Grazing for pollinators: The effects of grazing management on foraging and nesting pollinator communities and habitat

by

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Abstract

Native pollinators are a vital but threatened component of natural and agricultural systems worldwide, including grasslands. In the Great Plains, bison and prairie dogs were once among the most abundant mammalian grazers, while cattle grazing is a widespread management practice today. Grazers like cattle, bison, and prairie dogs shape the ecosystems around them through herbivory and behavior. However, their effects on pollinator habitat and pollinator communities in prairies are not well understood. This study investigated the effects of grazers on 1) foraging pollinator habitat, communities, and traits and 2) ground-nesting bee habitat and communities. During summer 2024 and 2025, I quantified plant-pollinator networks and measured ground-nesting bee communities across grazing regimes (bison, cattle, prairie dogs, and ungrazed areas) and intensities at sites spanning tallgrass and shortgrass prairies in the Great Plains (Konza Prairie, KS; American Prairie, Charles M. Russell National Wildlife Refuge, and Fort Belknap, MT). I found that grazers primarily influence pollinators indirectly, through effects on floral resources. In Kansas, floral resource availability was higher in bison- and cattle-grazed areas than ungrazed areas, and in Montana, bison and prairie dogs were associated with increased floral resources. In both regions, plant species richness, but not abundance, was positively associated with pollinator species richness. In addition, bee size (a proxy for dispersal ability) did not vary with grazing regime in either region, but larger bee species tended to interact with fewer plant species than smaller bee species in both regions. I found that nesting bee abundance was highest in bison-grazed sites in Kansas, and trended higher in bison-grazed sites in Montana. Nesting bee abundance was primarily driven by aboveground habitat characteristics, particularly floral richness, across regions. Identifying grazing practices that promote robust pollinator

communities is critical for the conservation and management of North America's grasslands, and for informing restoration decisions.

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Chapter 1 - Introduction

Pollinators have ascended in the conservation zeitgeist in recent decades, and for good reason—terrestrial ecosystems and humanity's food systems rely on them. Without pollinators—including bees, flies, butterflies, moths, wasps, beetles, bats, birds, lizards, and more—the nearly 90% of flowering plant species that require animal pollination would not be able to sexually reproduce (Ollerton et al. 2011). Additionally, 85% of major crop species rely on or benefit from animal pollination (Klein et al. 2007). Clearly, our world is better for this mutualism—we have squash, blueberries, almonds, chocolate, and tequila while ecosystems maintain genetically diverse plants.

Among terrestrial ecosystems, grasslands are one of the most expansive but most threatened. Grasslands make up almost 40% of Earth's land area, supporting agriculture and livestock and act as a major carbon sink (O'Mara 2012). Temperate grasslands have been reduced by more than 45% worldwide, one of the highest conversion rates of any ecosystem, and have declined vastly in North America since European colonization (Samson et al. 2004, Hoekstra et al. 2005).

Herbivores and fire, contemporarily mediated by human management, shape and maintain grassland systems. In North America, fire has long been used as a management tool by indigenous peoples, and historically grazers—including bison and prairie dogs—worked in tandem to shape the prairies (Axelrod 1985, Roos et al. 2018, Duchardt et al. 2025). Through colonization, cattle have taken the place of bison and prairie dogs in North America's grasslands and fire regimes have changed vastly (Samson and Knopf 1994). Today, most of the U.S.'s largest grassland remnants are areas where the landscape was not amenable to the plow and ranching livelihoods and grazers maintained the grasslands (Scholtz and Twidwell 2022).

Herbivores including bison, prairie dogs, and cattle play significant ecological roles in grasslands through their foraging preferences and physical impacts on their surroundings (Ratajczak et al. 2022, Duchardt et al. 2025, Rebh and Welti 2025).

Given the historic and current role of grazers in grassland systems, it is important to understand how grazers might influence habitat for pollinators in grasslands. What grazers eat and how they modify vegetation, nutrient cycling, and soil characteristics all may impact the quality and quantity of foraging and nesting habitat available to pollinators. Mammalian herbivores mediate plant community composition (Fahnestock and Detling 2002, Pringle et al. 2023), altering food resources for pollinators. Grazer impacts on grassland plant communities are variable but bison and cattle can boost plant species richness (McMillan et al. 2018, Ratajczak et al. 2022, Noble and Ratajczak in press). Grazers like bison, cattle, and prairie dogs vary in their foraging patterns and preferences, but all tend to forage on grasses more than on forbs—plants that provide pollinators most of their pollen and nectar resources (Fahnestock and Detling 2002, Towne et al. 2005, Ratajczak et al. 2022). The potential for reduction in grass competition due to grazing may benefit forbs and in turn, pollinator communities (Figure 1).

Grazers may further impact ecological characteristics that are important for nesting pollinators. Nesting is a critical, poorly understood life stage for insect pollinators including ground-nesting bees, which make up 80+% of bee species (Harmon-Threatt 2020). Bee nesting habitat, particularly among ground-nesters, is understudied (Antoine and Forrest 2021, Orr et al. 2022). A range of soil, soil surface, and above-ground characteristics have been identified as important for ground-nesting bees, but the specifics vary widely across studies. In several cases, bare ground cover and shorter vegetation are positively associated with bee nesting, and the effects of soil characteristics on nesting bees are variable (Tschanz et al. 2020, Gardein et al.

2022, Albrecht et al. 2023, Williams et al. 2024). The importance of nearby floral resources also ranges from unrelated to positively associated with bee nesting (Pane and Harmon-Threatt 2017, Williams et al. 2023). In general, studies examining direct measurements of bee nesting (e.g., measurements that do not infer nesting bee presence from foraging bee presence) are limited, particularly in grazed areas. It is possible that grazers not only affect bee foraging habitat, but influence characteristics that mediate bee nesting habitat, including plant community composition and heterogeneity, vegetation height, bare ground cover, soil compaction, and nutrient cycling (Whicker and Detling 1988, Towne et al. 2005, Kimoto et al. 2012, Beals et al. 2014, Borer et al. 2014, Horne et al. 2024, Rebh and Welti 2025).

Here I examine how grazers influence pollinator communities and their foraging and nesting resources. I spent two field seasons collecting data on pollinator communities in sites spanning tallgrass and short- to mixed-grass prairie: Konza Prairie in northeast Kansas (tallgrass), and American Prairie, Fort Belknap, and the Charles M. Russell National Wildlife Refuge in northeast Montana (short- to mixed-grass). In both Great Plains regions, I measured pollinator communities and their foraging and nesting habitats across a range of management practices: bison-grazed, cattle-grazed, and ungrazed sites at Konza, and bison-grazed (including two levels of grazing densities), cattle-grazed, prairie dog colony, and ungrazed sites in Montana. In Montana, I compared sites under varying bison grazing intensities.

I discuss my results from the study in two chapters: Chapter 2 focuses on foraging pollinator communities and how grazing management shapes floral resources for pollinators. Chapter 3 addresses ground-nesting bee communities, using direct measurements of bee nesting and asking how a range of habitat factors influence nesting bees across grazing regimes. By exploring how foraging and nesting pollinator communities vary with habitat characteristics and

across grazing practices, I aim to identify ecological characteristics that benefit pollinators and highlight ways in which grazers mediate pollinator habitats.

Supporting pollinators is critical for maintaining plant diversity in natural systems and for agricultural production (Ollerton 2017, Katumo et al. 2022). Pollinators in prairie habitats in particular face threats as their habitat is fragmented, converted to suburban development and row crops, or shifts to a woody state (Ratajczak et al. 2016, Comer et al. 2018, Wagner et al. 2021). The ecological and economic importance of grazers makes understanding pollinator habitat in grazed grasslands necessary. Linking grazers, pollinators, and the ecosystems they share can both highlight the possible historic dynamics between native herbivores and pollinators, and the role played by present-day grazing systems for pollinators. Identifying ways to support pollinator communities through management is one strategy for making sure our remaining prairies persist as healthy, biodiverse systems.

