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Influence of native ungulate herbivory on riparian floral resources and native bee communities

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ABSTRACT

Bees are essential pollinators in many natural and agricultural systems and declines of some species are well-documented. Threats to bees include habitat loss and degradation and uncertainty remains about how management practices influence bee communities. Globally, ungulates are common in many systems and though numerous studies have examined livestock effects on bees, native ungulate effects on bees are poorly studied. In the western US, two native ungulates, deer (*Odocoileus* spp.) and elk (*Cervus canadensis*), are widespread and may occupy large annual home ranges. Public land managers are tasked with managing deer and elk habitat in ways compatible with other land uses, including as pollinator habitat. To address the question of how these large herbivores influence bee communities, we conducted a three-year manipulative study in a Pacific Northwest riparian system. Half of 12 sites were protected from native ungulate herbivory and half were unprotected. We measured bloom availability and diversity each year, and quantified herbivory pressure and sampled bees in the third year. We found fewer blooms of plant species preferred by elk, the dominant large herbivore in the system, in unprotected sites than protected sites in the second and third years, and that blooming plant composition differed between protected and unprotected sites. Bee species richness was lower in unprotected areas in July of the third year and evidence suggests that bees specializing on plants consumed by ungulates may be at particular risk. Our work illustrates the importance of considering dietary overlap when investigating effects of ungulates on bee communities.

1. Introduction

The importance of invertebrate conservation has become more widely appreciated since the publication of E.O. Wilson's seminal essay on the subject over 35 years ago (Wilson, 1987). Not only are invertebrates one of the most specious animal groups, but they also

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fulfill ecological functions vital to humans, including food web provisioning, decomposition, nutrient cycling, and pollination (Wilson, 1987). The plight of pollinating insects, particularly, has received much attention in the last several decades, not only because of well-publicized declines of some species (Ollerton, 2017) but also because of the growing realization of the degree to which an increasing human population depends on insect-pollinated foods (Reilly et al., 2020). Bees have received the most attention both because of their efficiency in pollinating many important crops (Khalifa et al., 2021) and concern over the status of several high-profile species (e.g., Graves et al., 2020). Maintaining the diversity of bees and other pollinating insects is not only a top conservation priority because of their direct contribution to overall animal diversity and human food security, but also because of their role in pollinating many native plants, including those that occur in sensitive habitats (Gonzalez et al., 2013) or that rely on a narrow set of pollinators (Tubbesing et al., 2014; Baguette et al., 2020).

Although several factors threaten bee diversity, including non-native species, climate change, and pesticides, one key driver of bee declines is habitat loss and degradation (Potts et al., 2010; Harvey et al., 2023). A global challenge is protecting existing high-quality bee habitat and managing it in ways that support bees but also provide other needed ecosystem services (e.g., Ekroos et al., 2020; González-Robles et al., 2020; Balogun et al., 2022). In the United States (US), some of the largest and most intact landscapes supporting bee habitat occur on public lands – including those managed by federal and state agencies (Glenny et al., 2022). For example, just two federal agencies, the USDA Forest Service (USFS) and the Bureau of Land Management, manage over 177 million ha of grasslands, forests, and shrublands, most of which are located in the western US (Vincent, 2019). US public land managers are increasingly tasked with balancing not only traditional uses of those lands (e.g., timber and livestock production, recreation) but also a more diverse array of species and ecological functions (e.g., pollinators and pollination) (DeBano et al., 2016; Pollinator Health Task Force, 2015; Wojcik et al., 2018). Effective management in this context requires understanding how actions including riparian restoration, silviculture, and fire management, coupled with ecosystem processes such as herbivory, interact to affect pollinators (Glenny et al., 2022).

In the US, ungulate herbivory involving both domestic livestock (e.g., cattle (*Bos taurus*), sheep (*Ova aries*) and native ungulates (e.g., bison (*Bison bison*), elk, deer, pronghorn (*Antilocapra americana*)) can affect pollinators, such as bees, through various pathways that influence resource availability, including nesting habitat and nectar and pollen quantity and quality (DeBano et al., 2016; Watson et al., 2021; Thapa-Magar et al., 2022). Trophically-mediated effects arise directly from the consumption of plants by ungulates, which can alter plant chemistry, biomass, and reproduction and lead to cascading effects on bees (Kral-O'Brien et al., 2023). The importance of trophically-mediated effects in any given system may be influenced by various factors, including the system's aridity and evolutionary history with grazing animals, the grazer species, the season in which grazing occurs, and potential dietary overlap between ungulates and bees (DeBano, 2006; Cutter et al., 2021; Thapa-Magar et al., 2022; Mitchell et al., 2023). Bees in systems where ungulates and bees have a high degree of dietary overlap are more likely to be negatively affected by grazing compared to systems with relatively little overlap (DeBano et al., 2016). The degree of dietary overlap will be influenced by both the temporal and spatial availability of plants that are preferentially foraged on by both ungulates and bees, and the spatial and temporal overlap of both herbivore groups. Establishing dietary preferences of ungulates and bees can be challenging, often involving foraging observations, ungulate fecal analyses, and/or analyses of collected pollen from bees. Although new techniques, such as metabarcoding, are promising (e.g., Nichols et al., 2016; Scasta et al., 2019; Arstingstall et al., 2021, 2023), dietary preferences of co-occurring ungulates and bees are not well understood in most systems.

Although numerous studies have investigated effects of ungulates on bees, almost all have focused on domestic livestock (reviewed in Thapa-Magar et al., 2022) and the need to include native ungulates has been recently emphasized (Glenny et al., 2022). In the US, humans have had profound effects on native ungulate populations. Following a general decline of ungulate species in the western US in the 1800s and early 1900s due to settlement and harvest by non-indigenous people (Krausman and Bleich, 2013), deer and elk rebounded in the last century, and elk in particular may be occurring at historically high numbers due to the extirpation of top predators and changing land use practices (Painter et al., 2015; Beckett et al., 2022; Kohl et al., 2023; Larsen and McMillan, 2023). Other species, such as the American bison, remain at historically low numbers (Ranglack et al., 2023). Federal and state agencies make numerous decisions that can impact native ungulate populations and their habitats (e.g., timber sales, reintroduction of large carnivores, hunting regulations). However, management agencies in the US do not routinely monitor native ungulate effects on vegetation, as they do with livestock, and almost no work has been conducted to inform managers about the consequences of management decisions related to native ungulates on significant groups of pollinators, such as bees. One exception was work by Bruninga-Socolar et al. (2022), who found that spatial and temporal variation in prescribed fire and bison grazing led to a greater diversity of bees with different nesting habits. In another study, Beckett et al. (2022) found that Canadian islands with higher deer density had fewer flowering species and lower bumble bee abundance.

