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Original Research

Phenologically Targeted Grazing: A Potential Sustainable Strategy for Native Bees in Semiarid Rangelands ☆

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ABSTRACT

Rangelands may offer valuable habitat for invertebrate wildlife, helping conserve ecologically and economically significant organisms, like native bees. In some systems, livestock may affect bees by consuming or trampling blooming plants that bees rely on for food. One potential way to reduce potential negative effects of livestock on bees is to delay grazing on floristically rich parts of the landscape until after peak bloom (i.e., phenologically targeted grazing). To test the outcome of this method, we collected bees using pan traps and counted blooming stems from May to September in grazed and ungrazed sites. Our sites were located in two experimental cattle grazing systems in the Pacific Northwest, United States, in which cattle turnout did not occur until after peak forb bloom. One system was located in bunchgrass prairie, and the other was located in riparian meadows. Our objectives were to 1) quantify seasonal variation in bee and blooming plant communities and 2) measure how or if these communities responded to grazing. In both systems, bee and bloom species richness peaked in June and bloom abundance and diversity were highest in May and June. Bee abundance and diversity were more variable throughout the season. We observed significantly lower abundance, richness, and diversity of blooming species in the riparian system in response to grazing, potentially decreasing floral resource availability for bees, but did not detect a concomitant negative effect on bees. In the bunchgrass system, we observed no significant negative effects of grazing on bees or blooming plants. This suggests that for areas with high-quality bee habitat, site-specific, phenologically targeted grazing may moderate negative effects of livestock on bee and plant communities. Range managers could use alternative grazing locations (e.g., old fields, early senescing sites, more intensively managed pastures), if available, during peak bloom to mitigate potential herbivory effects on bees and blooms.

Introduction

Livestock grazing is one of the most widespread land uses in the world, with at least 25% of the earth's land area (~2.5 billion ha) grazed annually (Asner et al. 2004; Henderson et al. 2015). In the United States (US), livestock grazing is a dominant land use in many regions (Bigelow and Borchers 2017), where grazing-related activities contribute to regional economies (Vincent 2019) and cultures (Kirner 2015). Approximately 92 million ha of US Federal Land (Vincent 2019) and 256 million ha of private, state, local, and tribal lands are grazed each year in the United States (Butler et al. 2003), representing nearly 35% of total land area in the country.

On many of these lands, grazing takes place in conjunction with other land uses, such as timber production, recreation, en-

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ergy development, and wildlife management (Havstad et al. 2007; Brunson & Huntsinger 2008; Eastburn et al. 2017). Collaborations among multiple user groups (e.g., producers, recreationists, conservationists) have resulted in productive partnerships that benefit livestock, wildlife, and people (Hoogesteijn and Hoogesteijn 2010; Neilly et al. 2016; Wilmer et al. 2018). Although the term "wildlife" is often used to refer to vertebrates, invertebrates, by far, are the most abundant and species-rich assemblages of organisms in every terrestrial habitat (Zhang 2013) and can be important components of wildlife and rangeland management plans (Black et al. 2011; Grodsky et al. 2015). Beyond their sheer abundance and diversity, invertebrates contribute to the maintenance of overall ecosystem health and function through their roles in ecosystem services and processes (Noriega et al. 2018), making their conservation of utmost importance (Wilson 1987).

One critical ecosystem function that many invertebrates fulfill is pollination. Pollination is essential to the reproduction of many plant species, including rangeland plants, and is ultimately vital to maintaining healthy plant communities that underlie rangeland ecosystems (Black et al. 2011; Gilgert and Vaughan 2011). Although pollination is mediated by diverse animals, including mammals and birds, invertebrates are by far the most significant and speciose group of pollinators (Kearns and Inouye 1997; Roulston and Cane 2000; Potts et al. 2010). Bees (apiformes) are particularly significant pollinators by virtue of being frequent flower visitors and because they carry relatively large amounts of pollen compared with other invertebrates (Larson et al. 2018). Native bees are especially important pollinators on US rangelands and in wildland systems, where honey bees (*Apis mellifera* Linnaeus, 1758) can be uncommon (Kimoto et al. 2012b; Ballantyne et al. 2015; Cane and Love 2016; Roof et al., 2018).

There are approximately 4,000 species of native bees in North America (Cane and Tepedino 2001) that vary in size, flower preference, levels of floral specialization, nesting habits, and social organization (Michener 2007). Most native bees are small, solitary insects that emerge in spring or summer and feed on nectar while working to provision brood cells, primarily with pollen. Of native bees, 70–80% of species nest below ground in holes they construct, preexisting cavities, or abandoned rodent nests (Liczner and Colla 2019; Harmon-Threatt 2020). Other species use aboveground nesting resources, including downed wood, standing trees, and pithy stems (Michener 2007). Another key aspect of native bee biology is their diet. Most bees depend on a mix of nectar and pollen to provision their brood cells and feed themselves. Bees can range tremendously in their diet breadth, from specialists that forage on one or few plant species to broad generalists that forage on many plant species. Because rangelands are common across the globe and can support high densities of floral and nesting resources, they can provide good habitat for native bees (Black et al. 2011; Cane 2011; Kimoto et al. 2012a; Hanberry et al., 2021) and possibly spillover pollination services to neighboring cultivated agricultural land (Öckinger and Smith 2007; Garibaldi et al. 2011).

Across rangelands, grazing can not only influence ecosystem health, function, and structure (Jones 2000; Freilich et al. 2003; Krausman et al. 2009; Schönbach et al. 2011; Bailey et al. 2019; Goosey et al. 2019) but can also affect pollinators, including bees. In some systems, livestock grazing has been found to improve outcomes for bee populations (Vulliamy et al. 2006; Lázaro et al. 2016; Shapira et al. 2020; Lasway et al., 2022), whereas other studies have found grazing can negatively affect some bees (Kruess and Tscharntke 2002; Sjödin 2007; Xie et al. 2008; Yoshihara et al. 2008; Kimoto et al. 2012b). The variability in responses of native bees to livestock grazing may be due to myriad factors, including differences in the type of grazer, the intensity of grazing, the timing of grazing, plant growth stage, and the species traits of the particular bee species in the system (Kimoto et al. 2012b; Cutter et al., 2021). Several recent reviews suggest that the variability of insect pollinator responses to grazing may be mediated by the evolutionary history and habitat traits of a given system, with overall negative effects on pollinator abundance and richness (Glenny et al. 2022; Thapa-Magar et al. 2022), especially in regions that lack long-term evolutionary histories with herds of large mammalian grazers (Thapa-Magar et al. 2022). These effects may occur through multiple pathways, including dietary overlap (i.e., livestock and bees consuming the same floral resources) (DeBano et al. 2016), degrading nesting resources through soil and vegetation trampling (Kurz et al. 2006; Kimoto et al. 2012b; Schmalz et al. 2013), and by changing bee foraging behavior (Sjödin 2007).

One increasingly popular approach to livestock management that may have applications in pollinator conservation is targeted grazing (Launchbaugh and Walker 2006; Bailey et al. 2019). Targeted grazing is the practice of deliberately manipulating, timing, frequency, location, and/or intensities of grazing for the purpose of accomplishing specific vegetation and other ecosystem health goals (Launchbaugh and Walker 2006). Early uses of targeted grazing primarily focused on controlling invasive or pest plants in rangelands (Marchetto et al. 2021), but its use has expanded to include goals such as increasing the abundance and richness of native plants (Davy and Rinella 2019; Porensky et al. 2021) and enhancing wildlife habitat and rangeland biodiversity (James et al. 2017; Rhodes et al. 2021). Although recent research on targeted grazing approaches has expanded to include wildlife, this work has focused on vertebrates (Rhodes et al. 2021). Factors that can be manipulated in grazing plans include onset (turnout date), duration of grazing, stocking rate, livestock type, and grazing rotations (Bailey et al. 2019). Targeted grazing provides an opportunity to vary some of these factors in ways that may make grazing more compatible with, and potentially beneficial to, native pollinator populations.

Grazing timing, as it relates to the phenology of blooming plants and bee life cycles, may be a particularly important factor influencing bee community level responses to grazing (DeBano et al. 2016). Most studies that have detected negative effects of grazing on bee communities were conducted in systems where grazing was initiated early in the local growing season (Kruess and Tscharntke 2002; Xie et al. 2008; Kimoto et al. 2012b), when bloom and bee richness were more likely to be high. To our knowledge, only two studies have examined pollinator responses to late-season grazing. Sjödin (2007) observed that pollinator species in a Swedish grassland system visited flowers at higher rates and at greater species richness in sites where grazing was delayed until midsummer compared with sites grazed continuously since spring. Similarly, Lázaro et al. (2016) found that early-season grazing in Greece resulted in lowered pollinator species richness compared with late-season grazing. Given differences between European and North American grasslands, it is not clear that similar results would occur in the United States.