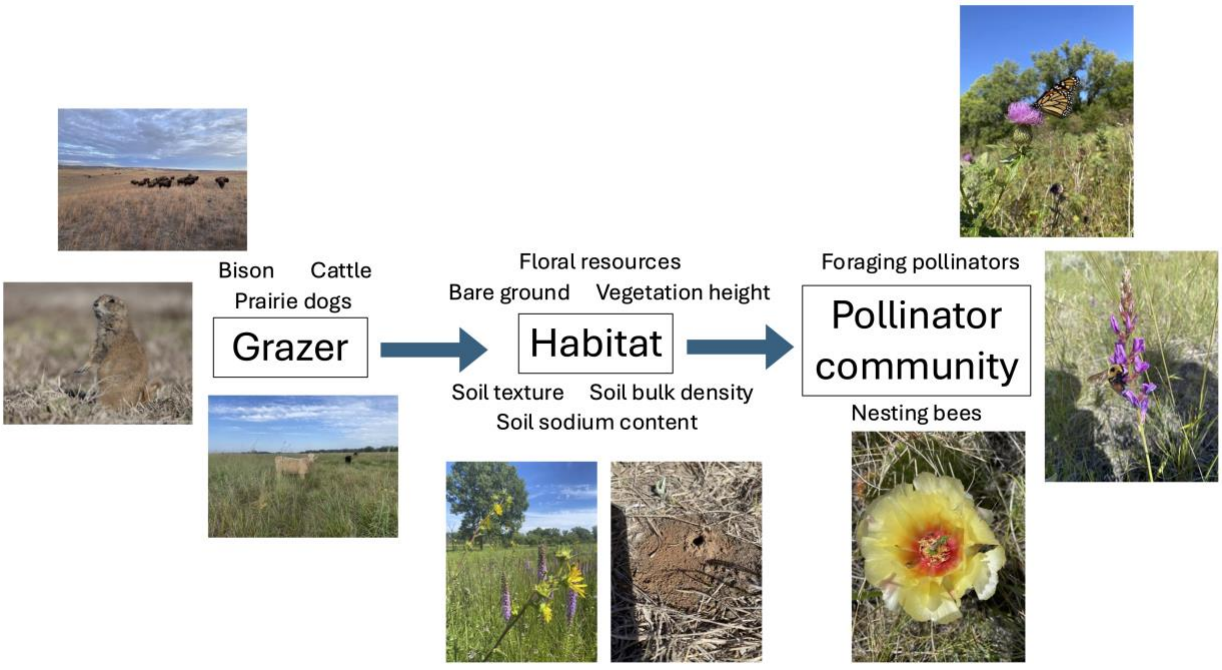

Figure 1.1. Hypothesized relationships between grazers, pollinator habitat, and pollinator communities in grasslands. Grazers considered in study are bison, cattle, and prairie dogs

(compared to ungrazed areas) in two Great Plains regions (Kansas and Montana). Adapted from Welti and Joern (2018). Prairie dog photo by Chris Helzer.

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Chapter 2 - The effects of bison, cattle, and prairie dogs on pollinator communities and floral resources

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Abstract

Native pollinators are a vital but threatened component of natural and agricultural systems worldwide, including grasslands. In many Great Plains grasslands, bison and prairie dogs were once the dominant mammalian grazers, while cattle grazing is a widespread management practice today. Grazers like cattle, bison, and prairie dogs shape the ecosystems around them through selective foraging and non-consumptive effects, which affect plant community composition, reducing the proportion of grasses in favor of forbs—the wildflowers that pollinators depend on. However, grazer effects on pollinator habitat and pollinator communities in prairies are not well understood. Our objectives are to investigate 1) the effects of grazers on floral resources for pollinators, 2) how pollinator communities vary with grazing and floral resource availability, 3) how bee size—a proxy for dispersal ability—varies with grazing regimes and floral resources, and 4) to characterize plants and pollinators on a spectrum from generalists to specialists in interaction networks. During summer 2024 and 2025, we quantified

plant-pollinator networks across grazing treatments (bison, cattle, prairie dogs, and ungrazed areas) and intensities at sites spanning tall- and shortgrass prairies in the Great Plains (Konza Prairie, KS; American Prairie and Fort Belknap, MT). Grazers primarily influenced pollinators through effects on floral resources. In Kansas, floral resources were higher in bison- and cattle-grazed areas than ungrazed areas, and in Montana, bison and prairie dogs were associated with increased floral resources. In both regions, pollinator richness was positively associated with plant species richness but not floral abundance. Bee size did not vary with grazing regime in either region, but larger bee species trended towards interacting with fewer plant species than smaller bee species in both regions. We identify several plants of high importance to pollinator species in each region, to aid grassland restoration seed mix design. Identifying grazing practices that promote healthy pollinator communities is critical for the conservation and management of North America's grasslands.

Introduction

Approximately 88% of Earth's flowering plant species are pollinated by animals, largely insects including bees, wasps, butterflies, moths, flies, and beetles (Ollerton et al. 2011). These key plant-pollinator interactions maintain the health of natural systems and contribute to the production of ~75% of major food crops globally (Klein et al. 2006). Pollinators are declining globally due to stressors including habitat loss and degradation, invasive species, and climate change (Winfree 2010, Burkle et al. 2013, Cornelisse et al. 2025, Edwards et al. 2025). Pollinators native to grassland ecosystems may be particularly vulnerable. For example, U.S. grasslands have been greatly reduced since European settlement, with only 5% of tallgrass prairie, 29% of mixed-grass prairie, and 52% of shortgrass prairie remaining today (Samson and Knopf 1994, Samson et al. 2004). Temperate grasslands, globally, have followed a similar

pattern and have among the highest percent of habitat conversion and lowest percent of protected areas of the major terrestrial biomes (Hoekstra et al. 2005).

The future of native pollinators in these threatened habitats depends in large part on how remaining grasslands are managed (Buckles and Harmon-Threatt 2019, Welti and Joern 2018). Disturbance, grazing animals, and variable climate are key determinants of grassland structure and the flow of ecosystem services (Axelrod 1985). Millions of bison and miles of prairie dog towns historically covered North America's grasslands prior to European settler colonization (Hornaday 1989, Knapp et al. 1999, Fahnestock and Detling 2002). In the 1800s, bison reached the brink of extinction, and today bison have largely been replaced by cattle in North America's remaining grasslands (Knapp et al. 1999, Allred et al. 2011). Globally, 26% of Earth's non-glaciated terrestrial area is used for grazing ruminant livestock (FAO 2012). Bison conservation has increased in recent decades, with the United States naming the bison its National Mammal and public and private herds growing in abundance to a current population of ~500,000 (Knapp et al. 1999, Sanderson et al. 2008, Allred et al. 2011). Similarly, prairie dogs have been eradicated from their grassland habitat since the 1800s and persist today at approximately 2% of their historic population size in the U.S. (Fahnestock and Detling 2002, Miller et al. 2007).

Grazing by mammalian herbivores can affect flowering plant community composition, vegetation structure, and soil characteristics (Damhoureyeh and Hartnett 1997, Kimoto et al. 2012, Koerner et al. 2018, Ratajczak et al. 2022), all of which may have cascading effects on pollinator communities (Fay 2003, Kimoto et al. 2012, Welti and Joern 2018, Cutter et al. 2022). Both cattle and bison selectively forage on grasses, allowing flowering plants to proliferate, and both grazers are generally thought to increase floral community diversity (Coppedge et al. 1998, Towne et al. 2005, Ratajczak et al. 2022). However, these effects are not always seen in drier

grasslands or post-agricultural contexts (Bennett et al. 2025, Noble and Ratajczak, in press). In addition to active grassland management involving ungulate grazers like cattle and bison, prairie dogs are native, typically unmanaged herbivores that strongly modify vegetation, creating distinct floral communities and habitat characteristics that may have a unique impact on pollinator communities (Whicker and Detling 1988, Fahnestock and Detling 2002, Beals et al. 2014). By altering pollinator food, shelter, and nesting resources, grazing mammals may mediate pollinator community makeup and plant-pollinator interaction network structure.

The cascading effects of grazing on floral resources are expected to influence pollinator communities. Grazed grasslands tend to have lower pollinator richness and abundance relative to ungrazed sites (Rosenberger and Conforti 2020, Thapa-Magar et al. 2020, Campbell et al. 2021, Rakosy et al. 2022), though in some cases pollinators are relatively unaffected by grazing (Stein et al. 2020, Mitchell et al. 2023). Pollinator abundance and richness can further vary with grazing intensity, and intermediate grazing pressure may support the greatest bee abundance and species richness (Kimoto et al. 2012, Lázaro et al. 2016, Lasway et al. 2022). Regardless of grazing practices, greater pollinator richness and abundance are typically associated with greater floral resource availability (Lázaro et al. 2016, Rosenberger and Conforti 2020, Stein et al. 2020, Thapa-Magar et al. 2020, Campbell et al. 2021, Lasway et al. 2022, Rakosy et al. 2022). In addition to the influence of grazing on pollinator community richness and abundance, grazing can influence plant-pollinator interactions, which may be important for plant and pollinator resilience to stressors (Welti & Joern 2018). Most studies on the effects of grazing on pollinators focus on cattle grazing (Kimoto et al. 2012, Stein et al. 2020, Thapa-Magar et al. 2020, Campbell et al. 2021, Lasway et al. 2022, Rakosy et al. 2022, Kral-O'Brien et al. 2023, Mitchell et al. 2023). When effects of multiple grazer species are examined, they are often considered as a

group across multiple species (e.g., Filazzola et al. 2020), despite evidence of differential effects by species (Cutter et al. 2022). Few studies address bison grazing, compare multiple grazer species (though see Welti & Joern 2018, Rosenberger & Conforti 2020, Cutter et al. 2022), or examine responses to prairie dog colonies.