Understanding management effects and their influence on ungulate herbivory is particularly important in sensitive habitats that support rich biological communities, such as riparian areas. Forming a transition between aquatic and upland habitats, riparian areas typically support high biodiversity and unique species assemblages (DeBano et al., 2003; Rood et al., 2020). Although few studies have focused on pollinators in riparian areas, work conducted thus far suggests this pattern holds true for bees as well (Williams, 2011; DeBano et al., 2016; Mitchell et al., 2022). However, riparian areas are also among the most altered habitats in western North America, with many riparian systems negatively impacted by past land uses (Naiman et al., 2005; National Research Council, 2002; Rood et al., 2020). Ungulates can have strong effects on riparian areas because they may concentrate their activity in riparian areas compared to uplands in certain seasons, resulting in preferential use of riparian vegetation (McCorquodale et al., 1986; Carson and Peek, 1987; Averett et al., 2017). Thus, the combination of high diversity, historical disturbance, and disproportionate use by ungulates in riparian areas increases the urgency of studying pollinator and ungulate interactions in these areas. Attempts to limit further disturbance and restore these sensitive areas require understanding specifically how land management affects pollinators in riparian areas versus other habitats (Naiman et al., 2005; National Research Council, 2002; Rood et al., 2020).

Here, we examined how blooming plant and native bee communities responded to a three-year manipulation of native ungulate herbivory in an inland Pacific Northwest riparian system. Because elk and deer are smaller than cattle and do not occur in large herds in this system, we predicted that their influence would be mediated primarily through trophic pathways rather than through effects on nesting habitat (e.g., trampling). Thus, we focused on floral resource availability rather than nesting habitat characteristics. Our study objectives were to: 1) use existing data on native ungulate diets in the region to group riparian forb and shrub species into three ungulate selection categories of selected, neutral, and avoided; 2) quantify responses of blooming forbs and shrubs to native ungulate herbivory, including changes in bloom abundance of the three preference groups, and overall blooming species richness, diversity, and community composition; 3) quantify how deer and elk herbivory pressure varied temporally and spatially in our system in the third year of the study; and 4) examine responses of bee abundance, richness, diversity, and community composition in the third year of grazing exclusion. This study is the first to manipulate native ungulate grazing, coupled with accounting for herbivore dietary selection, to understand the role of native ungulates in influencing floral resources and native bees. Through our work, we sought to provide insights that can inform wildlife and land management across a broad spectrum of land ownerships to benefit pollinator conservation.

2. Methods

2.1. Study area

The study was conducted in a 2,217-ha portion of the Meadow Creek drainage within the USDA Forest Service Starkey Experimental Forest and Range (Starkey) in northeastern Oregon (45°12′ N, 118°3′ W); the riparian study area comprised 157 ha (7.1 %), with uplands occupying the remainder. Elevations range from 1120 to 1240 m along Meadow Creek within Starkey and to 1448 m in the uplands. Average temperatures are −4°C in January and 18°C in summer (Kie et al., 2013), with mean annual precipitation of 510 mm (Rowland et al., 1997; Wisdom, 2005). Meadow Creek is used extensively spring through fall by two wild ungulate species - mule deer (*Odocoileus hemionus)* and elk - with densities comparable to those in adjacent herd ranges (2.8–3.6 per km^2 (deer), 5.6–6.8 per km^2 (elk)). Cattle historically grazed the entire Meadow Creek reach within Starkey but were excluded from the eastern and western portions where this study was conducted since 2012 and were not re-introduced into those portions until 2017, after this study was completed (Averett et al., 2017).

The riparian vegetation in the study area includes herbaceous species such as introduced meadow foxtail (*Alopecurus pratensis*), Idaho fescue (*Festuca idahoensis*), Canada goldenrod (*Solidago canadensis*), Northwest Territory sedge (*Carex utriculata*), panicled bulrush (*Scirpus microcarpus*), and California false hellebore (*Veratrum californicum*) (Averett et al., 2017). Common woody deciduous species are black hawthorn (*Crataegus douglasii*), snowberry (*Symphoricarpos albus*), Woods' rose (*Rosa woodsii*), and gray alder (*Alnus incana*) and overstory forest species include ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) (Averett et al., 2017). Due to legacies of past land uses along Meadow Creek (Holechek and Vavra, 1982, Skovlin, 1991) and a desire to improve habitat conditions for threatened fish, the USFS implemented a riparian restoration project along 13 km of Meadow Creek in Starkey in 2012–2013 that included planting native woody species and creating five new pastures to promote more sustainable cattle grazing (Fig. 1; Averett et al., 2017).

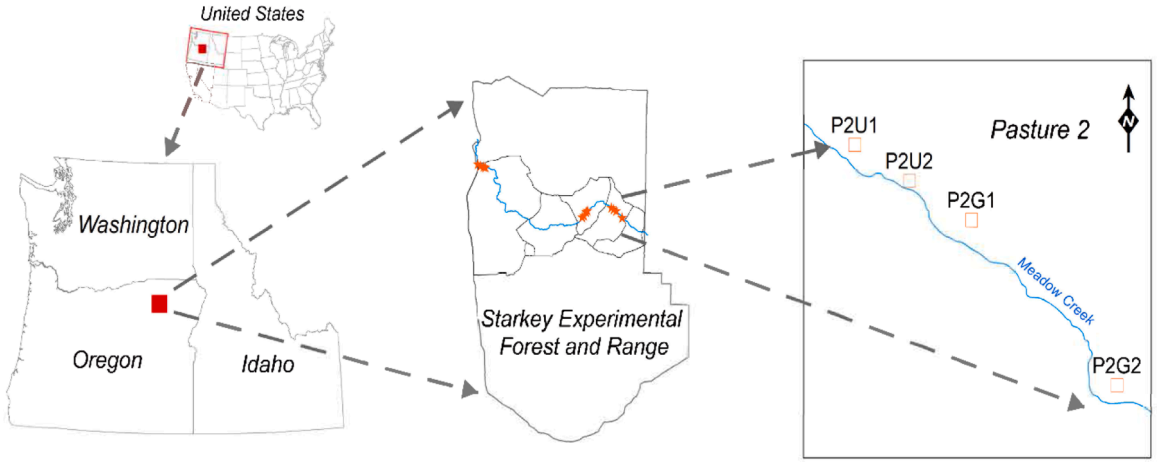

Fig. 1. Location of the USDA Forest Service Starkey Experimental Forest and Range in northeastern Oregon, United States. The center panel shows the 12 riparian study sites (denoted in red) located along Meadow Creek (denoted in blue) in three pastures, and the right panel shows the arrangement of four study sites within one of those pastures (Pasture 2). P2U1 and P2U2 are sites protected from native ungulates (i.e., ungrazed) and P2G1 and P2G2 are sites exposed to native ungulates (see text for details).