Here, we examine whether phenologically targeted grazing is an ecologically viable approach to minimizing potential negative effects on bee and blooming plant communities when they share rangelands with cattle (*Bos taurus* Linnaeus, 1758). We hypothesized that phenologically targeted grazing, set to begin after peak bloom, would have minimal effects on native bee and blooming plant communities. We conducted cattle grazing experiments in two graminoid-dominated systems in the Pacific Northwest, United States, to examine responses to grazing, when grazing began after peak bloom. Our specific objectives were to 1) quantify seasonal variation in abundance, richness, diversity, and community composition of blooming plant and bee communities; and 2) measure the responses of those communities as grazing was implemented throughout the season and compare those responses to ungrazed sites. We predicted that community composition of blooming plant

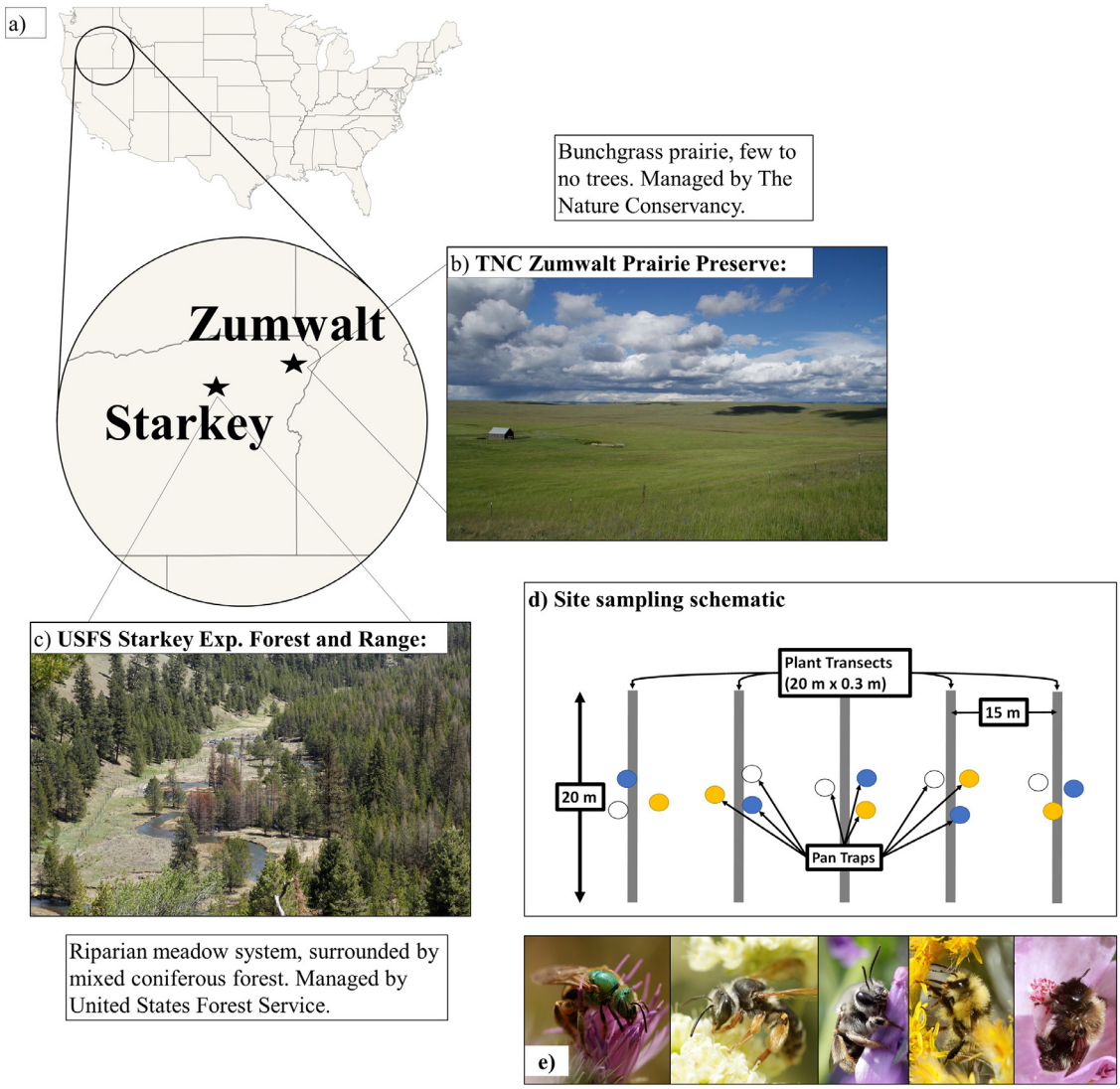

Figure 1. Study locations and sampling schematic. **a**, Study locations in Oregon, United States; **b**, The Nature Conservancy's Zumwalt Prairie Preserve; **c**, USFS Starkey Experimental Forest and Range; **d**, Sampling design; and **e**, Diversity of native bees, L→R: *Agapostemon* sp., *Andrena prunorum, Anthophora urbana, Bombus* sp., *Diadasia nigrifrons*. (See Table 1 for more information about each study system). All photos by SM.

and bee communities would vary through the growing season and that peak abundance, richness, and diversity of blooming plants and bees would occur early in the season (May and June). We also predicted that delayed-onset cattle grazing would not reduce bee abundance, richness, and diversity or alter community composition of blooming plants and bees compared with ungrazed sites. We examined plant and bee responses in the same season at two different locations to determine if observed trends were consistent between geographically isolated areas.

Methods

Study areas

Zumwalt Prairie Preserve

The Zumwalt Prairie Preserve (the Zumwalt) in Wallowa County, Oregon (45.55°N, 116.95°W, Fig. 1) is owned and managed by The Nature Conservancy (TNC). The preserve encompasses 13,269 ha of bunchgrass prairie, representing the largest remaining remnant of Pacific Northwest Bunchgrass Prairie (Tisdale 1982; Kennedy et al. 2009; Averett et al. 2020). Most of the Zumwalt is located between 1,060 and 1,680 m and receives an average of 48 cm of precipitation each year, mostly arriving between November and June (NOAA 2010). The coldest month of the year is December (average daily minimum, maximum temperature: −8.3, 1.7°C) whereas the warmest is July (average daily minimum, maximum temperature: 6.8, 29.5°C) (NOAA 2010).

Indigenous peoples lived on the bunchgrass prairie for thousands of years and began grazing horses in the early 1700s (Bartuszevige et al. 2012). After indigenous peoples were forcibly removed from the region and relocated to reservations in 1877, European-Americans continued grazing livestock in the region until the present (1880s–1940s, sheep [*Ovis aries* Lineaus, 1758]; 1940s–present, cattle) (Bartuszevige et al. 2012). Large portions of the bunchgrass prairie have relatively intact native plant communities dominated by bunchgrasses and > 300 species of forbs (e.g., prairie smoke [*Geum triflorum* Pursh, 1813], twin arnica [*Arnica sororia* Greene, 1910], lupines [*Lupinus* spp. Linneaus, 1753]); see Endress et al. (2019) and Averett et al. (2020) for descriptions of the dominant plant communities. Dominant soils in the area are Xerolls consisting primarily of silt loam, silty clay loams, and clay soils are most common across this study area (Schmalz et al. 2013).

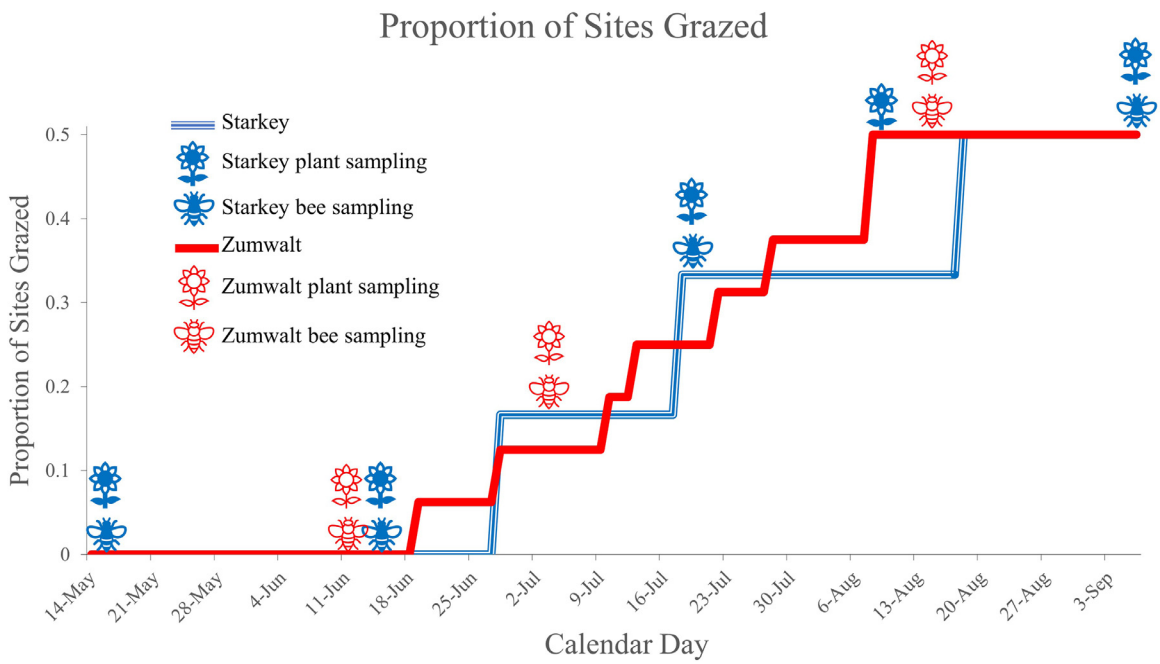

Figure 2. Proportion of all sites grazed by calendar date in 2018. Blue and red lines show proportion grazed at Starkey and the Zumwalt, respectively. Bee icons show bee sampling dates and flower icons show blooming plant sampling dates.