Functional traits can provide mechanistic insight into why individuals or species respond to altered environmental conditions. Trait-based research is expanding in insect ecology, including efforts to link bees' traits to their ecological roles as pollinators, their potential for survival amidst anthropogenic change, and their variation across ecological gradients (Garibaldi et al. 2015, Campbell et al. 2022, Greenop et al. 2023, Cardoso et al. 2025). Bee size is a proxy that correlated positively with foraging range, dispersal ability, and pollination function, as larger bees can travel farther and transport more pollen than smaller bees (Greenleaf et al. 2007, Földesi et al. 2020). Bee size tends to be positively associated with floral richness, in many (Wray et al. 2013, Smith et al. 2019, Cullen et al. 2021, Baltz et al. 2025), but not all cases (Raiol et al. 2021). Larger bees may be able to seek out florally rich habitats, as their larger body size allows greater dispersal range, while smaller bees with more limited dispersal ability may forage closer to where they emerge regardless of floral resource availability. Understanding how bee size varies across a range of grazing regimes and floral resource availabilities can identify bee community capacity for pollination and dispersal in variable grassland landscapes.

We asked how grazing regimes and habitat characteristics that are mediated by grazing affect pollinator community composition and plant-pollinator networks. In 2024 and 2025, we measured pollinator communities and pollinator habitat and constructed plant-pollinator networks in tall- and shortgrass prairies across the Great Plains. We assessed pollinator and plant communities in sites grazed by bison, cattle, and prairie dogs, as well as ungrazed sites. Our

objectives included **Obj. 1)** testing the hypothesis that the richness, abundance, and diversity of floral resources are higher in bison-, cattle-, and prairie dog-grazed sites and lower in ungrazed sites, and **Obj. 2)** testing the hypothesis that foraging pollinator richness, abundance, and diversity increase with greater floral resource availability—which we expect to find in grazed areas—and that pollinator community composition varies with floral resource availability. For both Objectives 1 and 2, we also compared plant and pollinator richness, abundance, and diversity among high and low bison grazing intensities in Montana. Our third objective **Obj. 3)** tested the hypothesis that larger bees would be found foraging in areas with greater floral resource availability. Lastly, **Obj. 4)** identified plant and pollinator species that played particularly important roles in the plant-pollinator networks of each region by highlighting generalist plant and pollinator and specialist pollinator species. Identifying these key species can guide pollinator conservation within prairie restoration efforts. Through this study, we aim to identify grazing management practices that support diverse plant and pollinator communities in grasslands.

Methods

Study sites

Fieldwork for this project took place at Konza Prairie Biological Station (hereafter "Konza") in the Flint Hills region of northeastern Kansas (Riley Co.), and at American Prairie, Fort Belknap Indian Reservation, and the Charles M. Russell National Wildlife Refuge in northeast Montana (Blaine and Phillips Co.s; "Montana" sites), USA (Figure 1).

Konza is a long-term ecological research site in the tallgrass prairie consisting of bison-grazed, cattle-grazed, and ungrazed units. Interannual climatic variation is high, but on average, the area has a continental climate with hot summers and receives approximately 840 mm of

rainfall annually. Konza is a hilly, untilled, unglaciated prairie characterized by rocky uplands with shallow soils, steep slopes, and lowlands with deeper soils, with soils cherty silty clay loams exemplified by the Florence series. Prairie vegetation consists of primarily perennial native grasses and forbs: perennial tallgrasses (*Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum nutans*) dominate; mid-height and shortgrasses (*Schizachyrium scoparium*, *Bouteloua curtipendula*, *B. gracilis*) and forbs (*Solidago* spp., *Asclepias* spp., *Vernonia baldwinii*) are abundant. In addition, woody shrubs (*Cornus drummondii*, *Rhus glabra*, *Gleditsia triacanthos*) make up an increasing component of the site's vegetation.

Bison were reintroduced to Konza between 1987 and 1992; cattle were introduced in 1992. Cattle (cow-calf pairs) are on-site approximately May-October and bison are present year-round. The species are stocked at similar rates (one cow per 10.8 acres, one bison per 10.9 acres). During the study period, cattle removed approximately 15% of annual net primary production and bison removed 25% (Jeff Taylor, pers. comm.).

American Prairie (AP) is an NGO-managed short- to mixed-grass prairie with bison, cattle, ungrazed, and prairie dog town sites, and the Charles M. Russell National Wildlife Refuge (CMR) is a Fish and Wildlife Service-managed site encompassing the Fort Peck Reservoir, adjacent to AP properties. Ft. Belknap is a tribal reservation northwest of AP properties and the CMR, and is home to the Nakoda and Aaniiih peoples, who graze bison and cattle on their land. Northeast Montana has a highly variable continental climate, with 310 mm of precipitation on average, and a growing season lasting approximately late May-early July. Soils are heterogeneous, with Harlake clay soils dominating. Gentle hills and winding creeks typify our study sites. The area's short- to mixed-grass prairie vegetation includes a mix of native and introduced grasses (native grasses: *Bouteloua gracilis*, *Hesperostipa comata*, *Nassella viridula*,

Pascopyrum smithii; nonnative grass: *Agropyron cristatum*) and forbs (native forbs: *Opuntia polyacantha*, *Tetraneuris acaulis*, *Astragalus* spp.; nonnative forbs: *Medicago sativa*, *Melilotus officinalis*). The pollinator community in Montana includes at least 28 bumblebee species (Dolan et al. 2017), and this study region has a high diversity of bees overall (particularly in the family Andrenidae).

At the American Prairie study sites, cattle (cow-calf pairs) are stocked at a rate of approximately one cow per 36.5 acres, and bison are stocked at approximately one bison per 62.5 acres. At Ft. Belknap, cattle are stocked at similar rates and bison are stocked at a higher rate than at AP, approximately one bison per 13.5 acres. The CMR sites had no bison or cattle grazing during the course of this study, with cattle removed from different sections between 1976-2021.

Field sampling

We repeated data collection across two growing seasons, during May-August of 2024 and 2025. Data collection was broken into several weeklong "sampling rounds" during which one round of surveying was conducted at a given site. At Konza, we conducted four to five sampling each summer. Montana has a much shorter growing season; at AP/CMR we conducted two sampling rounds each season, while at Ft. Belknap we conducted one sampling round per season. Across study locations, we selected study sites in areas with burn regimes consistent with current burning practices in each region (annually burned sites at Konza and infrequently burned sites in Montana).

Each year, we collected data at Konza for two weeks in May, one week in July, and one to two weeks in August. We collected data in two sampling sites each of cattle, bison, and ungrazed sites (six Konza sites total), returning to the same approximately ~1-acre locations for

each sampling round. Within each sampling site, we split sampling evenly between the upland and sloped parts of the site to account for the hilly topography of Konza. We spent June of each year at the Montana sites to capitalize on the short (approximately late May-early July) growing season in this high latitude, low rainfall region. At AP/CMR we collected data in two replicates each of cattle, bison, ungrazed, and prairie dog town sites (eight sites total), and at Ft. Belknap we collected data in two replicates each of bison- and cattle-grazed sites (four sites total).

Each sampling round involved hand-netting pollinators and recording floral and other habitat characteristics along transects. We conducted plant-pollinator network surveys in two approximately one-acre replicates in each grazing treatment. Per sampling round, we conducted one person-hour of plant-pollinator network surveys via random walk in each replicate, searching for foraging pollinators (we included bees, wasps, flies, butterflies, and moths) and hand-netting any pollinators observed interacting with the reproductive parts of flowers, pausing the timer while handling insects. We recorded the flowering species each insect was collected on and preserved small-bodied pollinators in 90% ethanol. Larger pollinators, such as bumblebees, moths, and butterflies, were photographed in the field and released with one exception: we did collect bumblebees in Montana, as the state's bumblebee diversity is extremely high and is currently undergoing documentation (Dolan et al. 2017).

Additionally, we recorded the species and number of inflorescences of forbs flowering along four 1x50-m transects per sampling site during each sampling round. We counted all angiosperm flowering stems within one meter to the left of the 50-m transect tape. We haphazardly selected transect starting points using GIS maps of study sites and generated an angle at random for the direction of each transect. We used the same transects during each sampling round.

Sample processing

Following each field season, all insects collected were pinned and identified to the lowest taxonomic level possible and subsequently verified by experts. Keys used for bees included Michener et al. (1994), Dolan et al. (2017), and the Great Plains Bumblebee Atlas Kansas Identification Guide (Xerces Society 2022); keys used for flies included Kits et al. (2006) and Miranda et al. (2013). Flies in the families Syrphidae, Bombyliidae, Nemestrinidae, Stratiomyidae, and some Tachinidae were identified to genus or species, Lepidoptera and other Diptera were identified to species, family, or morphospecies, and wasps were identified to family. Following the conclusion of the study, insects collected will be deposited with the University of Kansas Entomology Collection.