2.2. Experimental design

To quantify effects of ungulate herbivory on riparian plantings and other resources, including native bees and small mammals (DeBano et al., 2016, Averett et al., 2017, Millward et al., 2022), we constructed grazing exclosures in three of the five pastures. Exclosures were fully functional in January 2014. For this study, we established four sampling sites along Meadow Creek in each of three pastures ($n = 12$). In each pasture, two sites were placed in exclosures that excluded deer and elk and two were exposed to wild ungulate herbivory (Fig. 1). Sampling sites ranged from 0.73 to 3.29 ha ($\bar{x} = 1.28$ ha). Within pastures, mean distance between grazed and ungrazed sites ranged from 151 m (pasture 5) to 377 m (pasture 2) and mean distance between sampling site centers across pastures was 4143 m (Fig. 1). For plant and bee sampling we established five parallel, 20-m belt transects (0.3 m wide) at each site, positioned perpendicular to the stream and separated by 15 m. We sampled flowering plants for three years (2014–2016). Bees were sampled in 2016, when we established an array of trail cameras for quantification of deer and elk detections in areas in and adjacent to our sample sites.

2.3. Herbivore preferences

Because we expected plants readily consumed by native ungulates to be most responsive to ungulate exclusion, we classified blooming plants encountered in our sampling into three dietary selection categories. These categories were determined from foraging trials using captive, trained elk in forested ecosystems of the Blue Mountains of northeastern Oregon during mid-April through October 2004–2006 (Cook et al., 2014) and in Starkey during August 2005 – 2012 (Cook et al. unpublished data). At each foraging site, plant species encountered were assigned a selection category based on Ivlev's Electivity Index (Ivlev, 1961). The IVLEV score was then averaged by plant species across foraging sites (e.g., Cook et al., 2016). Species with a positive mean IVLEV score with a confidence interval (CI) that did not include zero were categorized as selected. The selected category indicates the species was consumed in higher proportion than available and is often referred to as "preferred" in the electivity literature (e.g., Lechowicz, 1982). Species with a negative mean IVLEV score with a CI that did not include zero were categorized as avoided – i.e., consumed in lower proportion than available. Species with a mean IVLEV score that had a CI that overlapped zero were categorized as neutral – i.e., consumed equal to available. We focused on elk versus deer forage preferences because elk are much more abundant than deer in this system, consume much more forage daily than deer, and little is known about dietary selection of deer in our study area.

2.4. Plant sampling

To quantify floral resources available to bees, we sampled blooming stems on the five belt transects at each of the 12 sites from 2014 to 2016. We sampled in May, June, July, and September in 2014 and 2016, and June, July, and September in 2015 (see Table S1 for specific dates). All blooming stems were identified, counted, and summed for all five transects at each site using methods consistent with previous studies (e.g., Roof et al., 2018; Graham et al., 2021). Blooms were identified to species except for the following groups of species that we combined into one taxon: *Trifolium repens* and *T. pratense*; *Arnica sororia* and *A. chamissonis*; *Noccaea fendleri* and *Thlaspi arvense*; and *Symphyotrichum spathulatum, S. eatonii,* and *Canadanthus modestus*. In addition, *Penstemon* stems, except for *Penstemon procerus*, were identified to genus only, as was one species of *Descuriana*. Scientific names for plants follow USDA NRCS PLANTS Database conventions (http://plants.usda.gov).

2.5. Herbivory pressure

Beginning in 2016, a series of motion-activated trail cameras (Bushnell Trophy Camera HD with infrared flash) was established at 600 m-intervals along the entire 13-km stretch Meadow Creek reach within Starkey to document occurrence of elk and deer and their potential effects on vegetation and other response variables. Cameras were placed in open areas to maximize the field of view, along the stream edge, and facing parallel to the stream. Cameras were mounted ~ 1 m above the ground on trees or t-posts. Cameras operated continuously over the study period and each detection was identified to species and counted. We selected 14 cameras stationed within a 600-m buffer of the mid-points of our 6 grazed sampling sites for tallying counts of herbivores (4 cameras were used to characterize ungulate use for Pasture 2 and 5 cameras were used for each of the other two pastures).

We estimated daily cumulative herbivory pressure at the six grazed sites by selecting cameras with continuous data streams during the entire sampling period that ranged from 6 May to 8 September 2016 and filtering data such that individual detections were ≥ 1 minute from the last event. We then selected any camera within the circular buffers surrounding the two grazed sites in each of the three pastures and compiled counts of the number of deer and elk in all detection events. Counts were then averaged across cameras for each pasture each day. Herbivory pressure was calculated at the pasture level rather than by site because the distance between the two grazed sites in each pasture was substantially less than daily ungulate movements. Using these data, we estimated the daily cumulative ungulate herbivory pressure as the 2016 growing season progressed. Like others (e.g., Weber et al., 2025), we use the term "herbivory pressure" to reflect counts of herbivores recorded on camera traps, even though detection events are not equivalent to documenting grazing or browsing. We assume that ungulates spend a proportionally equivalent amount of time foraging in each location, i.e., there was no spatial bias in foraging bouts across our sites, so that counts of animals observed on cameras provide a sound index for which to compare relative grazing effects across sites.

2.6. Bee sampling

We sampled bees at each site in May, June, July, and September 2016 concurrent with plant sampling – see Table S2 for specific dates. We used 15 236-ml pan traps at each site that included 5 UV-reflective blue, 5 UV-reflective yellow, and 5 white traps that were each filled with soapy water (Levenson et al., 2024). Although all bee sampling approaches have biases (Levenson et al., 2024), pan traps have been found to be an effective and efficient method for sampling bee communities (Westphal et al., 2008). Pan traps were placed on the ground, with one trap of each color located at the center of each of the five transects. Traps were placed in a triangular orientation; each trap was separated from the other by ~0.5 m. We collected pan traps after two days and noted any disturbed traps. Bees were taken to the laboratory, washed, pinned, and subsequently identified using methods described in Kuhlman and Burrows (2017).

2.7. Statistical analysis

To investigate blooming plant responses to herbivory, we used generalized linear models (GLMs) to determine whether deer and elk exclusion affected 1) the total number of blooming stems during all sampling periods for each of the three dietary selection categories, 2) blooming plant species richness, and 3) Shannon diversity. We analyzed years separately, blocking on pasture. Because blooming stem abundance and richness data were counts and because of evidence of overdispersion, we used a negative binomial instead of a Poisson distribution to examine effects of ungulate exposure on these variables. We used a normal distribution for analyses of diversity. For bees, we also used blocked GLMs to determine whether treatment affected bee abundance, richness, and diversity during each month. To adjust for trap disturbances by wildlife and minor differences in trapping duration, we calculated bee abundance as a rate for each site (number of bees per trap per hour). Consequently, we used a normal distribution for analyses of bee abundance and diversity, and a negative binomial distribution for richness, analyzing months separately. R was used for all GLM analyses (Version 4.0.3; R Development Core Team, 2020).