Table 1
Comparison of the two locations sampled for this study, including sampling sites.

Systems by the numbers		
	Zumwalt	Starkey
Annual precipitation	48 cm	42 cm
Elevation	1 300-1 500 m	1 100-1 200 m
Stocking rate (AUM/acre)	0.28-0.3	0.03-0.9 (site dependent)
Total management area	13 350 ha	10 125 ha
Median site size	39.9 ha	1.3 ha
Median nearest neighbor dist.	518 m	103 m
Median dist. between all sites	2 825 m	1 718 m
2018 cattle turnout date	June 19	June 28
Months sampled	Jun, Jul, Aug	May, Jun, Jul, Aug (plants only), Sept
Bee taxa richness	122	128
Blooming species richness	85	102
Management	The Nature Conservancy	US Forest Service

We sampled 16 sites in the Zumwalt in 2018. Eight sites served as a control and were not grazed by cattle at any time in 2018. At the other eight sites, a deferred rotation grazing system was used where cattle were rotated through sites from June 19 to August 9, with stocking rates ranging from 0.28 to 0.30 animal unit month [AUM]/acre (Table 1; Fig. 2). As a result, as the season progressed, the system moved from being dominated by ungrazed sites to having half of all 16 sites grazed by cattle by the end of the season (Fig. 2). The grazing history of all sites before 2018 is described in the appendix. Wild ungulates (deer [*Odocoileus* spp. Rafinesque, 1832] and elk [*Cervus canadensis* Erxleben 1777]) were present in the Zumwalt during our study; however, their abundance and presence were not measured as our focus was on experimentally manipulated cattle grazing regimes.

Starkey Experimental Forest and Range

The US Forest Service Starkey Experimental Forest and Range (Starkey) is in Union County, Oregon (45°12′N and 118°3′W, see Fig. 1). Similar to the Zumwalt, Starkey's climate is characterized by warm dry summers and cool wet winters. Annual average precipitation is 42 cm (NOAA 2010), mostly falling between November and June.

The coldest month is December (average daily minimum, maximum temperature: −4.6, 3.1°C), while the warmest month is July (average daily minimum, maximum temperature: 12.1, 29.7°C) (NOAA 2010).

Since 1955, Starkey has been used for long-term research on cattle grazing (Rowland et al. 1997; Wisdom et al., 2004). Our study was conducted along an 11-km section of Meadow Creek (tributary to the Upper Grande Ronde River), a perennial stream characterized by a narrow band of riparian meadows surrounded by upland coniferous forests. The elevation of Meadow Creek is 1,100–1,200 m, with surrounding uplands reaching 1,500 m. The riparian meadow system is dominated by grass and sedge species; annual forb species (e.g., strict forget-me-not [*Myosotis stricta* Link ex Roem & Schultes, 1819], tiny trumpet [*Collomia linearus* Nuttall, 1818], spring draba [*Draba verna* Linnaeus, 1753]); perennial forb species: (e.g., slender cinquefoil [*Potentilla gracilis* Douglas, 1830], Nuttall's violet [*Viola nuttallii* Pursh 1813], yarrow [*Achillea millefolium* Linaeus, 1753]); flowering shrubs; and scattered trees (DeBano et al. 2016; Averett et al. 2017). Most of the soils in Starkey are classified as silt-loams (Strickler 1965).

In 2018, we sampled 12 sites located in the graminoid-dominated habitat along Meadow Creek. Six sites served as a control and were not grazed by cattle at any time in 2018. The remaining six sites were grazed using a deferred rotation grazing system, where cattle were rotated through the six sites from June 28 to September 27 with stocking rates ranging from 0.03 to 0.9 AUM/acre (see Table 1; Fig. 2; Table S1, available online at…). As a result, as the season progressed, the system moved from being dominated by ungrazed sites to having half of all sites grazed by cattle by the end of the season (see Fig. 2). The grazing history of

all sites before 2018 is further described in the appendix. Wild ungulates (deer and elk) were present in some Starkey sites during our study; however, as at the Zumwalt, their abundance and presence were not measured.

Field methods

Plant community sampling

We surveyed blooming plant communities once per month at the Zumwalt (June–August) and Starkey (May–September) (see Fig. 2). We sampled plants along five parallel belt transects (each 20-m long and 0.3-m wide) separated by 15 m (see Fig. 1). At the Zumwalt, we centered transects within each site and oriented transects north to south, whereas at Starkey, we arranged all transects perpendicularly to Meadow Creek. We identified, counted, and summed all blooming stems by species (forbs and shrubs) along transects except for two genera at the Zumwalt (Hawk's-beards [*Crepis* spp. Linaeus, 1753] and *Lupinus*) that we only identified to genus. Data from all five transects were combined, creating a single dataset for each site. As in other pollinator studies (e.g., Roof et al., 2018; Graham et al. 2021; Mitchell et al. 2021), we defined blooming stems as individual flowers or clusters of flowers arranged on a stem.

Bee community sampling

Plants and bees were sampled concurrently except for August at Starkey when plants were sampled but bees were not (see Fig. 2). At every site, fifteen 240-mL pan traps, filled with 180–200 mL of slightly soapy water, were arranged in five groups of three (one each fluorescent blue, fluorescent yellow, and white) centered on each plant transect and left for approximately 48 h (see Fig. 1). Upon collection, the number of disturbed traps (e.g., knocked over by animals) was noted and later used to adjust for sampling effort (e.g., bees/trap/hour). In the laboratory, collected specimens were washed and pinned. Bees were identified to species, if possible, using methods described in Kuhlman and Burrows (2017). Cellophane-cuckoo bees (*Epeolus* spp. Latreille, 1802), metallic sweat bees (*Lasioglossum* [subgenus *Dialictus*] spp. Robertson, 1902), nomad bees (*Nomada* spp. Scopoli, 1770), blood bees (*Sphecodes* spp. Latreille 1804), and cuckoo carder bees (*Stelis* spp. Panzer, 1806) were often not identified to species due to a lack of available identification resources for the western United States.

Statistical analyses

Abundance, richness, and diversity

We evaluated univariate community responses to grazing for each sampling month using one-way analysis of variance (ANOVA, alpha = 0.05). The response variables we analyzed included bloom abundance (total number of blooming stems counted on transects), bloom species richness, and bloom Shannon-Weiner diversity (hereafter "diversity") (Shannon and Weaver 1949); for bees, we analyzed bee abundance (bees/trap/hour), rarefied bee species richness, and bee diversity. We examined responses to grazing in both systems each month by classifying "grazed sites" as any site that had been grazed by livestock in 2018 before sampling (e.g., a site grazed in July was classified as "ungrazed" if sampled in June and as "grazed" if sampled in July and August; see Fig. 2). We conducted ANOVAs in R (R Core Team 2019), and graphs were made using R's ggplot2 (Wickham 2016) package. Rarefied species richness was calculated using the vegan package in R (Oksanen et al. 2008).

Blooming plant and bee community analyses

We characterized communities using nonmetric multidimensional scaling (NMDS) ordinations with taxa abundance data and a Sorenson's distance measure to locate sites in plant community and bee community space (Kruskall and Wish 1978; McCune and Mefford 2006). We used the following settings: maximum 500 iterations, random starting point, step-length of 0.20, 250 runs real data, and 250 runs randomized data. We used NMDS analyses to visualize plant and bee communities across sample months and treatments, and differences in species composition between months and treatments were statistically evaluated using multiresponse permutation procedures (MRPP) (Biondini et al. 1985). MRPP analysis returns a probability value that estimates how likely a grouping is according to chance (McCune et al. 2002), as well as an agreement statistic, or A-value, which is a measure of within-group homogeneity. A-values closer to 1 indicate higher within-group homogeneity, and values close to 0 indicate within-group heterogeneity as expected by chance. All multivariate analyses were conducted in PC-ORD Version 7 (McCune and Mefford 2006).