We measured bee size for bees collected during hand-netting surveys via intertegular distance (ITD), a measurement of the breadth of the mesosoma commonly used as a proxy for bee body size (Figure 2; Cariveau et al. 2016). We used Swift Imaging 3.0 software (Swift Microscopes, camera model SC1603) to take photos of bees under a microscope and measured the distance between each bee's tegulae using ImageJ (Schneider et al. 2012). To create a dataset of interspecific values of ITD, we averaged measurements of ten haphazardly selected bees for each species when available; for bees with fewer than ten individuals, we measured all available specimens. The average ITD for each species was calculated and used as the best estimate of ITD for each sampled individual of that species. Community weighted means (CWMs) of ITD per site and sampling round were calculated to obtain estimates of average community-level bee ITD. For the six bumblebee and carpenter bee species we did not lethally collect at Konza, we used average ITD measurements from existing trait research (Dean et al. 2015, Cortina et al. 2022, Ostwald et al. 2024). Altogether, measured ITDs supplemented with existing

measurements covered 91% of the bee species (103/113 species), and 98% of individual bees in the dataset. Bees collected during the final Konza sample round of 2025 (early August) were not measured due to time constraints.

Statistical analysis

We conducted data analysis on Konza and the Montana sites separately, as their climates, ecology, and historic and current management practices are largely distinct and our sampling intensity varied by region. We conducted all analyses on both the Konza and Montana data, except for the grazing intensity comparisons which were only conducted for Montana bison sites. For the plant community, we calculated floral richness (number of flowering species), floral abundance (number of ramets of flowering species), and Shannon's diversity index ($-1*\Sigma(p_i \ln [p_i])$ of plants flowering during sampling rounds, where the proportional abundance of species, p_i, was calculated on per-species abundance. For the foraging pollinator community, we calculated pollinator richness (number of pollinator species observed), pollinator abundance (number of individual pollinators), and Shannon's diversity index. We calculated diversity using the package vegan (Oksanen et al. 2025). At Konza, we tested models both with and without topography (slope vs. upland) included as a random effect, to investigate if landscape position influenced the forb community, and had comparable results; here we report models without the topography random effect. We used R version 4.4.3 for all statistics and the ggplot2 package for graphics (Wickham 2016, R Core Team 2025).

To address Obj. 1, we examined the responses of mean floral richness, abundance, and Shannon's diversity to grazing regimes using generalized linear mixed effects modeling (package lme4, Bates et al. 2015). Separate models included floral richness, abundance, diversity as responses and grazing regime as a fixed effect, with a random effect of sampling site to

account for spatial autocorrelation. For floral richness and abundance, we used a Poisson distribution, and for diversity used a Gaussian distribution. We performed post-hoc Tukey's honest significant difference (HSD) tests to make pairwise comparisons of floral richness, abundance, and diversity among grazing regimes.

To address Obj. 2, we examined the responses of pollinator species richness, abundance, and Shannon diversity to grazing regimes using generalized linear mixed effects modeling (package lme4, Bates et al. 2015). We also investigated the relationship between floral resource availability and pollinator species richness using generalized linear mixed effects models. We modeled the effects of grazing regime and floral resources on pollinator communities separately, to examine the direct and indirect effects of grazers on foraging pollinators. One set of models included pollinator richness, abundance, and diversity as responses to grazing regime, and the other examined pollinator species richness as a response to floral richness and floral abundance. All models included the random effect of sampling site to account for repeated sampling. In models comparing pollinator richness, diversity, and abundance by grazing regime, we first included all pollinator observations and then repeated analyses on bee species alone to determine if patterns varied between the bee and broader pollinator communities. We performed post-hoc Tukey's HSD tests to make pairwise comparisons of pollinator richness, abundance, and diversity across grazing regimes.

To investigate whether pollinator community composition varied with floral resource richness and abundance, we performed direct ordination via constrained analysis of principal components (using the capscale function in the vegan package). For the direct ordinations, we excluded pollinator species present in less than three samples, and square root-transformed the community matrices. One Konza observation included an unusually high value for floral

abundance, and we tested the models investigating the response of pollinator richness and pollinator community composition to floral richness and abundance both with and without this observation. The results did not change in significance with or without this observation; therefore, we report results with it included, but removed it from graphics depicting these models for visual clarity.

To address Obj. 3, we analyzed differences in average bee size (CWMs, see Sample Processing section; Greenop et al. 2023) among grazing treatments using generalized linear mixed-effects modeling that included grazing regime as a main effect and sampling site as a random effect. We followed these analyses with pairwise comparisons using Tukey's HSD tests. To test responses of bee size to habitat characteristics and plant interaction partners, we constructed three generalized linear models, two of which modeled the relationship of CWMs of ITD with A) average floral richness and B) average floral abundance per sampling site and sampling round. The third model investigated the relationship between bee species ITD and the number of plant species interactions observed across all sampling rounds for a given bee species.

To address Obj. 4, we constructed interaction webs for all plant and pollinator species interactions observed in our sampling for each site and grazing regime (see Figures S1-S2 for full interaction webs). Using the full interaction webs for each region (Konza and Montana), we focus on species-level metrics: for plant species we calculated the number of pollinator species observed visiting their flowers. We considered the inverse as well, for each pollinator species calculating the number of unique mutualist plant species interactions. To identify generalist plants and pollinators, we summed the number of unique mutualist species interactions for each plant and pollinator species. We identified specialist pollinators using this information and MA's expert knowledge of bee ecology.

Results

Konza

We observed 171 pollinator species interacting with 46 plant species at Konza during this study. This included 1699 foraging individuals, with 714 observed in 2024 and 985 in 2025. Among the orders, 10.7% of insect pollinators observed were Diptera, 16.9% were Lepidoptera, and 72.4% were Hymenoptera. Among bees, Halictidae dominated (~76% of bees), followed by Apidae (~19% of bees), Colletidae (~3%), Megachilidae (~2%), and Andrenidae (<1%).

Montana

Across all Montana study sites, we observed 183 pollinator species interacting with 64 plant species during the study. This included 1361 individual foraging pollinators; with 670 observed in 2024 and 691 in 2025. Among the orders, 52.1% of our observations were Diptera, 6.0% were Lepidoptera, and 41.9% were Hymenoptera. Among bees, Halictidae were the most abundant (~61% of bees), followed by Apidae (~19%), Andrenidae (~13%), Megachilidae (~7%), and Colletidae (<1%).

Floral resource availability and grazing

We hypothesized that there would be more floral resources in grazed areas than ungrazed areas due to herbivores preferentially grazing on grasses (Obj. 1).

Konza

Floral richness, abundance, and diversity were higher in bison and cattle-grazed sites, compared to ungrazed sites at Konza (Figure 3; Tables A1-2). No differences between bison and cattle treatments were detected.

Montana

In Montana, floral richness was higher in the high-intensity bison grazing regime (Ft. Belknap) than in the ungrazed sites (Figure 3; Table A3). The low-intensity bison grazing regime (AP/CMR) and the prairie dog grazing regime also had significant positive overall effects on floral richness, but did not have significant pairwise comparisons (Table A3). Floral abundance was higher in the high-intensity bison grazing regime at Ft. Belknap than in the ungrazed sites, the low-intensity bison grazing regime, and all Montana cattle-grazed sites (Figure 3; Table A3). The prairie dog colony sites had higher floral abundance than the ungrazed sites and the Ft. Belknap cattle sites (Figure 3; Table A3). The high-intensity bison grazing regime had a significant positive effect on floral diversity in the overall model, but post-hoc tests did not detect pairwise differences (Figure 3; Table A4).

Foraging pollinator community patterns

We hypothesized that pollinator richness would increase in sites with more floral resources, which we expected to find in grazed areas (Obj. 2).

Konza

Floral resource richness, but not floral abundance, influenced the Konza pollinator community. Increased flowering species richness was associated with increased pollinator species richness (Figure 4; Table A5). Floral abundance was not associated with variation in pollinator species richness (Table A5). Additionally, floral richness, but not abundance, influenced pollinator community composition (Figure 4; Table A6).

Grazers had a limited direct influence on pollinator communities at Konza. Pollinator abundance was higher in cattle-grazed sites than ungrazed sites (Figure 5; Table A7). Cattle grazing also had a positive effect on pollinator species richness in the overall model, but was insignificant in post-hoc tests (Figure 5; Table A7). Pollinator diversity did not vary with grazing

management (Figure 5; Table A8). When we included only bee species rather than all foraging pollinator taxa, we observed the same results (Table S1-S2).

Montana

Pollinator species richness increased with flowering plant species richness in Montana and did not vary with flowering abundance (Figure 4; Table A9). Floral richness and abundance did not significantly influence pollinator community composition (Figure 4; Table A10).

Pollinator species richness, abundance, and diversity did not vary with grazing management or grazing intensity (Figure 5; Table A11-A12), nor did bee species richness, abundance, or diversity (Table S3-S4).