To evaluate whether herbivore exclusion affected overall patterns of blooming plant and bee community composition, we used permutation-based nonparametric multivariate analysis of variance (perMANOVA) (Anderson, 2001). For blooming plants, we examined effects of treatment, year, and their interaction and for bees, we examined effects of treatment, month, and their interaction. We used Sørensen's distance measure and 4999 randomizations to evaluate significance. We employed indicator species analyses (ISA) (Dufrêne and Legendre, 1997) to determine whether certain blooming plant or bee species were associated with treatments. ISA generates indicator values (IV) ranging from 0 (no indication) to 100 (the species is present in all treatment replicates and is exclusive to that treatment) (McCune et al., 2002). We evaluated significance of indicator values with 4999 Monte Carlo randomizations. We used PC-ORD, Version 7.09 (McCune and Mefford, 2006) for all multivariate analyses and an α level of 0.05 to evaluate statistical significance.

3. Results

3.1. Blooming plant availability and elk selection categories

We counted 25,050 blooming plant stems of 118 species over three years, with 7644 of 74 species counted in 2014; 3656 of 53 species in 2015; and 13,750 of 100 species in 2016 (see Table S1 for a list of species and number of stems counted each month and year and Supplementary Material Fig. S1 for yearly weather conditions). We categorized over 96 % of blooming stems of 80 species into three elk selection categories: selected (23 species), neutral (26 species), and avoided (31 species) (Table 1). We were unable to assign selection categories for the remaining 38 species (Table S3), but all but one of those species made up less than 1 % of observations of blooming stems. *Monardella odoratissima*, which accounted for 4 % of all blooming stems, was the only species that made up more than 1 % of all observations that could not be categorized.

3.2. Plant responses to herbivory

In 2014, the first year that exclosures were functional, we found no significant differences in the number of blooming stems in sites exposed to native ungulate herbivory versus protected sites for any elk selection category (Fig. 2; Table S4). However, in 2015 and 2016 we found fewer blooming stems of plants classified as selected by elk in grazed versus ungrazed sites ($z = 3.6$, $p = 0.0004$; $z = 2.7$, $p = 0.007$, respectively), but no differences for neutral and avoided plant species (Fig. 2; Table S4). Blooming plant richness and diversity did not differ significantly between grazed and ungrazed sites in any year (Table S4).

Blooming plant community composition differed between grazed and ungrazed sites and by year, but there was no significant interaction between treatment and year (Table 2). Seven species were significant indicators for ungrazed sites (four selected species, two neutral, and one of unknown preference), and three species for grazed sites (two selected species and one neutral species; Table 3). Of the 10 indicators, six were relatively weak, with IV values less than 50 (Table 3).

3.3. Herbivory pressure

In 2016, we tallied 2223 elk and deer in 1405 separate detection events across the 14 cameras in the three pastures. Of these detections, 2006 were elk (1232 events), 226 were mule deer (172 events), and 1 was a white-tailed deer (*Odocoileus virginianus*).

Table 1
Blooming plant species observed during the study classified into three elk selection categories (selected = consumed in higher proportion than available, neutral = consumed in proportion to available, avoided = consumed in lower proportion than available) and the number of stems of each species, arranged in descending order by count. Species that comprised more than 1 % of all observed blooming stems are indicated with an asterisk. We classified plants into selection categories based on three years of data from captive elk foraging trials in the northeastern Blue Mountains of OR (mid-April through October; Cook et al. 2014) and eight years in the USDA Forest Service Starkey Experimental Forest and Range (August; Cook et al. unpublished data). We were unable to assign a selection category for 38 species that comprised less than 4 % of all flowers documented to be blooming on transects (see Table S3).

Plant Species	Count	> 1 % of all Stems
Selected Plants		
Potentilla gracilis	2790	*
Eriogonum heracleoides	2378	*
Achillea millefolium	2172	*
Viola vallicola	972	*
Trifolium repens/pratense	755	*
Ribes cereum	507	*
Symphyotrichum eatonii/S. spathulatumi/Canadanthus modestus	501	*
Trifolium wormskioldii	217	
Taraxacum officinale	211	
Medicago lupulina	202	
Prunella vulgaris	191	
Viola adunca	154	
Camassia quamash	74	
Potentilla glandulosa	45	
Thalictrum fendleri	17	
Valeriana dioica	16	
Viola palustris	13	
Grindelia nana	9	
Symphoricarpos albus	4	
Rosa nutkana	2	
Neutral Plants		
Solidago missouriensis	738	*
Galium boreale	416	*
Penstemon procerus	317	*
Senecio serra	308	*
Rumex acetosella	227	
Sidalcea oregana	154	
Dianthus armeria	148	
Stellaria longipes	141	
Collomia linearis	115	
Sanguisorba canadensis	114	
Montia linearis	106	
Fragaria virginiana	94	
Penstemon sp.	91	
Lomatium ambiguum	83	
Arnica chamissonis/sororia	101	
Triteleia grandiflora	31	
Cirsium arvense	27	
Polemonium occidentale	25	
Potentilla recta	22	
Veratrum californicum	20	
Erigeron speciosus	19	
Tragopogon dubius	16	
Lomatium cous	9	
Cirsium vulgare	5	
Lomatium macrocarpum	3	
Avoided Plants		
Myosotis stricta	1544	*
Draba verna	1489	*
Lotus unifoliolatus	1021	*
Microsteris gracilis	746	*
Collinsia parviflora	693	*
Perideridia gairdneri	538	*
Ranunculus uncinatus	536	*
Agoseris glauca	485	*
Sedum stenopetalum	446	*
Veronica serpyllifolia	414	*
Vicia cracca	261	
Polygonum douglasii	218	
Epilobium brachycarpum	216	
Fragaria vesca	138	

(*continued on next page*)

Table 1 (*continued*)

Plant Species	Count	> 1 % of all Stems
Noccaea fendleri ssp. *glauca/Thlaspi arvense*	135	
Thermopsis montana	97	
Hypericum anagalloides	93	
Hypericum perforatum	89	
Cerastium fontanum	75	
Lithophragma parviflorum	65	
Madia glomerata	39	
Gentianopsis simplex	34	
Antennaria rosea	31	
Urtica dioica	27	
Geum macrophyllum	26	
Ranunculus orthorhynchus	23	
Verbascum thapsus	13	
Epilobium ciliatum	8	
Galium aparine	5	
Madia gracilis	4	

Among all detections, > 90 % were elk, suggesting the importance of elk relative to deer in contributing to herbivory pressure. Deer and elk consistently used all three pastures throughout the growing season (Fig. 3).