Results

General results

We counted 45,642 blooms from 85 plant species at the Zumwalt and 22,926 blooms from 102 species at Starkey. Some plants (31 species) occurred in both study systems. We collected 7,128 bees from 172 taxa across the two systems (Table S2, available online at …). At the Zumwalt, 3,608 bees were collected, of which 3,317 were identified to one of 122 species or morphospecies. Of the remaining specimens, 284 were identified to subgenus, 283 of which were *Lasioglossum (Dialictus)* and 7 were identified to genus-level only. At Starkey, we collected 3,520 bees, 3,362 of which were identified to one of 119 species or morphospecies. Of the remaining specimens, 119 were identified to subgenus, 117 of which were *Lasioglossum (Dialictus),* and 39 were identified to genus. Of bees, 69 species or morphospecies, representing approximately 40% of all taxa identified, occurred in both systems.

Seasonal variation in blooming plant and bee communities

Abundance, richness, and diversity

Blooming plant abundance, richness, and diversity varied by season, with all three metrics peaking in June at the Zumwalt and declining steadily in July and August (Fig. 3). Ninety percent of all blooms were accounted for by 18 plant species in June, 11 in July, and 4 in August (Table S3, available online at …). At Starkey, average bloom abundance was also highest during the first month of sampling (May), while average bloom richness and diversity were highest from May to July and declined markedly by September (see Fig. 3). The number of species comprising 90% of blooms was 9 in May, 11 in June, 15 in July, 6 in August, and 3 in September (Table S4, available online at …).

Similar to blooming plants, bee abundance, rarified richness, and diversity varied seasonally. At the Zumwalt, average abundance peaked sharply in August, average rarefied bee richness was highest in June and July, and bee diversity peaked in June (Fig. 4). The number of bee species making up 90% of specimens collected at the Zumwalt decreased throughout the season, reflecting the peak richness and diversity early in the season, with 30 species in June, 27 in July, and 14 in August (Table S5, available online at …). By August, 60% of all bees collected were one of two species of sweat bees: *Lasioglossum incompletum* (Crawford 1907) and *Halictus tripartitus* (Cockerell 1895). Similar to the Zumwalt, average rarefied bee richness at Starkey was highest early in the season (May–July), but average bee abundance and diversity were highest in July (see Fig. 4). The number of species comprising 90% of bees collected

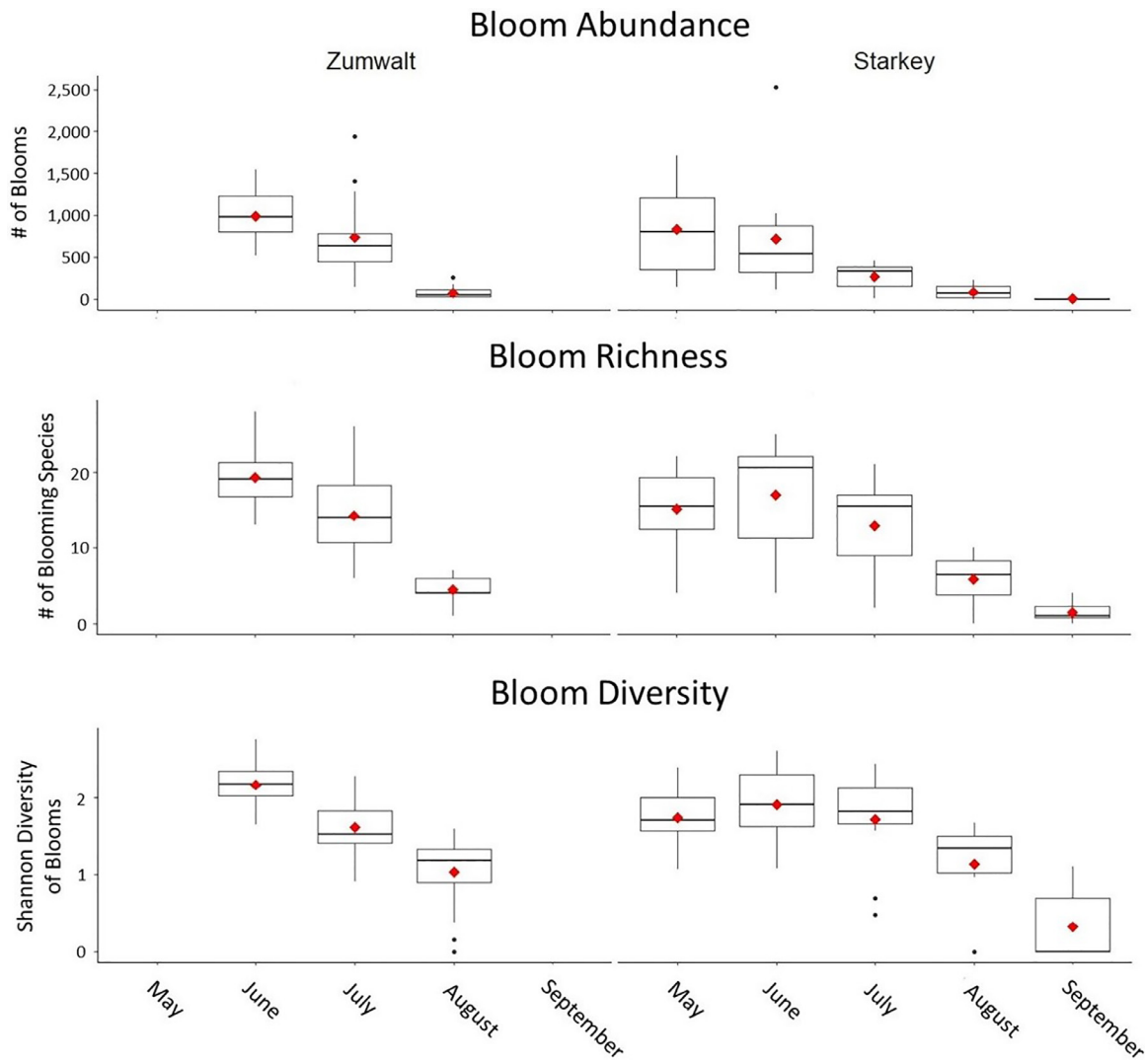

Figure 3. Boxplots of seasonal variability in 2018 by site in blooming plant abundance, richness, and diversity. Red diamonds: group means.

was 23 in May, 24 in June, 25 in July, and 16 in September (Table S6, available online at …). By September, 58% of bees collected at Starkey were one of two sweat bee species: *H. tripartitus* and *Halictus ligatus* (Say 1837).

Patterns in plant and bee community composition

In both systems, blooming plant and bee communities were strongly structured by sampling month (Fig. 5). In the Zumwalt plant ordination (see Fig. 5a), axis 1 explained 62% of the variance in the data and axis 2 explained 5%. Final stress of this ordination was 11.7. Month-to-month groupings of blooming plants differed significantly at the Zumwalt (MRPP: A = 0.2, $P < 0.001$). Plant species most positively associated with axis 1 were Gardner's yampah (*Perideridia gairdneri* Mathias, 1936), shaggy fleabane (*Erigeron pumilus* Nuttall, 1818), and Missouri goldenrod (*Solidago missouriensis* Nuttall, 1834). These were also plants that were associated with late-season blooming communities. The plants most negatively associated with axis 1 include twinflower arnica *(A. sororia),* strict forget-me-not (*M. stricta*), lupines (*Lupinus* sp.), meadow deathcamas (*Zigadenus venenosus* Watson, 1879), and slender phlox (*Microsteris gracilis* Greene, 1898), which are abundant early-season plants at the Zumwalt. Several plant species were positively or negatively correlated with axis 2 (see Fig. 5a, Table S7, available online at …).

In the Starkey plant ordination, axis 1 explained 38% of the variance in the data and axis 2 explained 11% (see Fig. 5b), and final stress of the ordination was 8.9. Month-to-month groupings of blooming plants differed significantly at Starkey (MRPP: A = 0.2, $P < 0.001$). Only one plant species *(P. gairdneri)* was strongly positively correlated with axis 1. The plants most negatively associated with axis 1 included blue-eyed Mary (*Collinsia parviflora* Douglas, 1829), *M. stricta, D. verna,* blue violet (*Viola adunca* Rees, 1817), and dandelion (*Taraxacum officinale* Weber ex Wiggins, 1780). These were mostly abundant early-season annuals at Starkey. Only one plant *(T. officinale)* was strongly positively correlated with axis 2. Plants negatively correlated with axis 2 included *P. gracilis,* little flower penstemon (*Penstemon procerus* Douglas ex Graham, 1829), blue umber-lily (*Triteleia grandiflora* Lindley 1830), *C. linearis,* and long-stalk starwort (*Stellaria longipes* Goldie, 1822) (see Fig. 5b, Table S7).