Bee size

We hypothesized that larger bees would be found in sites with more floral resources, which we expected to find in grazed sites (Obj. 3).

Konza

At Konza, cattle grazing was significantly negatively associated with bee size in the overall model, but pairwise effects were not significant (Figure 6; Table A13). The average bee ITD measurements for each treatment were 2.43 $\pm$ 0.09 SE mm in ungrazed, 2.10 $\pm$ 0.08 SE mm in bison-grazed, and 1.66 $\pm$ 0.04 SE mm in cattle-grazed sites. Bee size declined with increasing floral abundance (Figure 6; Table A14) and exhibited a negative trend with floral richness (Figure S3; Table A14). There was no relationship between body size and the number of plant species interactions per bee species, although we observed a weak negative trend (Figure 6; Table A15).

Montana

Bee size did not vary with grazing regime in Montana. The average ITD ranged from 2.46 ± 0.16 SE mm on prairie dog colonies, 1.99 ± 0.10 SE mm on bison-grazed sites, 1.90 ± 0.07 SE mm on cattle-grazed sites, to 1.83 ± 0.07 SE mm on ungrazed sites (Figure 6; Table A13). Bee size was not significantly associated with flowering species richness or abundance, but trended towards negative relationships (Figures 6 and S3; Table A14). There was no relationship between body size and the number of plant species interactions per bee species, although the relationship trended weakly negative (Figure 6; Table A15).

Plant-pollinator networks

We aimed to identify important generalist plant and pollinator and specialist pollinator species (Obj. 4).

Konza

Plants varied in the number of pollinator species they were observed associating with, from one to 42 plant species (with an average of 11.2 ± 1.6 SE unique pollinator species interactions per plant species; Figure 7). The plant species serving the highest number of pollinator species were *Solidago canadensis*, *Asclepias viridis*, *Dalea candida*, *Asclepias verticillata*, *Dalea purpurea*, *Vernonia baldwinii*, *Verbena stricta*, *Psoralidium tenuiflorum*, and *Euphorbia marginata* (Table 1).

Pollinators also varied in the number of plant species they were observed visiting, ranging from interacting with one to 35 plant mutualists (with an average of 3 ± 0.3 SE unique plant species interactions per pollinator species). The pollinators visiting the largest numbers of plant species were bees, particularly sweat bees in the family Halictidae (Table 2).

Several plants also served specialist bees, including *Dalea* spp., which were visited by the *Dalea* specialists *Tetraloniella albata* (we observed four individuals of this species that is rare in

the eastern Great Plains on *D. purpurea* in 2025) and *Colletes robertsonii* (we observed two in 2024 and 27 in 2025). *Salvia azurea* was visited by its specialist bee, *Tetraloniella cressoniana* (14 in 2024), *Vernonia baldwinii* was visited by its specialist *Melissodes vernoniae* (three in 2025), and various legume species served multiple *Megachile* legume specialists. Other bee species uncommon in the eastern Great Plains that we observed included *Colletes willistoni* (caught one on *Psoralidium tenuiflorum* in 2025), *Megachile comata* (one on *Psoralidium tenuiflorum* in 2025), *Megachile addenda* (one on *Baptisia bracteata* in 2024), and *Andrena macra* (one on *Comandra umbellata* in 2024).

Montana

Plant species varied in the number of pollinator species they interacted with, ranging from one to 55 unique pollinator species interactions observed per plant species (for an average of 8 ± 1.1 SE unique pollinator species interactions per plant species; Figure 7). The plant species serving the greatest numbers of pollinator species in Montana sites were *Achillea millefolium*, *Opuntia polyacantha*, *Erigeron pumilus*, *Dieteria canescens*, *Sisymbrium altissimum*, *Melilotus officinalis*, *Astragalus agrestis*, *Hymenoxys richardsonii*, and *Medicago sativa* (Table 3).

Pollinator species interacted with one to 25 unique plant species overall and averaged 2.8 ± 0.3 SE plant species partners per pollinator species. The pollinator species visiting the greatest numbers of plant species were primarily flies, along with a few sweat bee species (Table 4).

A handful of plant species served specialist bees, including *Sphaeralcea coccinea*, which was visited by the possible *Sphaeralcea* specialist *Panurginus beardsleyi*, and *Toxicoscordion venenosum*, visited by *Toxicoscordion* specialist *Andrena astragali*.

We also observed several bee species uncommon in eastern Montana: *Melissodes dagosa* (three caught on *Opuntia polyacantha* in 2025), *Colletes nigrifrons* (one on *Eremogone congesta*

in 2025), *Andrena cupreotincta* (three in 2025 and one in 2024, all on *Sisymbrium altissimum*). Additionally, we observed a handful of parasitic *Lasioglossum* (three in 2025 on different plant species).

Discussion

Grazers affected pollinator communities, but this was primarily mediated through their effects on floral resources. This pattern was strongest at Konza and more moderate in Montana. At Konza, floral resources were richer and more abundant in cattle- and bison-grazed areas than in ungrazed areas, while in Montana, only bison at higher grazer densities were associated with heightened floral resource availability. Across regions, pollinator species richness was positively associated with plant species richness. These findings suggest that through selective grazing on grasses, grazers can benefit pollinator communities by mediating plant competition among grasses and forbs.

Grazers and floral resources

In grasslands globally, the impact of grazers on plant community composition varies from beneficial to neutral to detrimental for native plant richness and abundance depending on environmental context, abiotic factors, grazing intensity, and evolutionary history (Milchunas and Lauenroth 1993, Bakker et al. 2006, Filazzola et al. 2020, Staver et al. 2021, Voysey et al. 2024). At Konza, there is strong support for a beneficial role of grazers in shaping diverse plant communities (Towne et al. 2005, Eby et al. 2014, Ratajczak et al. 2022). The effects of grazing on grassland plant community composition are moderated by ANPP, with stronger grazer effects on plant communities as ANPP increases (Milchunas and Lauenroth 1993). In higher-ANPP grasslands, herbivory plays a more important role in modulating competition for light among plants, which can lead to increasing plant richness (Bakker et al. 2006). This may explain the

more consistent positive relationship between grazers and floral resources at Konza (tallgrass prairie, higher ANPP) compared to Montana (short/mixed-grass prairie, lower ANPP).

Bison and cattle had similar effects on pollinator habitat at Konza. This partially contrasts with previous studies at Konza that identified plant community differences in bison- compared to cattle-grazed areas (Towne et al. 2005, Ratajczak et al. 2022). In our study there were no significant contrasts between floral resource richness, abundance, or diversity between bison- and cattle-grazed sites; however, in comparison to previous studies that examined long-term trajectories, this is a relatively short (two-year) study and did not address total plant community composition. Nonetheless, it is encouraging to see that, at least in the annually burned sites we sampled, native and domestic grazers both promote floral resources for pollinators in Kansas tallgrass prairie.

In Montana, bison stood out as the grazer with the strongest effect on floral richness, aligning with work from the region finding greater plant species richness in bison-grazed than cattle-grazed or ungrazed areas (McMillan et al. 2019). We observed limited effects of prairie dogs on pollinator communities despite their large impacts on soil and plant nutrients, plant biomass, and overall prairie ecosystem dynamics (Rebh and Welti 2025, Duchardt et al. 2025), though prairie dog colony sites did have higher floral diversity than ungrazed areas.

Bison and cattle are generally managed differently. Bison often graze grasslands year-round while the majority of cattle in the Great Plains graze on pasture during the growing season before being transported to winter feeding sites. As a result, comparisons of bison and cattle pastures are tests of grazing management system in addition to tests of grazer species effects. In addition, prairie dogs are native herbivores that are relatively unmanaged in comparison to both ungulate species. Despite these factors, comparisons are valuable given the relative consistency

of these grazing regimes and the historic and current importance of all three grazers in North American grasslands.

Pollinators, floral resources, and grazing

Increases in floral resources benefit pollinators (Potts et al. 2003, Hegland and Boeke 2006, Hyjazie and Sargent 2022, Ojija and Silabi 2024), and evidence for a potentially complementary role of grazers in facilitating this pattern is emerging (Welti and Joern 2018). We found support for a positive association between grazers, floral resources, and pollinators at Konza, and moderate support for a positive link between bison grazing, floral resources, and pollinators in Montana. Our results differ from studies in which grazers were associated with reduced pollinator richness, abundance, and/or diversity compared to ungrazed sites (Thapa-Magar et al. 2020, Rosenberger and Conforti 2020, Campbell et al. 2021, Rakosy et al. 2022) and contrast with one study where bison had a direct negative influence on bee abundance (Griffin et al. 2021). However, several of these studies used pan and vane traps (Thapa-Magar et al. 2020, Campbell et al. 2021, Griffin et al. 2021), methods which may not accurately record foraging pollinator preference for an area (Baum and Wallen 2011, Kuhlman et al. 2021, Westerberg et al. 2021). Our study suggests that where grazers promote floral resources, pollinator communities benefit.