3.4. Bee responses to herbivory

In 2016, we collected 2895 bees in May, June, July, and September comprised of 110 species and 24 morphospecies. See Table S2 for a list of species and the number collected each month. Although there were no significant differences in bee abundance in sites exposed to native ungulate herbivory versus protected sites in any month (Table S5), there were significantly fewer bee species in grazed sites compared to ungrazed sites in July ($z = 3.2$, $p = 0.001$; Fig. 4), with seven fewer species, on average, at grazed sites compared to ungrazed sites that month. Shannon diversity was also lower in grazed sites compared to ungrazed sites in July, although the difference was not statistically different ($z = 1.97$, $p = 0.08$). By contrast, species richness and diversity were similar between treatments for May, June, and September (Fig. 4; Table S5). While bee community composition varied monthly, it did not differ significantly between grazed and ungrazed sites and there was no significant interaction between treatment and month (Table 4). Two bee species were significant, albeit relatively weak, indicators for ungrazed sites (Table 5).

4. Discussion

Using a multi-year study that manipulated exposure to herbivory, we demonstrated that native ungulates influence floral resources and native bee communities in an Inland Pacific Northwest riparian system; camera trap data confirmed that elk were the most common herbivore and allowed us to quantify spatial and temporal patterns of herbivory. In addition, existing data on ungulate and bee foraging preferences helped us detect and interpret patterns in blooming plant and bee responses. Floral communities responded to herbivory in the second and third years of the study, with fewer blooms of elk-selected species in sites exposed to grazing compared to protected sites. The lack of response in the first year was not surprising given that ungulate-mediated changes in floral abundance should become more pronounced after multiple years of grazing exclusion. Preferential selection for particular plants by deer and elk also resulted in blooming plant community composition differing significantly between sites exposed to herbivory versus protected sites.

We detected 10 blooming plant indicator species; however, only 4 were relatively strong (indicator values > 50) and all were associated with ungrazed areas, with three in the "selected by elk" category and one in the neutral category. All four species began blooming in late May or later, exposing them to increasing cumulative herbivory pressure as indicated by native ungulate detections quantified with camera traps in 2016 (Fig. 3). One selected species, *Viola vallicola*, was only a weak indicator of ungrazed areas, potentially because it blooms early, and therefore may have been partially through the blooming period before deer and elk exerted significant herbivory pressure (Table 3, Fig. 3). Conversely, plants avoided by elk were not indicators of grazed or ungrazed sites, an unsurprising result because the presence and relative abundance of these species should remain similar in grazed and ungrazed sites alike. In areas grazed consistently for many years, grazed sites may support relatively more avoided species than ungrazed areas because of competitive release (Segre et al., 2016), but we did not detect those responses during the three-year study period. Contrary to our expectations, the three indicator species for grazed areas were categorized as either selected or neutral species, but all were relatively weak indicators (IV < 50). One of those indicators was *Trifolium repens* (white clover), which has a prostrate, stoloniferous growth form. Because of this, its growth and production of flowers and seeds can be suppressed by overshading herbaceous vegetation (Brougham, 1959; Pasumarty and Thomas, 1990). If ungulates remove herbaceous cover that shades white clover, it may allow white clover to produce more blooms. Other studies have found that frequent livestock grazing can promote white clover growth (Brougham, 1959) and reduced overstory shading can increase flower and seed production as well as result in flowering occurring earlier in the season (Stern and Donald, 1962; Pasumarty and Thomas, 1990; Ehret et al., 2015).

The impact of fewer blooms on which bees can forage may potentially be quite detrimental to native bees. Many plant species

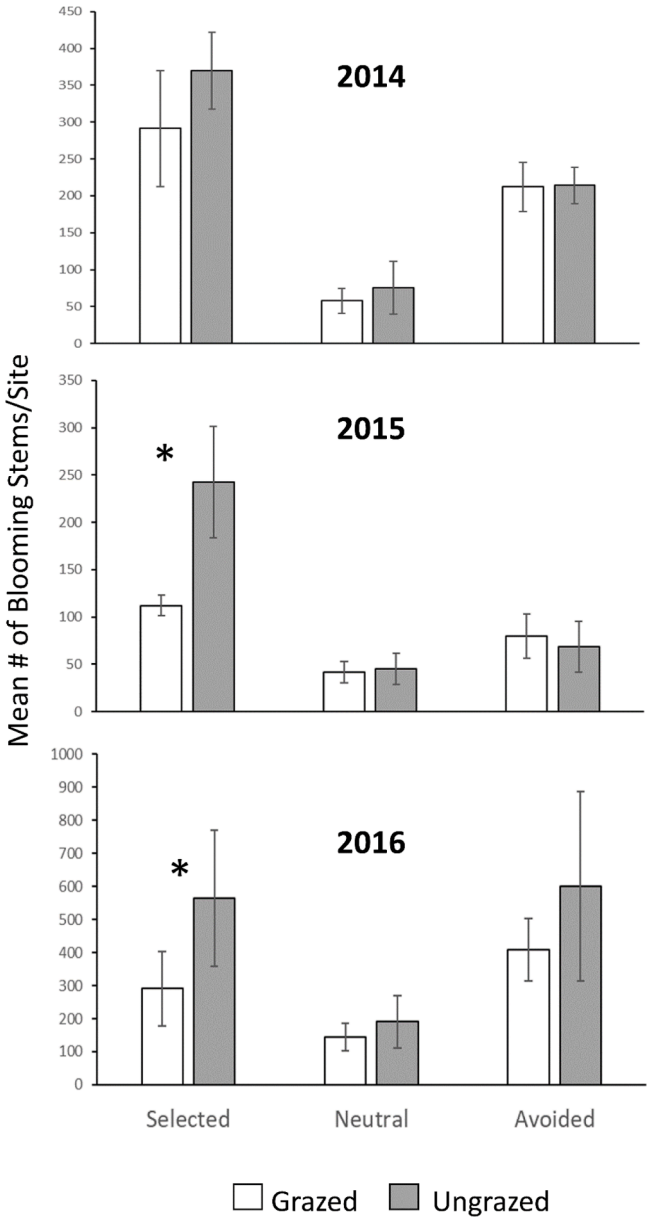

Fig. 2. Mean number of blooming stems of plants in three elk selection categories (selected, neutral, and avoided) in 2014, 2015, and 2016 for sites exposed to deer and elk herbivory (grazed) and sites protected from herbivory (ungrazed). Error bars are standard errors and significant differences ($p \leq 0.05$) are indicated with an asterisk.