Bee communities were also strongly structured by month (see Fig. 5c and 5d). In the Zumwalt bee ordination (see Fig. 5c), axis 1 explained 58% of variance in the data and axis 2 explained 25%. Final stress of this ordination was 13.4. Month-to-month groupings of bees differed significantly at the Zumwalt (MRPP: A = 0.3, $P < 0.001$). Bee species most negatively associated with axis 1 included two mining bee species (*Andrena* spp. Fabricius, 1775), one mason bee species (*Osmia trevoris* Cockerell, 1897), one long-horned bee

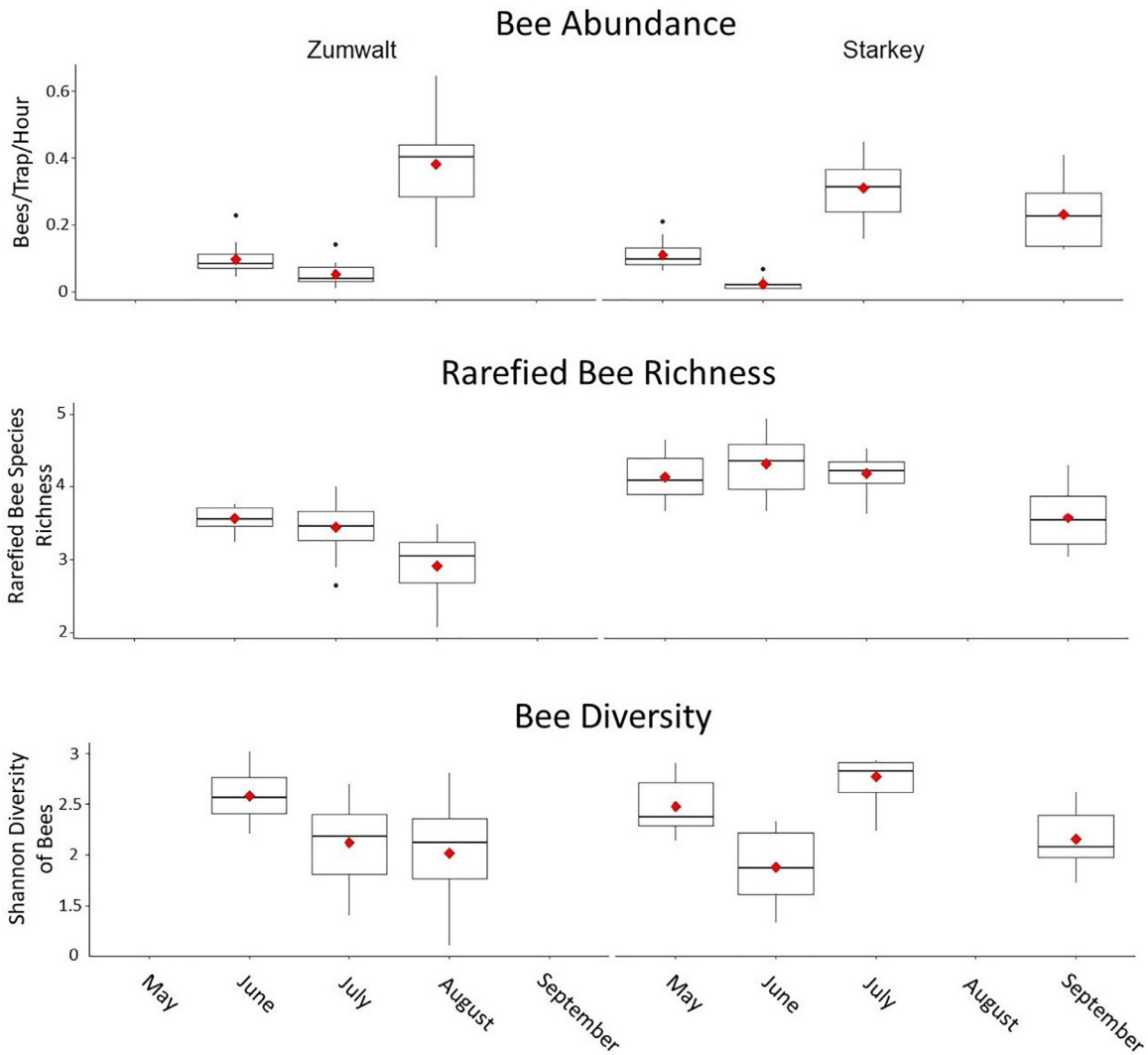

Figure 4. Boxplots of seasonal variability in 2018 by site in bee abundance, rarefied richness, and diversity. Red diamonds: group means.

species (*Eucera frater* Cresson, 1879), and one cuckoo bee (*Nomada* sp. Scopoli, 1770), all of which were early-season, solitary bees. Bee species most positively associated with axis 1 included four sweat bee species and one bumblebee species (*Bombus californicus* Smith 1854). All five of these species were primarily caught during the month of August. Only two species (a mason bee species (*Osmia melanopleura* Cockerell, 1916) and a fairy bee species (*Perdita wyomingensis* Cockerell, 1922), were strongly positively correlated with axis 2. Bees negatively correlated with axis 2 included three mining bee species, one sweat bee species (*Lasioglossum* sp.), and one long-horned bee species (*Eucera edwardsii* Cresson, 1879) (see Fig. 5c, Table S8, available online at …).

In the Starkey bee ordination, axis 1 explained 60% of variance in the data and axis 2 explained 19%. The final stress of this ordination was 12.7. Month-to-month groupings of bees differed significantly at Starkey (MRPP: $A = 0.3$, $P < 0.001$). Four sweat bee species (three *Lassioglossum* spp. and *Halictus rubicundus* Christ, 1791) and one bumblebee species (*Bombus bifarius* Cresson 1879) were most positively associated with axis 1. Two mining bee species (*Andrena* spp.), two sweat bee species (*Lasioglossum* sp. 2 and *Dufourea dilatipes* Bohart, 1948), and one long-horned bee species (*E. frater*) were most negatively associated with axis 1. Two mason bee species (*Osmia* spp.), two bumblebee species (*Bombus* spp.), and one mason bee species (*Hoplitis fulgida* Cresson, 1864) were most strongly positively correlated with axis 2. Bees negatively correlated with axis 2 included four sweat bee species (*Halictus tripartitus* Cockerell, 1895; *H. ligatus* Say, 1837; *Lasioglossum versans* Lovell, 1905; and *Agapostemon texanus* Cresson, 1872) and one pebble bee species (*Dianthidium subparvum* Swenk, 1914) (see Fig. 5d). See Table S8, available online at... for complete list of species correlations.

Blooming plant and bee responses to grazing

We predicted that bee and blooming plant abundance, richness, and diversity would not differ significantly between grazed and ungrazed sites in delayed-onset grazing systems. There were no statistically significant differences in blooming plant abundance, species richness, or diversity between grazed and ungrazed sites in July or August at the Zumwalt (Table 2). However, we found significantly lower average bloom abundance, richness, and diversity ($P < 0.02$) in grazed sites at Starkey in both July and August, but not September (see Table 2, Fig. 6).

We found no significant differences in bee abundance, richness, or diversity between grazed and ungrazed sites at Starkey in any sampling month (see Table 2). At the Zumwalt, bee abundance and