Grazing intensity and plant-pollinator communities

Variation in grazer density or stocking rate can further influence vegetation and soil characteristics (Kimoto et al. 2012) and is often a more realistic management recommendation compared to altering grazer species at a site. Stocking rate information is often lacking in studies on grazing and pollinators (Kral-O'Brien et al. 2023), but we were able to include a comparison of high and low bison grazing intensity in Montana. Bison stocking rates at Ft. Belknap were

~4.6x higher than at neighboring American Prairie sites. Floral richness and abundance, and bee species richness were higher in the high bison grazing intensity site, while overall pollinator communities did not differ in richness, abundance, or diversity between the sites. These results suggest that healthy flowering plant and pollinator communities can persist across a wide range of bison grazing intensities.

Bee traits, grazing, and floral resources

We expected, but did not find, larger bees to be associated with areas with higher floral resource richness. In both regions, average bee size per species was not associated with the number of plant species we observed each bee species interacting with, although a negative trend was present in both regions. This may be explained by larger bees' capacity to travel greater distances to reach patches of a single plant species where they can efficiently forage (Charnov 1976). Bumblebee colonies can achieve larger colony sizes when located near a large patch of a single flowering species (Spiesman et al. 2017), suggesting that these large-bodied bee species take advantage of single-plant species patches when available. On multiple occasions during our study, we observed Apidae bees (bumblebees and eucerines) in Montana preferentially visiting large patches of flowering plants like *Astragalus agrestis* and *Melilotus officinalis*, and at Konza, we observed larger-bodied bees (primarily *Halictus parallelus* and *Colletes robertsonii*) primarily visiting *Dalea* species. Our results align with previous studies finding that specialist bees tend to be larger than bees with greater diet breadths (Raiol et al. 2021, Anderson et al. 2024). As we only observed a nonsignificant trend, further data collection and study may help clarify the relationship between bee size and diet breadth.

Plant-pollinator interactions

At Konza, the number of plant and pollinator species interacting were very similar between bison- and cattle-grazed sites, and were markedly smaller in ungrazed sites. In Montana, bison-grazed sites generally had the largest number of plant and pollinator species. The average numbers of mutualist species interactions observed per plant and pollinator species were similar across regions. For plants, there was an average of approximately 11 pollinator species interactions per plant species at Konza, and eight pollinator species interactions per plant species in Montana. For pollinators, in both regions there was an average of approximately three plant species interactions per pollinator species. The generalist pollinators visiting the greatest number of plant species at Konza were all bee species, while in Montana, a mix of fly and bee species served as the dominant generalist pollinators. Several of the plants we observed interacting with the greatest number of pollinators in Montana were introduced species (*Sisymbrium altissimum*, *Melilotus officinalis*, *Medicago sativa*).

Land-use history considerations

Our results tended to be more consistent with our hypotheses at Konza than in Montana. One potential factor in explaining this contrast may be variation in the land-use history of sites, as Konza is a prairie remnant that has been managed for research for 50 years, resulting in a consistent and well-documented long-term management history. In contrast, the Montana sites, like many grasslands, have a more complex history, potentially including areas of former agricultural land or that have been historically planted with nonnative forage species for cattle, all of which may influence present-day plant and pollinator community makeup. Land with a longer history of grazing management can have higher present-day plant and pollinator richness

and foraging pollinator abundance compared to land that was historically farmed (Cortina et al. 2022).

Historic land-use can have strong effects on ecological communities but is often harder to measure or find in records. Sites with consistent, well-recorded long-term management like Konza are extremely useful for identifying ecological patterns and relationships, but such sites are also unusual in the Great Plains' matrix of private, public, tribal, and nonprofit-owned grasslands. Long-term research sites with well-documented management records are critical for understanding responses across a range of ecosystems and should be prioritized for continuous investment while more broadly, work to document grassland legacies presents an ongoing knowledge gap.

Conclusions and future directions

Future work on pollinator habitat across management regimes should incorporate fire along with grazing, as grazing and fire can be used in tandem to promote grassland heterogeneity (e.g., patch-burn grazing, Spiess et al. 2025), and may interact to influence pollinator communities and plant-pollinator interactions (Welti and Joern 2018). Measuring how pollinator communities and their floral resources vary within different stages of a patch-burn or rotational grazing system would illuminate how pollinators interact with the "shifting mosaic" such management practices can yield (Fuhlendorf and Engle 2004, Duquette et al. 2022). Additionally, further investigation into the pattern we observed of larger bees tending to visit areas of high floral abundance and fewer flowering species than smaller bees could help illuminate the drivers of this observation and the regularity with which it occurs in plant-pollinator networks. Higher replication is challenging in ecological studies like ours that aim to

sample entire plant and pollinator communities, but our conclusions regarding pollinators and management must take into consideration our limitations in number of sampled sites.

Floral resource availability influenced foraging pollinator communities in Kansas and Montana. Grazers strongly influenced floral resources, but pollinators did not vary strongly across grazing regimes or grazing intensities, indicating that where grazers promote floral resources, pollinators will benefit. Floral richness, more than floral abundance, was associated with increased pollinator richness, highlighting the importance of a variety of plant species for supporting a wide range of pollinators. Our results suggest that grazers and pollinators can coexist, and that especially in more productive grasslands, grazing can promote floral resource availability for pollinators.

Figures

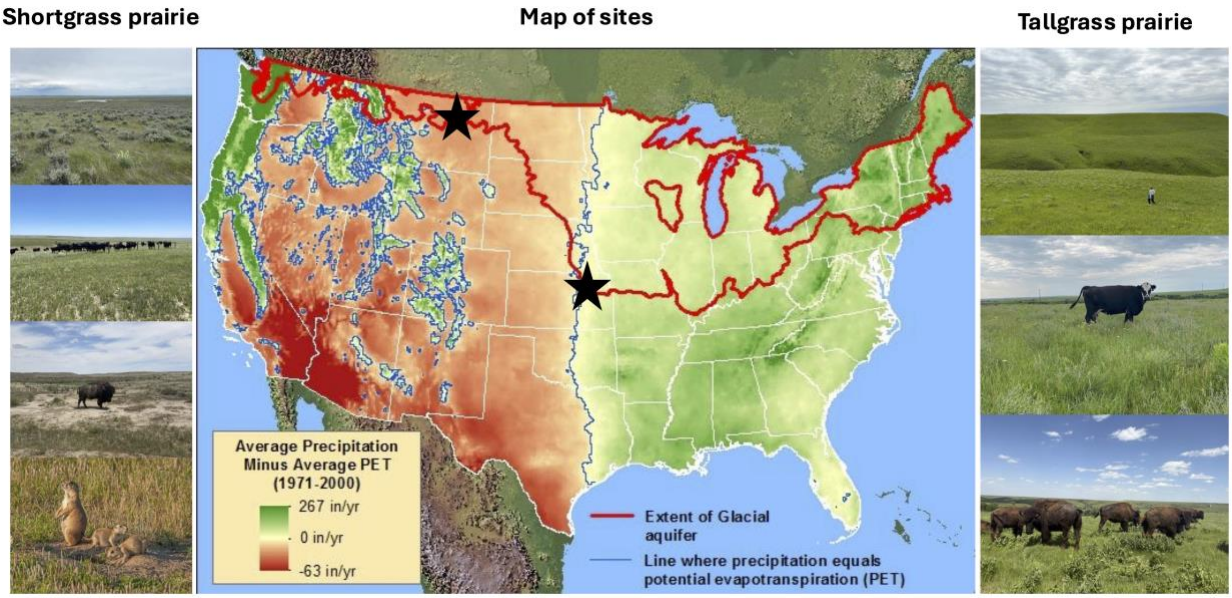

Figure 2.1. Map of study site locations (black stars) and grazing regimes included in this study. Sites include tallgrass prairie in Kansas (Konza Prairie Biological Station), and short-to mixed-grass prairie in Montana (American Prairie, Charles M. Russell National Wildlife Refuge, and Ft. Belknap). The grazing regimes at Konza included bison grazing, cattle grazing, and ungrazed areas. The grazing regimes in Montana included bison grazing, cattle grazing, prairie dog colonies, and ungrazed areas. Map from Wikimedia Commons. Prairie dog photo by Chris Helzer.

Figure 2.2. Photo illustrating the intertegular distance (red line) for an Agapostemon virescens bee (Halictidae family). The image was taken on a dissecting microscope using Swift Imaging 3.0 software. Intertegular distance is a commonly-used proxy for bee size and approximates bee dispersal distance and pollen-carrying capacity. Photo by America Zarate.