Table 2
Effects of grazing treatment, year, and their interaction on blooming plant composition, using perManova tests (see text for details).

	DF	F	P-Value
Grazing Treatment	1	2.54	0.001
Year	2	3.75	0.0002
Grazing x Year Interaction	2	0.90	0.63

preferred by elk are also key food sources for bees in the system (DeBano et al., 2016; Roof et al., 2018). Notably, the three species with the most blooming stems recorded in this study (*Potentilla gracilis*, *Eriogonum heracleoides*, and *Achillea millefolium*) were all categorized as "selected" by elk in previous research (Cook et al., 2014). Prior publications have also revealed that some of these species are key

Table 3
Significant ($p \leq 0.05$) blooming plant species associations resulting from indicator species analyses, listed by decreasing indicator value (IV) within each treatment.

Species (# blooms)[a]	Preference[b]	Treatment	Bloom Period[c]	IV	P-Value
Achillea millefolium (2172)	Selected	Ungrazed	June 10-Sept 7	66.1	0.04
Sidalcea oregona (154)	Neutral	Ungrazed	June 10-Sept 8	61.9	0.004
Potentilla gracilis (2790)	Selected	Ungrazed	May 25-Sept 8	59.6	0.05
Eriogonum heracleoides (2378)	Selected	Ungrazed	June 10-July 31	57.5	0.04
Viola vallicola (972)	Selected	Ungrazed	May 8–26	38.2	0.05
Noccaea fendleri ssp. *glauca*[d] (135)	Unknown	Ungrazed	May 26-June 14	31.9	0.05
Veratrum californicum (20)	Neutral	Ungrazed	June 13-July 25	31.7	0.04
Trifolium repens[e] (755)	Selected	Grazed	May 8-Aug 1	48.2	0.001
Potentilla glandulosa (45)	Selected	Grazed	May 9-July 31	38.9	0.007
Lomatium ambiguum (83)	Neutral	Grazed	May 9–26	32.5	0.05

[a] # of blooms observed on transects from 2014 to 2016; [b]Elk preference categories from Cook et al., unpublished data; [c] Bloom period indicates the first and last date in any year that the species was noted blooming on transects; [d]This species may also include *Thlaspi arvense*; [e]This species may also include *Trifolium pratense*.

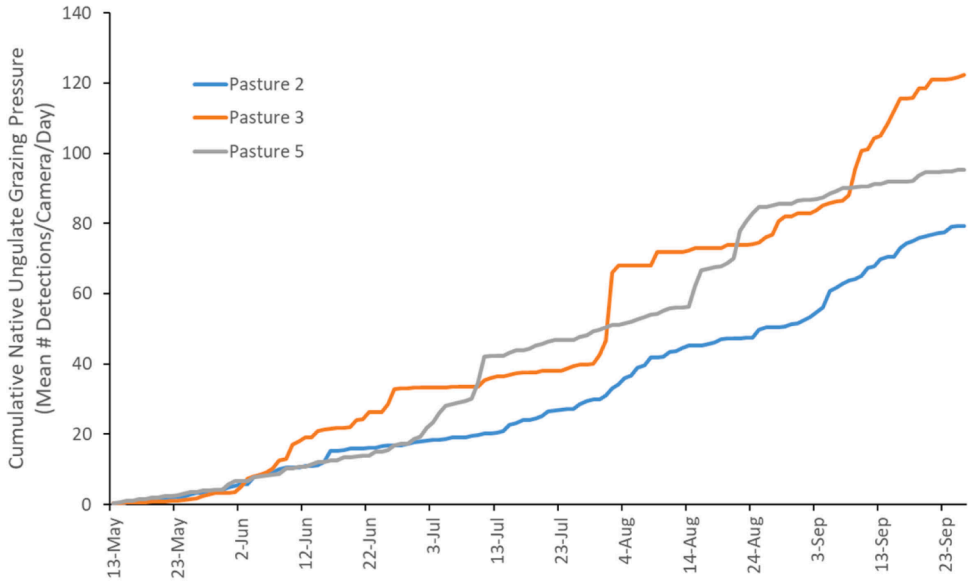

Fig. 3. Cumulative grazing pressure by deer and elk in 2016, estimated using camera traps (daily average count/trap/day) located in a 600-m circular buffer around grazed sites in three pastures for the Meadow Creek Riparian Study, USDA Forest Service Starkey Experimental Forest and Range.

resources for bees. For example, Roof et al. (2018) studied the same riparian system and found that *Potentilla gracilis*, a strong indicator of ungrazed sites in this study, was the second most frequently visited plant by bees. This species also had the greatest diversity of bee visitors (31 species) among the 92 plant species examined over a two-year period. The same project also revealed that the second strongest indicator species of blooming plants for ungrazed areas in our study, *Sidalcea oregona*, was a preferred forage species for bees (Roof et al., 2018). In addition, *Sidalcea oregona* is a member of the Malvaecea, a plant family known to support specialist bees (e.g., *Diadasia*) (Sipes and Tepedino, 2005).

Our study also revealed several bee responses to native ungulate grazing in the third year. Bee species richness in July was 40 % lower in sites exposed to herbivory compared to protected sites. Shannon diversity also showed a similar, but statistically insignificant, trend. The lack of response to ungulate herbivory in May and June may have been due to insufficient cumulative herbivory pressure by that time to impact bees through effects on floral resources. The lack of grazing effect on bee richness in September is not surprising – species richness late in the summer in these systems is low and a few generalist species often dominate the community (Mitchell et al., 2023). Abundance did not differ between treatments in any month, potentially because generalist bees may be able to forage on a wide variety of plant species, including those avoided by elk. Alternatively, trap efficiency may have declined in areas protected from elk, which is one potential limitation of passive sampling methods (Levenson et al., 2024). Although overall bee community composition did not differ between treatments, two bee indicator species were detected for ungrazed areas. Both were weak indicators; one (*Halictus confusus*) is a eusocial, generalist sweat bee (Sheffield et al., 2014) that was active throughout the sampling season, and the other (*Diadasia nigrifrons*) is a specialist on *Sidalcea* (Linsley and MacSwain, 1957; Kuta, 2003; Zimmerman and Reichard, 2005) and was