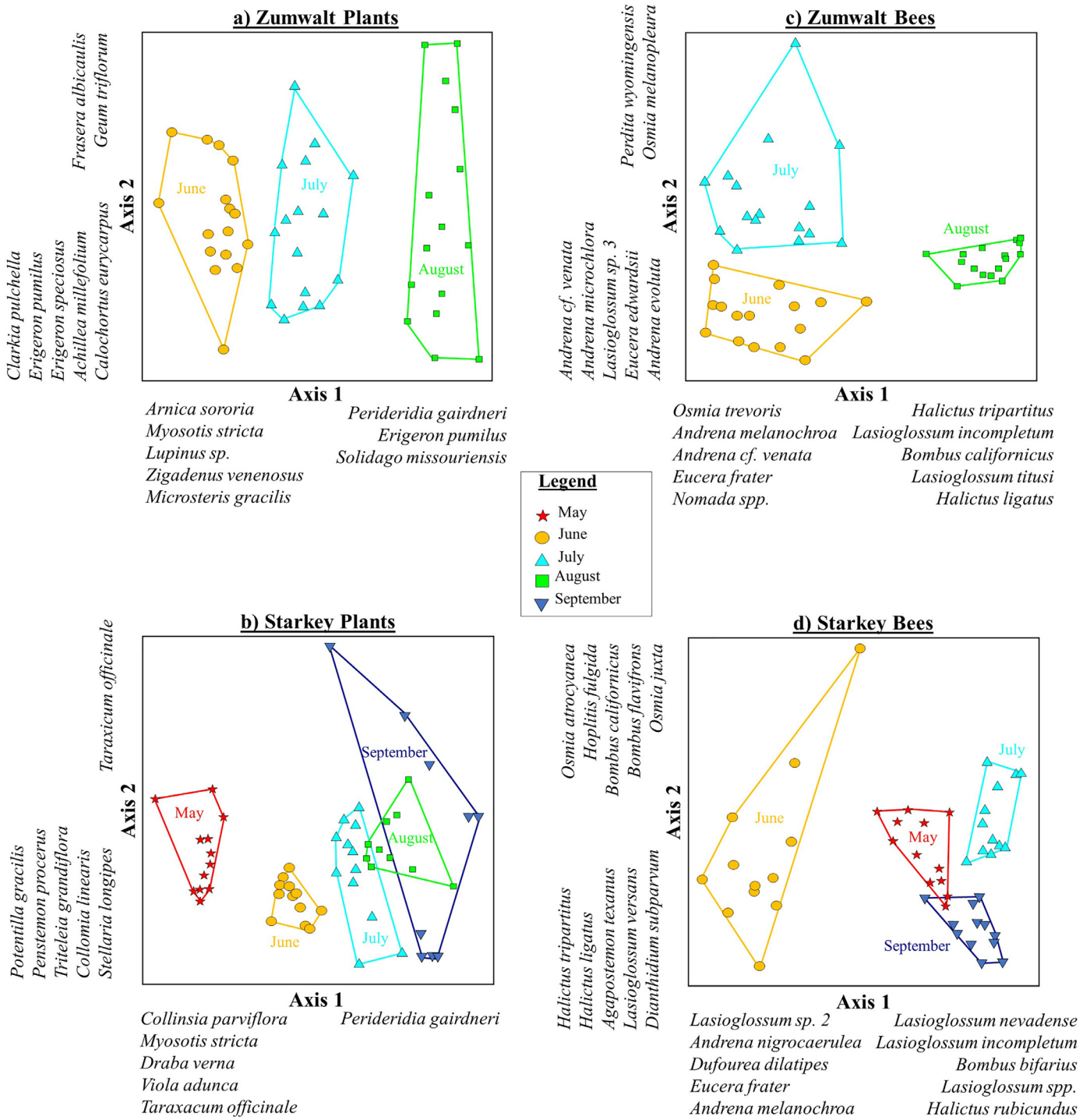

Figure 5. Nonmetric multidimensional scaling ordinations of bee and plant communities by month in 2018. Species with r^2 values ≥ 0.1 are shown. Species Pearson correlations with axes are listed in Tables S7 and S8. Subgenera for specimens not identified to species: *Lasioglossum* spp. (subgenus *Dialictus*), *Lasioglossum* sp. 2 (subgenus *Hemihalictus*), *Lasioglossum* sp. 3 (subgenus *Hemihalictus*). Species distant from the origin are positively correlated with the axis, and those listed close to the origin are negatively correlated with the axes.

richness, but not diversity, were significantly greater ($P = 0.04$) at grazed sites in July (see Table 2, Fig. 6). By August, however, these differences were no longer observed.

There was little separation between grazed and ungrazed sites in multivariate, community space, and community composition of bee and blooming plant communities did not differ relative to whether they were grazed in July, August, or September in either system (Table 3).

Discussion

The use of targeted grazing is gaining traction among land managers and livestock producers as a sustainable approach to rangeland management. This approach allows for livestock production while supporting additional goals related to ecosystem health and wildlife habitat enhancement (James et al. 2017; Davy and Rinella 2019; Porensky et al. 2021; Rhodes et al. 2021). Using focused

Table 2
Effects of grazing on bee and plant communities. Significant effects are bolded and shown in Figure 6.

Zumwalt							
		Blooming plants			Bees		
Month	Parameter	dF	F-stat	*P* value	dF	F-stat	*P* value
July	Abundance	1, 14	0.02	0.9	1, 14	5.2	**0.04**
	Species richness	1, 14	0.2	0.7	1, 14	5.4	**0.04**
	Diversity	1, 14	0.4	0.6	1, 14	1.9	0.2
August	Abundance	1, 14	1.8	0.2	1, 14	2.0	0.2
	Species richness	1, 14	0.07	0.8	1, 14	0.02	0.9
	Diversity	1, 14	0.05	0.8	1, 14	1.2	0.3
Starkey							
		Blooming plants			Bees		
Month	Parameter	dF	F-stat	*P* value	dF	F-stat	*P* value
July	Abundance	1, 10	11.9	**0.006**	1, 10	0.4	0.6
	Species richness	1, 10	16.9	**0.002**	1, 10	2.3	0.2
	Diversity	1, 10	42.4	**< 0.001**	1, 10	2.4	0.2
August	Abundance	1, 10	7.9	**0.02**	–	–	–
	Species richness	1, 10	8.1	**0.02**	–	–	–
	Diversity	1, 10	8.6	**0.01**	–	–	–
Sept	Abundance	1, 10	0.1	0.7	1, 10	0.002	0.97
	Species richness	1, 10	0.8	0.4	1, 10	0.3	0.6
	Diversity	1, 10	0.9	0.4	1, 10	0.1	0.7

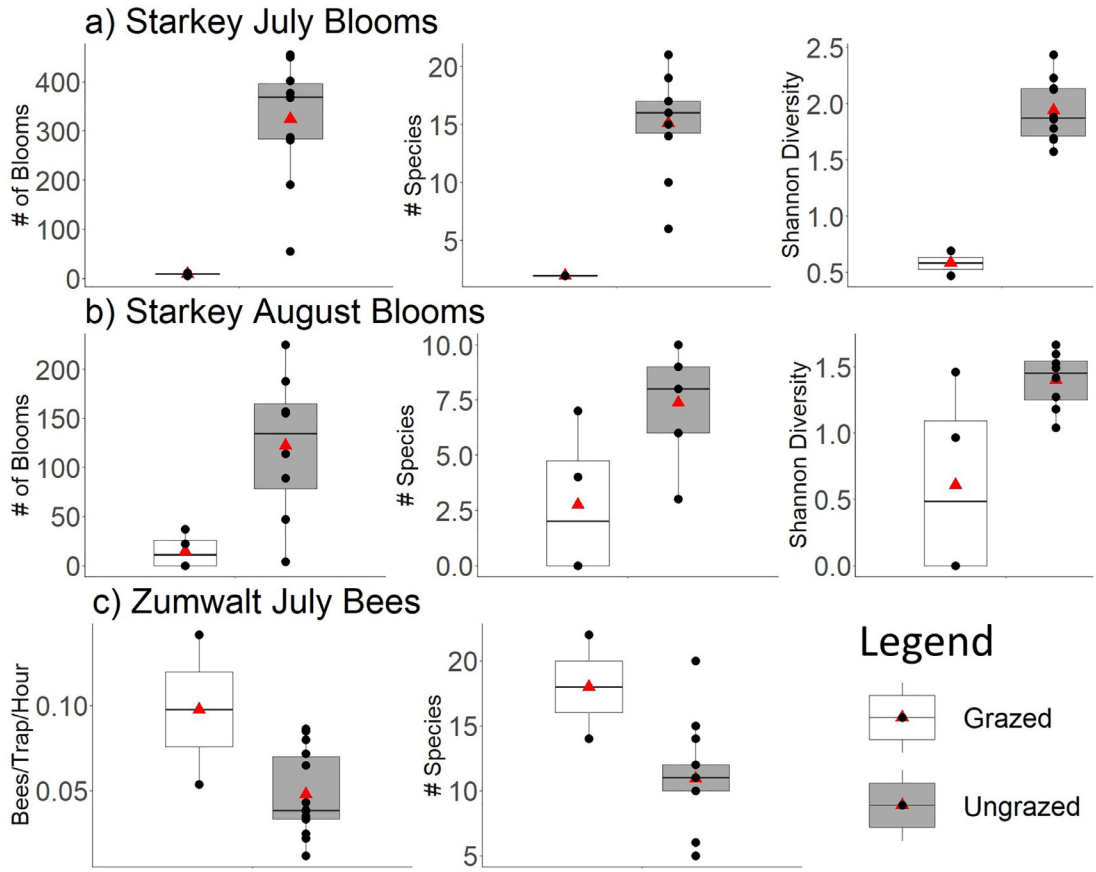

Figure 6. Boxplots showing **a**, Effect of grazing on plants at Starkey in July 2018 (2 grazed, 10 ungrazed sites). **b**, Effect of grazing on plants at Starkey in August 2018 (4 grazed, 8 ungrazed sites). **c**, Effects of grazing on bees at the Zumwalt in July 2018 (2 grazed, 14 ungrazed sites). Only statistically significant results are displayed. See Table 2 for analysis of variance results. Red triangles: group means.

and intentional decision making about where, when, and how to graze livestock to accomplish multiple goals across working landscapes can be expanded to include a wider variety of objectives, where cost-effective, or where nonmonetary motivations exist (e.g., enhancing pollinator habitat, accomplishing specific stewardship goals). To our knowledge, our study is the first to specifically examine whether a form of targeted grazing that focuses on plant phenology may be an effective way to manage grazing lands for the benefit of one type of invertebrate wildlife—native bees. Our predictions that blooming plant and bee abundance, richness, and diversity would peak early in the season were supported by our findings that all these measures (with the exception of bee abun-

Table 3
Multiresponse permutation procedures (MRPP) results, comparing grazed and ungrazed sites, for each month and grazing system.