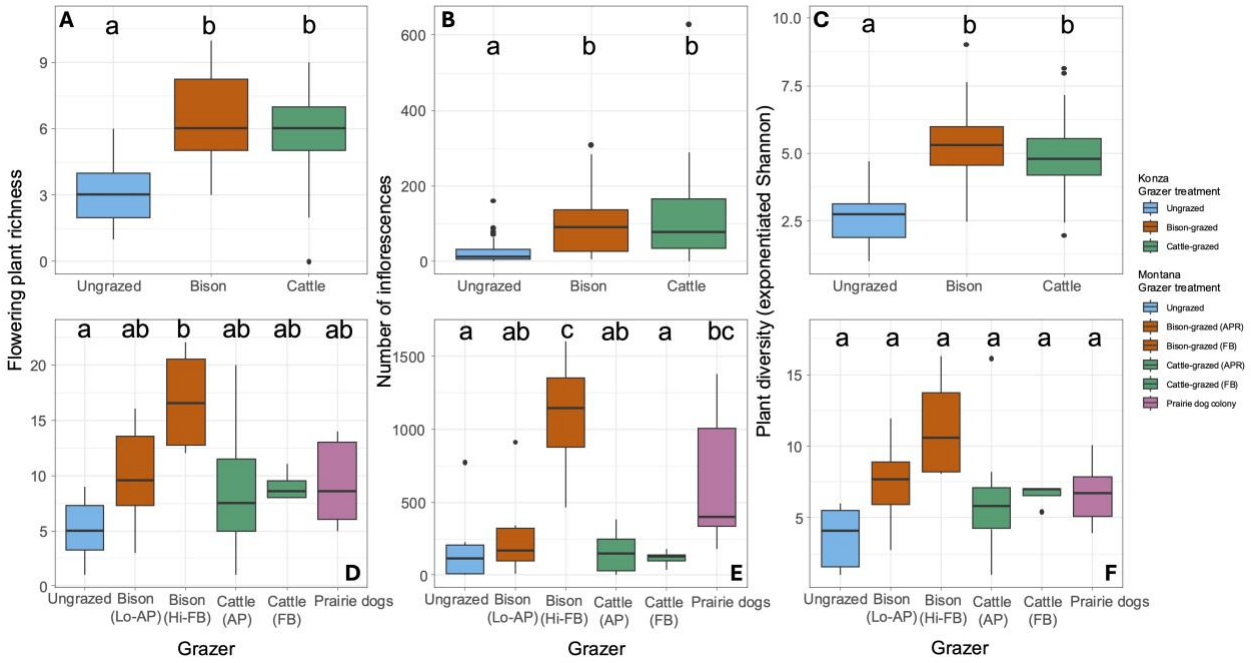

Figure 2.3. Boxplots illustrating floral resource availability by grazing regime. Boxes A-C show data from Konza, D-F show data from Montana. Boxes A and D show flowering plant richness by grazing regime, B and E show floral abundance (measured as the number of inflorescences) by grazing regime, and C and F show flowering plant diversity by grazing regime.

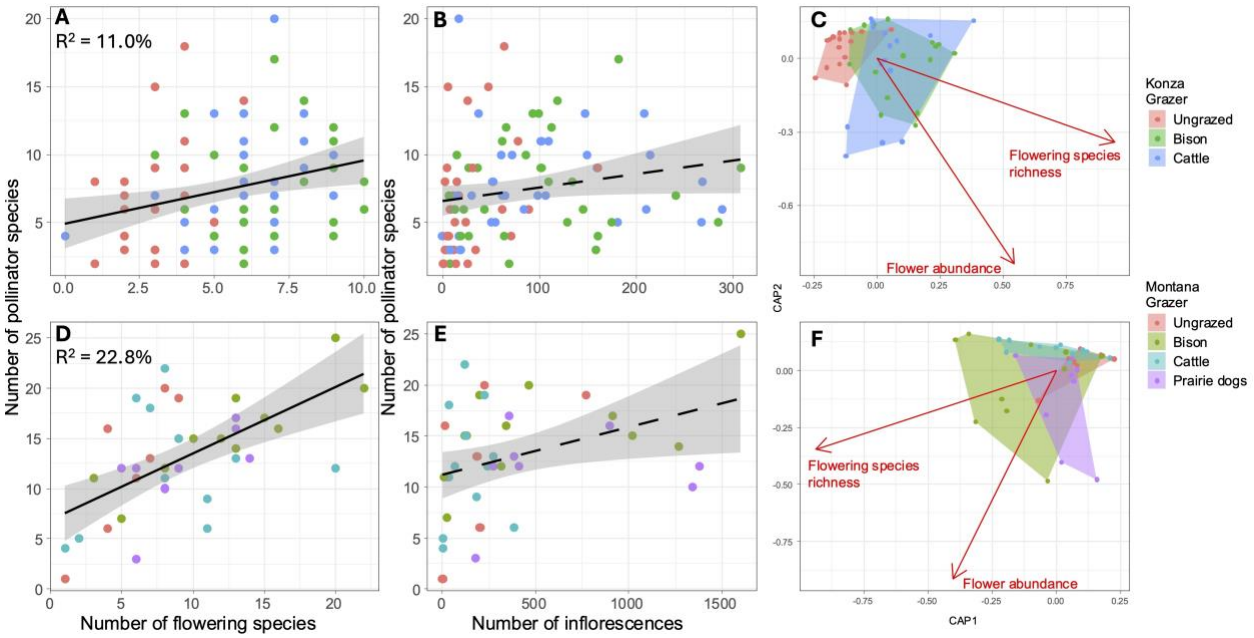

Figure 2.4. Plots showing the relationships between floral species richness (A and D) and abundance (B and E) and pollinator species richness, and between floral richness and abundance and pollinator community composition (C and F). Boxes A-C show data from Konza, and D-F show data from Montana. In A, B, D, and E, solid lines indicate statistically significant

relationships and dashed lines are nonsignificant relationships. The marginal R2 values on plots A and D are for reduced models that include floral richness as a fixed effect and sampling site as a random effect. In all plots, points are colored by grazing regime.

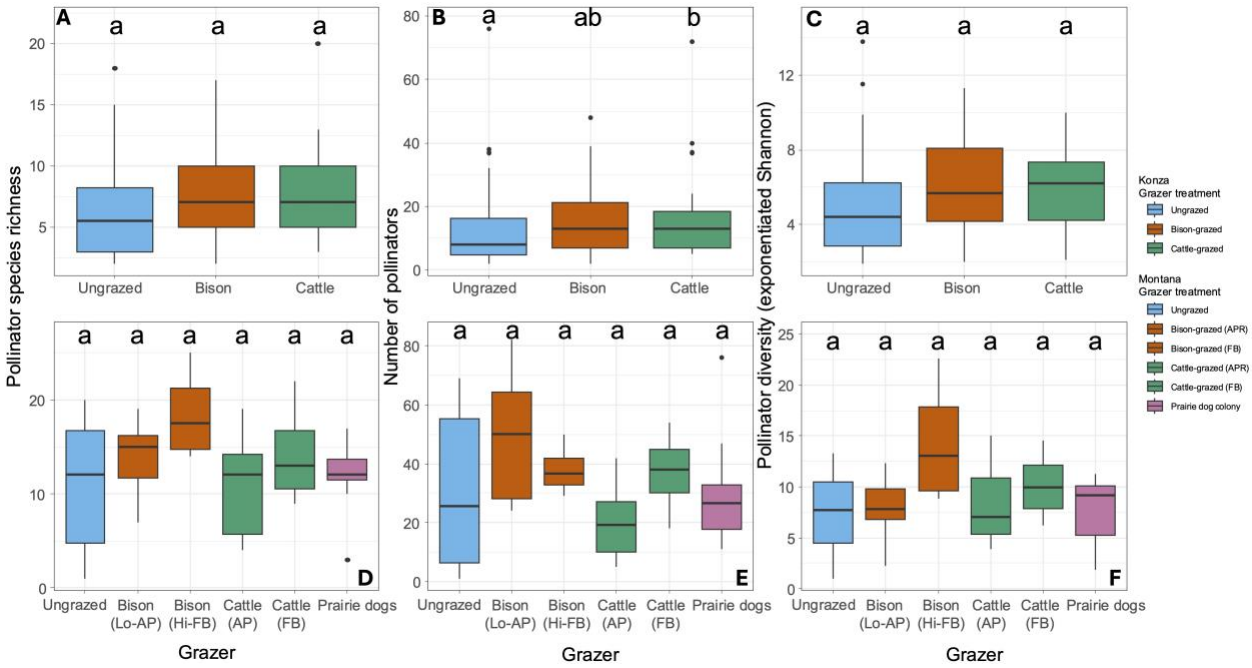

Figure 2.5. Boxplots illustrating pollinator species richness, abundance, and diversity by grazing regime. Boxes A-C show data from Konza, D-F show data from Montana. Boxes A and D show pollinator species richness by grazing regime, B and E show pollinator abundance by grazing regime, and C and F show pollinator diversity by grazing regime.