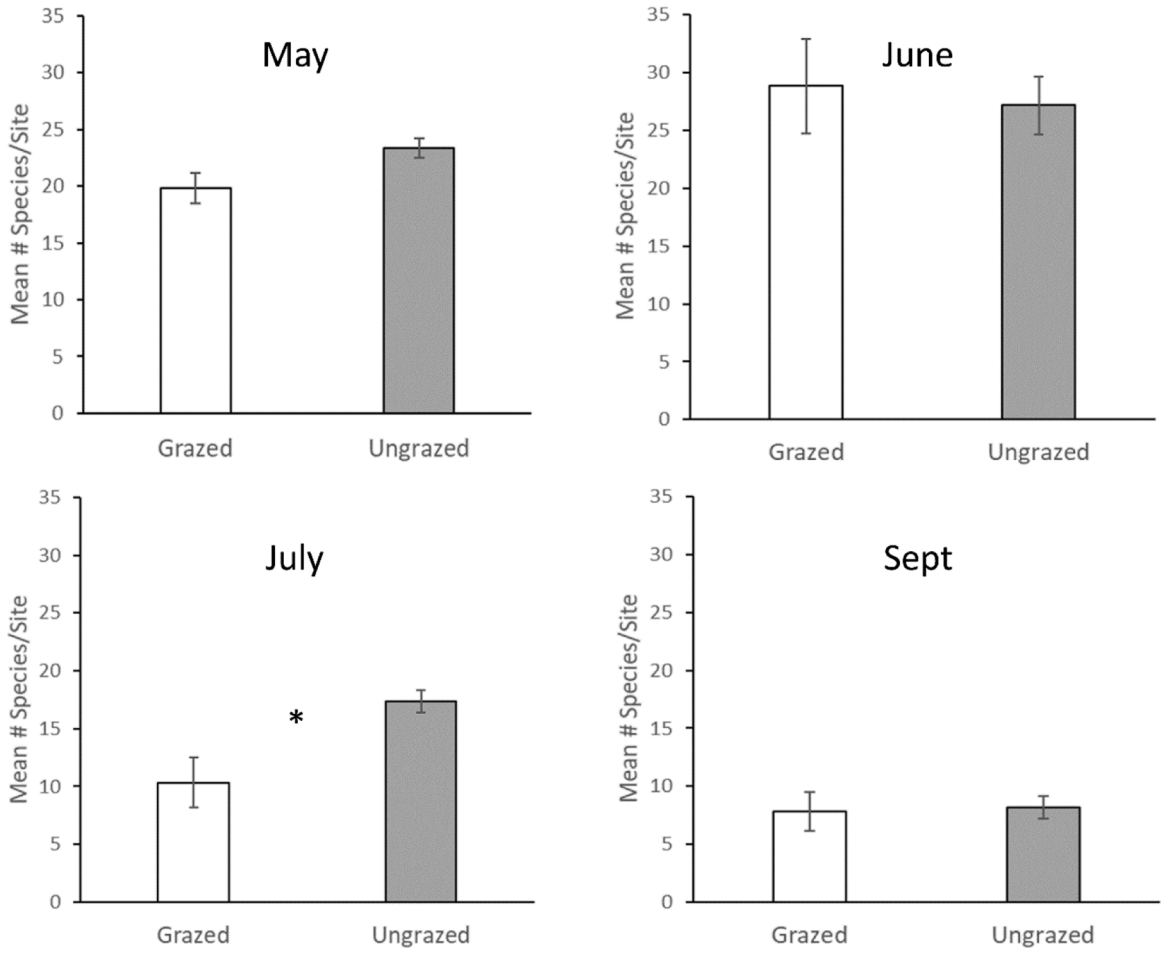

Fig. 4. Mean bee species richness site in 2016 for sites exposed to native ungulate herbivory (grazed) and protected sites (ungrazed). Error bars are standard errors and significant differences ($p \leq 0.05$) are indicated with an asterisk. See Table S5 for generalized linear model results.

Table 4
Results from perManova test on the effect of grazing treatment and sampling month individually and as an interaction on bee community composition.

	DF	F	P-value
Grazing Treatment	1	0.65	0.79
Month	3	11.76	0.0002
Grazing x Month Interaction	3	0.69	0.91

Table. 5
Indicator species analysis results for significant bee species associations ($p \leq 0.05$). Both species are ground nesters.

Species (# individuals)[a]	Treatment	Diet Breadth[b]	Activity Dates[c]	IV[d]	P-value
Halictus confusus (14)	Ungrazed	Polylectic	May 6-Sept 10	26.5	0.04
Diadasia nigrifrons (8)	Ungrazed	Oligolectic (*Sidalcea* specialist)	June 11-July 21	21.9	0.05

[a] # of individuals collected in 2016; [b] Sheffield et al. (2014), Kuta, (2003); [c] First and last dates in 2016 that the species was collected; [d] "IV" denotes indicator values.

active from mid-June through July. The finding that the only *Sidalcea* species in our study (*S. oregona*) was an indicator species of ungrazed sites illustrates one way in which native ungulate grazing may decrease bee species richness – if plant species that support specialist bees are regularly consumed by ungulates, bee species richness may decline in areas grazed by that ungulate.

Although this is only the third study of which we are aware that examined native ungulate effects on pollinators in North America,

and the first that included elk, our results align with a growing body of knowledge about ungulate effects on pollinators. Consistent with other work, we found that bee communities appear to be sensitive to trophically-mediated effects of ungulate herbivores, a process partially influenced by dietary overlap between herbivores and some bee species (DeBano et al., 2016). For example, Kimoto et al. (2012b) found increased cattle grazing intensity was associated with lower bumble bee abundance and richness. The authors measured both vegetation and soil variables and concluded that the removal of floral resources by grazing cattle was likely the major driver of bumble bee responses (Kimoto et al., 2012b). Likewise, other studies that have demonstrated either positive or negative effects of livestock on bees have identified changes in floral resources as the major driver of detected effects (Carvell, 2002; Hatfield and LeBuhn, 2007; Sjödin, 2007; Xie et al., 2008; Lasway et al., 2022), as has recent work on deer effects on bumble bees (Beckett et al., 2022). Beckett et al. (2022) found that Pacific Northwest islands with black-tailed deer had fewer flowering stems than islands without deer. Moreover, islands without deer supported more native plant species than islands with deer. The authors hypothesized that effects of deer on native plants may have been particularly important in reducing bumble bee abundance on islands with deer because most bumble bee species in their system foraged primarily on native, versus exotic, plants (Beckett et al., 2022).

Although we did not examine responses of nesting resources in this study, ungulates can affect ground- or stem nesting bees if their activities change soil properties, soil cover, and/or vegetation structure (Thapa-Magar et al., 2020; Hanberry et al., 2021; Bruninga-Socolar et al., 2022). For example, ground-nesting bees may be affected if soil properties are altered by the trampling or wallowing actions associated with large-bodied ungulates that typically forage in substantial herds. Changes in soil properties have been documented in response to not only cattle and bison (Knapp et al., 1999; Schmalz et al., 2013) but also to elk, with increased bulk density in some habitat types supporting high densities of elk compared to areas in which elk had been excluded (Binkley et al., 2003). Changes in soil bulk density or compaction, however, can influence some bee species positively. For example, some sweat bees prefer to nest in bare and compacted soils (Potts and Willmer, 1997, 1998; Vulliamy et al., 2006). However, highly compacted soils can prevent females in some bee species from initiating nests (Harmon-Threatt, 2020). Although elk and deer in our study system occur at relatively low densities and were unlikely to lead to trampling or soil compaction, future studies of the effects of elk and deer on soil properties, especially where they occur at very high densities or in very confined areas, are warranted.