		Plants		Bees	
	Mo	A value	*P* value	A value	*P* value
Zumwalt	June	−0.010	0.76	−0.007	0.67
	July	−0.008	0.60	0.003	0.36
	August	−0.011	0.62	0.030	0.10
Starkey	May	−0.021	0.78	−0.008	0.56
	June	−0.008	0.57	−0.035	0.95
	July	−0.012	0.70	−0.015	0.71
	August	−0.005	0.50	–	–
	Sept	−0.091	0.96	−0.015	0.71

dance) were highest in the first 2–3 mo (May–July) in both locations. Our hypothesis that phenologically targeted grazing would have minimal effects on native bee and blooming plant communities was supported by our results indicating no negative effects on bees and effects on plants in just July and August in Starkey. We found evidence that this grazing approach can be an effective strategy for reducing negative effects of livestock grazing on this important group of pollinators in Pacific Northwestern riparian meadows and grasslands, where past research has documented negative effects of livestock grazing on some bee taxa in the past (e.g., Kimoto et al. 2012b).

The extent to which phenologically targeted grazing minimizes negative effects on bees depends in part on the degree to which it successfully reduces dietary overlap between bees and livestock. The first step in determining whether the approach will be useful is to demonstrate that blooming flower and bee communities vary through the growing season, with peaks in species richness occurring at similar times and early enough in the season that grazing onset can either be delayed until after that time, or previously degraded habitats can be grazed first (i.e., before the peak has diminished in higher-quality sites). Our results showed that the species composition of blooming plant and bee communities varied widely through the growing season. Peaks in species richness occurred relatively early in both systems (before or during June), a result consistent with previous work in the western United States (Golet et al. 2011; Kimoto et al. 2012a, 2012b; Rhoades et al. 2018; Endress et al. 2022). In addition, peaks in bee and blooming forb richness occurred at generally the same time in both systems, a pattern also observed elsewhere (Potts et al. 2003; Ebeling et al. 2008; Holzschuh et al. 2012). The initiation of grazing at most sites in both systems did not begin until July or later, a practice that is a viable option in the region. For example, only ~20% of permittees on three ranger districts in the Wallowa-Whitman National Forest turn out cattle on their allotments before June 1 (pers. comm., M. Laverty, USFS Range Program Lead). In areas where cattle are turned out early in the season (e.g., before June 1), managers could take advantage of natural phenologic variation (e.g., dry grassland habitats with peak blooms in May) and less sensitive habitats (e.g., old fields or managed, seeded pastures) to promote landscape sustainability for pollinators. In this proposed scenario, livestock could be rotated onto more sensitive habitats after peak bloom had passed.

The next step in determining whether a phenologically targeted grazing approach is useful in the context of bee conservation is to demonstrate that when grazing is implemented under these conditions, bees do not show negative responses to grazing. Our study detected no changes in bee species composition or negative responses in abundance, richness, or diversity in bee communities in response to delayed grazing in either system. These results are consistent with European studies that found delayed grazing benefitted bees relative to early-season grazing (Sjödin 2007; Lázaro et al. 2016). The lack of any negative effects of grazing on bees in our study contrasts with other studies in which grazing occurred before or during peak blooming periods (including a study conducted in one of our study systems) and found negative effects of grazing on bee communities (Kruess and Tscharntke 2002; Xie et al. 2008; Kimoto et al. 2012b). Taken together, the results of our study in the context of previous research suggest that delayed-onset grazing, beginning after peak blooming flower abundance and richness, may be effective in mitigating potentially negative impacts of grazing on bee communities.

Although we found no negative effects of livestock grazing on bees, our results provide clear evidence for the potential of dietary overlap between bees and livestock and, thus, the importance of trying to limit that overlap temporally and spatially. In one system (riparian meadows), we found significantly lower abundance, richness, and diversity of blooming forbs in response to grazing in July and August. For sites where grazing began late, these effects occurred later in the season and no significant effects on bee communities were observed. The lack of effect on bees due to delayed-onset grazing may occur for several reasons. First, bee communities are typically less species rich and diverse late in the season, so fewer species will be affected by late-season grazing. In addition, by virtue of having fewer species overall late in the season, the bee community may have fewer specialist bee species. Specialist bees are particularly vulnerable to the loss of floral resources on which they depend. Our results in both systems were consistent with these expectations: we found fewer species of bees late in the season and the bee community was dominated by generalists. For example, late in the season in each study system, two species of generalist sweat bees accounted for more than half of all individuals sampled. Delayed-onset grazing may also have less of an effect on bees because floral resource richness and abundance are also declining as the season progresses. Thus, grazing by livestock is less likely to remove as many blooming species or blooming stems available to bees as it would early in the season. In addition, any reductions in the number of blooming species that do occur are less likely to affect a bee community dominated by generalists relative to one with many specialist species because generalists can seek out alternative resources.

In contrast to effects of livestock on blooming stems observed in the riparian meadow system, we did not detect significant responses to grazing by blooming plants in the bunchgrass prairie system. A variety of reasons may explain this difference, including variation in livestock diets between the two systems. The relative composition of grasses and forbs in livestock diets is influenced by numerous factors, including the dynamics of forage availability and quality and herbivore preferences. For example, although cattle generally prefer grass over forbs or shrubs, Walburger et al. (2007) found that the composition of grass in cattle diets in eastern Oregon can range from 65% to 90% and composition of forbs can range from 8% to 31%. This variation in diet composition may be due to seasonal changes in availability and quality. In systems where grasses become less available or decline in nutritional qual-

ity or palatability, cattle will be more likely to eat forbs (Walburger et al. 2007). However, in areas where grasses are abundant and high quality, such as at the Zumwalt Prairie, forb consumption may decline throughout the grazing season (Holechek et al. 1982; Uresk and Paintner 1985). The different responses of the blooming plant communities to grazing may also reflect a greater sensitivity of riparian areas to grazing (Schulz and Leininger 1990; Belsky et al. 1999; Samuelson and Rood 2011).

By considering the variability of bloom phenology on a landscape, range managers could graze cattle on sites with lower bloom richness and abundance (e.g., old fields, uplands) first, moving after peak bloom to sites with more abundant and species-rich blooming communities, thereby helping to reduce dietary overlap between most bee species and cattle (DeBano et al. 2016). Because bloom abundance and richness can be visually estimated quickly with minimal training, we propose that using phenologically targeted grazing is a general approach that could be adopted across the United States and elsewhere. Before widespread implementation of this approach, range managers should evaluate the economic viability of delayed or phenologically targeted grazing in their specific geographies.

One unpredicted result of our work was that bee abundance in both systems was greatest in the latter part of the growing season. As mentioned earlier, the higher abundance of bees observed in the latter part of the growing season was driven by a large number of generalist sweat bees. In the bunchgrass prairie system, the two dominant late-season species were *Lasioglossum incompletum* and *Halictus tripartitus,* and in the riparian meadow system they were *H. tripartitus* and *H. ligatus*. All three species are primitively eusocial generalists (Packer et al. 2007; Minckley 2008; Sheffield et al. 2014; Kremen and M'Gonigle 2015; Ponisio et al. 2019). The ubiquitous range of these particular species of sweat bees and their dominance in bee communities have been documented in several other studies in North America (Packer et al. 2007; Richards et al. 2011; Ponisio et al. 2019). At least two of these species (*L. incompletum* and *H. tripartitus*) appear to be fairly robust in the face of disturbance, being found in high quality and highly disturbed habitat alike (Sardiñas et al. 2016; Ponisio et al. 2019). The degree to which other systems are dominated by similar highly resilient species, the greater the potential for late-season grazing to have fewer negative effects on the overall bee community compared with early-season grazing.

Another unexpected result was that grazed sites had more bees than ungrazed sites late in the season in the bunchgrass prairie system. A partial explanation for this result may be the type of bee common during that time period. Some species of sweat bees may prefer certain habitat conditions (e.g., nesting substrate) associated with grazing, such as compacted soils (Kimoto et al. 2012b). The higher abundance of bees in grazed sites in the bunchgrass prairie system may also have been influenced by the trapping technique. The efficiency of passive traps can be influenced by local floral abundance or alteration of the physical structure of vegetation, which can affect the total abundance of bees collected (O'Connor et al. 2019). The higher abundance and richness of bees in grazed sites compared with ungrazed sites late in the season at the Zumwalt may also be due to fewer floral resources in grazed areas, or increased visibility of traps because of reduced vegetation structure. Despite potential limitations of pan traps for estimating bee abundance (O'Connor et al. 2019; Westerberg et al. 2021), they remain useful for comparing treatment effects on rarified richness, diversity, and community composition (Vrdoljak and Samways 2012).