Stem-nesting bees may be more likely to be affected by deer, who generally prefer to browse on shrubs (DeBano et al., 2016; Stewart et al., 2011), than by other large herbivores. Although deer were relatively rare in our system, with less than 10 % of ungulate detections being deer, they can be hyperabundant in other systems (Beckett et al., 2022). Thus, further research is needed to determine if browsing by deer in areas of high density affects habitat for stem-nesting bees. Shrubs browsed by deer typically have higher stem densities than unbrowsed plants (Russell et al., 2001), which could increase nesting habitat availability for stem-nesters in the long-term. However, if deer browse stems with active nests or if ungulate herbivory occurs at high enough levels to decrease the growth and survival of shrubs (Averett et al., 2017), then stem-nesting bees may be negatively affected. Thus focused studies on how browsing by native ungulates on shrubs affects stem nesting-habitat is another area in which future research is needed.

This study also illustrates potential approaches for improving research about effects of ungulate herbivory on invertebrate communities. The large number of species that comprise even select groups of invertebrates (e.g., native bees) makes examining individual species responses impractical. Instead, approaches often depend on examining larger, community-level patterns (e.g., species richness, diversity indices, species composition). Such broad approaches, however, can make it difficult to detect management effects on invertebrate communities, especially given natural variation in space and time, confounding factors often associated with observational studies, and knowledge gaps about the temporal and spatial impacts of management on factors expected to impact pollinators (Williams et al., 2001; Kimoto et al., 2012a; Debinski, 2023). We addressed some of these challenges by conducting a three-year manipulation of native ungulate herbivory exposure, a rare opportunity to more directly investigate causal relationships.

We were also able to document native ungulate herbivory with camera trap data to describe spatial and temporal gradients in herbivory pressure. These data allowed us to infer that herbivory pressure was not appreciable at our grazed sites until late May to early June, such that temporal overlap in floral resources used by bees and native ungulates was more likely to occur mid-season or later. Native ungulate herbivory in this system thus may have less impact on early emerging forbs and shrubs with short bloom periods, as well as the early season bee community, which often includes more oligolectic species than later-season communities (Mitchell et al., 2022). In addition, we determined that herbivory pressure was similar across our three study pastures. However, one limitation of our camera data was the degree of spatial resolution. Because of the movement capabilities of elk and deer and the spacing of cameras, we were unable to generate credible sampling site-level measures of ungulate pressure, which would have helped tease apart treatment effects (i.e., by having a continuous variable to estimate grazing rather than just presence/absence) (Kimoto et al., 2012b).

A novel approach in our study was incorporating a dietary overlap context that allowed us to refine our focus on plant species used as resources by both ungulates and bees. Our previous review (DeBano et al., 2016) demonstrated the high likelihood of dietary overlap between elk and bees in this system, and our past research had established native bee floral preferences in the study area (Roof et al., 2018) that provided valuable insights into potential mechanisms underlying observed effects. Additional work by others on native ungulate dietary preferences (Cook et al., 2014, 2016) enabled us to focus on those plants most likely to be affected by ungulate herbivory.

Findings from our study can inform larger-scale conservation and management of pollinators and their habitat. For example, the Center for Pollinator Conservation (https://www.fws.gov/program/center-pollinator-conservation) is working to increase pollinator habitat throughout the US, including increasing the availability of native seeds and plants. Tailoring seed mixes to minimize the potentially negative impacts of ungulate herbivory can lead to higher success rates in restoration projects and make best use of often limited funds.

5. Conclusions

Increasing populations of native ungulates, particularly deer and elk, and associated herbivory and crop damage, are a management and socio-economic concern in many locales worldwide (e.g., Rooney and Waller, 2003; Putman et al., 2011; Warren, 2011; Corgatelli et al., 2019). In the US, the effects of wild ungulates such as deer and elk on ecosystems are not generally considered when developing species-specific management plans (including hunting regulations) or livestock grazing plans for public lands. Moreover, the consequences of native ungulate herbivory for biodiversity and conservation of pollinators are not well-studied (Gómez, 2003; Glenny et al., 2022). Effective management of wild ungulate populations in an ecosystem context requires understanding how herbivory affects a variety of taxa, including pollinators, and the ecological functions they provide. Our research provides another line of evidence that the impacts of deer and elk on ecosystems should be explicitly considered for management of those species. We found that native ungulates influence flowering plant communities and the bees that forage upon them, and that these relationships are temporally and spatially dynamic. Management that accounts for the potential temporal and spatial dimensions of dietary overlap between ungulates and bees will be more effective at minimizing unintended negative outcomes for pollinators. In addition, special attention should be paid to requirements of specialist bees and conserving the plants they depend upon. Focused management of native and domestic ungulates in riparian areas is especially vital given the high biodiversity in these sites, importance as habitat for species of concern, legacy of anthropogenic disturbance, and current restoration priority (National Research Council, 2002; Rood et al., 2020). The results of this work can inform future co-management of pollinators and native ungulates. For example, exclusion fencing along special features such as riparian area and aspen stands (Gage and Cooper, 2009; Rolf, 2001; VerCauteren et al., 2007) is one tool used by public land management agencies in the US to protect these sites, which are often a small but biodiverse portion of the landscape. Other solutions include increasing hunting permits to reduce ungulate populations (e.g., Rolf, 2001).

This study points to several lines of additional research. First, future work should examine the effects of native ungulates on pollinator nesting habitat, including how ungulate density relates to soil characteristics and plant architecture (e.g., stems, twigs). Second, although native bees are a key component of the pollinator community, many other invertebrates are important in providing these services, indicating that further research examining a wider breadth of pollinating species in these systems is needed. Finally, a key need for managing public lands in the western US is a better understanding of how native ungulates and domestic livestock interact in time and space to influence pollinators.

CRediT authorship contribution statement

Mary M. Rowland: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Conceptualization. **Sandra J. DeBano:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Skyler Burrows:** Writing – review & editing, Methodology, Investigation. **Samantha M. Roof:** Writing – review & editing, Methodology, Investigation. **Joshua P. Averett:** Writing – review & editing, Methodology, Investigation.

Ethics

Not applicable: This manuscript does not include human or animal research.

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Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03661.

Data availability

Data will be made available on request.

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