Another important finding of our study is that neither system showed legacy effects from grazing in previous years, even though the treatment sites in the bunchgrass prairie system had been grazed at various times from spring to fall of each year by cattle at moderate rates (0.2–0.4 AUM/acre) since at least 2004 or 2005 (depending on the particular site). We did not detect any legacy effects of grazing from our sampling in early-season months before grazing onset in 2018 (see Fig. S1a and S1b). The lack of detectable effects on sites grazed annually over a 10-yr period may indicate that at moderate stocking rates, this ecosystem is resilient to short "pulse" disturbances and may "reset" each year (Lake 2000). However, studies have indicated that perennial forbs can be long-lived. Some studies indicate average lifespan for perennial plants is upwards of 36 yr (Treshow and Harper 1974; Ehrlén and Lehtilä 2002); thus, longer-term surveys could help determine if blooming plant abundance changes with longer-term exposure to grazing than sites used in this study were exposed to (12 yr of grazing). Additionally, it is unclear whether the results we observed in this study would remain consistent with different grazing systems, higher stocking rates, and/or different types of livestock. In fact, previous studies have indicated that when higher stocking rates resulted in higher utilization, abundance of certain bee taxa may decrease (Kimoto et al. 2012b) and that cattle influence bee and blooming plant communities less than other stock such as sheep (Cutter et al. 2021). Since the riparian meadow sites at Starkey were only grazed for 1 yr (in recent history) before our sampling in 2018, it will be important to continue monitoring bee and blooming plant communities there to determine if they respond to longer-term exposure to grazing.

Implications

Our results suggest that management approaches aimed at developing more sustainable livestock grazing practices that benefit pollinators may be an effective strategy for western US rangeland systems. Targeted grazing has been used to successfully control invasive plants while increasing native plant abundance and richness (James et al. 2017; Davy and Rinella 2019; Rhodes et al. 2021). Incorporating a targeted grazing strategy centered on bloom phenology may offer a straightforward way to increase sustainability for pollinators. On the basis of our study, integrating phenology into targeted grazing approaches may be a viable option for range managers interested in reducing negative effects of grazing on bee and blooming plant communities, where it occurs, and improving overall ecosystem health and sustainability. Many rangelands have at least some areas that lack abundant blooming plants (e.g., previously cultivated fields) (Smith DiCarlo et al. 2020; Watson et al., 2021). By surveying sites for plant diversity, richness, and abundance, range managers could identify "sensitive habitats" (e.g., native bunchgrass prairie, riparian meadows) that support complex bee communities and "less sensitive" or more resilient sites (e.g., old fields, upland forests) that contain fewer blooming plants and bees but still have valuable forage resources for livestock such as the introduced species Kentucky bluegrass (*Poa pratensis* Linnaeus, 1753), intermediate wheatgrass (*Thinopyrum intermedium* Barkworth and Dewey, 1985), and crested wheatgrass (*Agropyron cristatum* Gaertner, 1770) (Stubbendieck et al. 2017; Averett et al. 2020). Range managers could graze cattle in less sensitive areas before and during periods of peak floral abundance and richness, when bees are most vulnerable, and rotate cattle onto more sensitive habitats late in the season after most blooms have senesced.

While permanent fencing can be expensive, range managers could consider using alternatives such as temporary electric fencing or virtual fencing to keep livestock out of sensitive habitats early in the season (Campbell et al. 2018; Lomax et al. 2019). In other instances, range managers could leverage herders employed for other purposes (e.g., as predator deterrents) to monitor and move stock animals to targeted, less sensitive habitats until plant blooms in more sensitive areas have begun to senesce (Barnes 2015; Stephenson et al. 2016). Two added benefits of delayed-onset

grazing in native bunchgrass prairie are 1) native bunchgrasses are less sensitive to overgrazing later in the year (Schroeder and Johnson 2019) and 2) many culturally important forbs are early-emerging plants or blooms harvested in spring or early summer, which senesce later in the season (Endress et al. 2022). Both benefits suggest that phenologically targeted grazing can benefit more than just bees and flowering plants. Furthermore, phenologically targeted grazing that is timed to occur after peak bloom may be a particularly useful strategy for minimizing any potentially negative effects of livestock on pollinators in the context of a globally changing climate. Many bee species likely rely on the same cues for emergence timing as plants rely on for bloom timing (Bartomeus et al. 2011). This linkage between bee emergence and plant bloom means bloom phenology may remain a robust cue for developing grazing schedules, even with warming climates and associated changes in bee and plant phenology. To better understand bee community responses to sustainable grazing practices, future research should focus on the effects of grazing on taxa of conservation concern, undertake longer term studies, and investigate the effects of native ungulate grazers and how grazing interacts with other disturbances (e.g., fire). Future studies could also examine how much of a landscape needs to be excluded each year from grazing during peak bloom periods and how livestock could be rotated through different parts of the landscape from year to year to maintain robust pollinator and plant communities.

Competing Interests Statement

All authors declare no competing interests.

Author Contributions

SM, SD, MR, LM, HS, and SL conceived the ideas and designed the methodology; SM and SD collected the data; SB identified all bee specimens; SM and SD analyzed the data; SM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2023.06.001.

Appendix

Description of grazing history, grazing systems and estimated grazing intensity

United States Forest Service Starkey Experimental Forest and Range (Starkey)

Although historically grazed, cattle have been excluded from four of the Starkey Meadow Creek study sites since 1990 (Case & Kauffman 1997) and from the other eight since 2012. Cattle grazing was reintroduced along Meadow Creek in 2017 using a deferred rotation grazing system as part of a long-term experiment. In 2018, 80 cow/calf pairs were used to graze five main pastures. Of those five pastures, three contained the 12 study sites used in this study. Two sites of the four sites within each of the larger pastures excluded cattle grazing with fencing. One grazed site in each larger pasture was enclosed by a fence so a subset of cattle were introduced into the fenced area during a period of time when the larger pasture was being grazed. Cattle were first turned out in the system on June 4, 2018, when soil moisture was low enough to tolerate cattle, but they were not rotated into the study site pastures until June 28, 2018.

Although stocking rates of grazed sites at Starkey varied because the sizes of the areas within which our study sites were located differed as well as the duration for which they were grazed, their management was based on estimated use of the area where our study sites were located. Cattle were rotated through pastures as different greenline vegetation thresholds were reached, following protocols described in the Bureau of Land Management's *Multiple Indicator Monitoring (MIM) of Stream Channels and Streamside Vegetation* manual (Burton et al. 2011). Because cattle tended to concentrate in the riparian area of these pastures, we focused on documenting use in the riparian meadows where our study sites were located. These sites were monitored weekly for various MIM variables, including stubble height. When stubble height reached 19 cm, cattle were rotated out of the study site area. Using stubble height and other MIM variables as triggers for rotation resulted in similar utilization in all grazed Starkey sites in our study and reflect common use of grazing allotments in the Pacific Northwest.

The Nature Conservancy's Zumwalt Prairie Preserve

Cattle have been excluded from eight of the Zumwalt sites since 2004 or 2005 (depending on the particular site), whereas eight sites have been grazed using a deferred rotation grazing system since 2004 or 2005 at a moderate rate (0.2 – 0.4 AUM/acre), which is considered representative for the region (Kimoto et al. 2012b; Averett et al. 2020). Grazing occurred on some sites prior to 2004, however records were not kept regarding which sites were grazed or the stocking rate used. At the Zumwalt, 180 cow/calf pairs, 98 yearlings, and 10 bulls (with the exception of two grazed sites where bulls were not used) were rotated through sites. Cattle remained in pastures between three and seven days depending on the pasture size and the time needed to reach particular AUM/acre goals (0.29-0.3 AUM/acre in 2018). The resulting level of utilization associated with each pasture was measured within one week after cattle were removed from the pasture using the NRCS Key Forage Method (NRCS, 1999). In 2018, the stocking rates resulted in an average utilization of 37.7 ± 3.3% (mean ± standard deviation) and ranged from 31.2 to 41.8%, which is associated with moderate use in the region (Kimoto et al. 2012b).

Other Ungulates

Native ungulates (deer and elk) were present in both Starkey and the Zumwalt, and were likely present, at least some of the time, in some of our study areas. Since the focus of our study was on the experimentally manipulated cattle grazing treatments, we did not make any attempts to measure the presence or abundance of native ungulates in either landscape and did not account for native ungulate herbivory in our models.

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