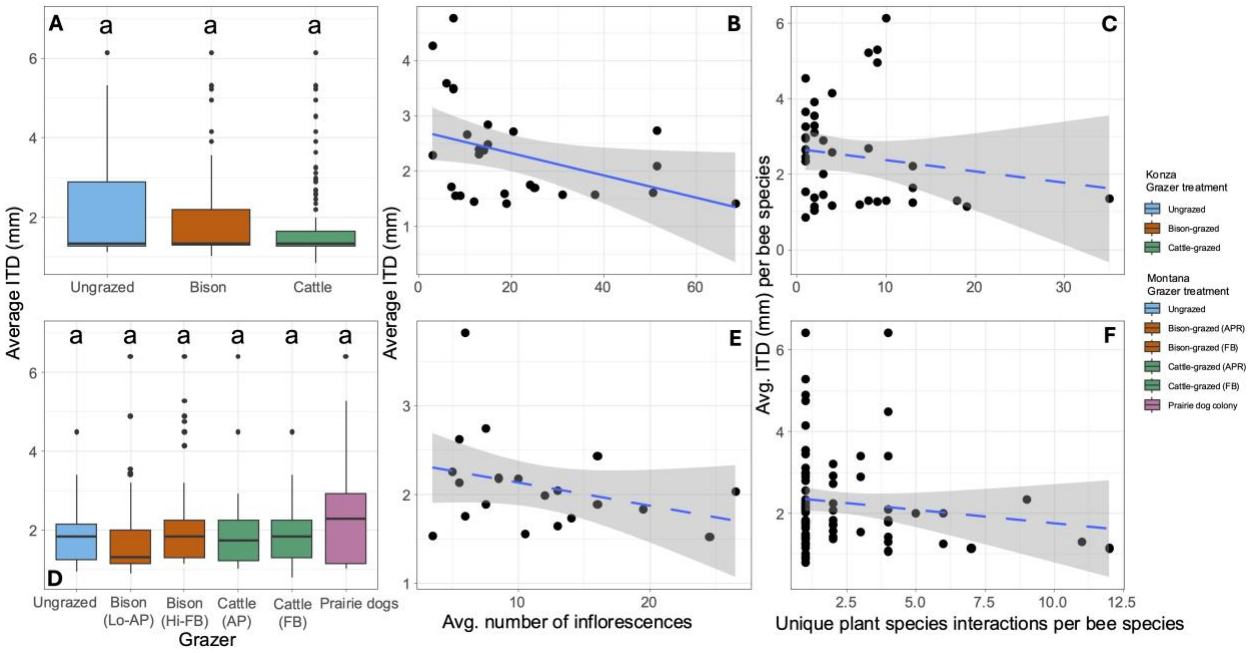

Figure 2.6. Plots showing the relationships between average bee size and grazing regime (A and D), between average bee size and average floral abundance (measured as number of inflorescences, B and E), and between average bee size per species and the number of unique plant species interactions observed per bee species (C and F). Plots A-C show data from Konza, and D-F show data from Montana. Bee size is measured via intertegular distance (ITD).

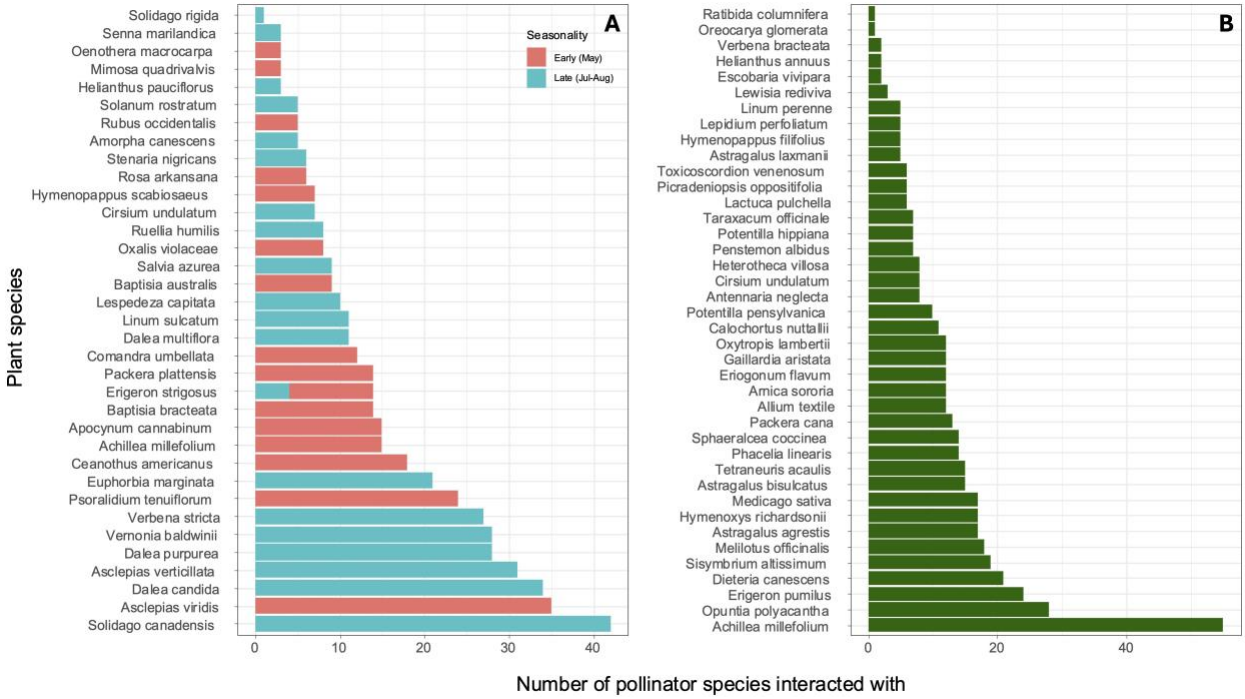

Figure 2.7. Graphs showing the number pollinator species we observed each plant species interacting with during the study (summed over both years of data collection). Plot A shows data

from Konza, and B shows data from Montana. Only plants observed interacting with pollinators more than five separate times are included in each graph. The bars on graph A (Konza) are color-coded by season with red bars representing observations made in May, and blue bars representing observations made in July-August. All observations in Montana (graph B) were made during June.

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Chapter 3 - The effects of grazing management on bee nesting habitat

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Abstract

Bees are highly effective pollinators that support ecosystems and agriculture. However, native bees in ecosystems like grasslands face threats of habitat loss and fragmentation and many are declining in the Anthropocene. How we manage these systems will help determine whether bees can persist and continue to provide critical ecological services. Bees rely on floral resources for food, but other aspects of their life histories are less well understood, including their nesting needs. The majority of native bee species nest in soil. Nesting habitat may be influenced by grassland management strategies like grazing, as herbivores can alter both aboveground and belowground characteristics important for bee nesting. To investigate the responses of ground-nesting bees to grassland grazing regimes, we conducted a two-year field study in tallgrass and shortgrass prairies in the Great Plains (Konza Prairie, KS; American Prairie, Ft. Belknap, and the Charles M. Russell National Wildlife Refuge, MT) under a range of grazing practices (high and

low bison-grazing intensities, cattle-grazing, prairie dog colonies, and ungrazed sites). We captured bees emerging from their ground nests in sites across grazing regimes and related their abundance to measured aboveground and belowground habitat characteristics. We tested the hypotheses that H1) grazers alter habitat characteristics for ground-nesting bees (floral resources, bare ground cover, vegetation height, and soil bulk density); H2) more bees nest in grazed than ungrazed areas; and H3) nesting bee abundance is associated with greater floral resources, more bare ground, shorter vegetation, intermediate soil bulk density, sandier soils, and soils higher in sodium. We report that grazers shape floral resource availability, with more floral resources in bison- and cattle-grazed areas at Konza, and in bison-grazed areas in Montana. Nesting bee abundance was largely driven by aboveground habitat characteristics, particularly floral species richness, in both regions, as well as by bare ground and vegetation height at Konza. Nesting bee abundance was highest in bison-grazed areas at Konza, and trended higher in bison-grazed sites in Montana. These results suggest that grazers, particularly bison, influence bee nesting habitat, particularly through the maintenance of high floral resource richness.

Introduction

Pollinators support native plant communities and the yields of 75% of crop species globally, including coffee, chocolate, and fruits (Klein et al. 2006, Winfree 2010). Bees are highly effective pollinators, due to their bodies being covered by branched hairs creating ample surface area to transport pollen. Insects including bees are rapidly declining due to climate change, habitat loss and fragmentation, and other anthropogenic impacts, threatening the health of native and agricultural systems worldwide (Wagner et al. 2021, Cornelisse et al. 2025). Bees native to grasslands are particularly threatened, with grasslands globally facing fragmentation and extensive land-use conversion to agriculture and suburban/urban areas (Samson and Knopf 1994,

Samson et al. 2004, Hoekstra et al. 2005). Habitat conversion for grasslands varies with suitability for agriculture and proximity to urban areas, with North American Great Plains grasslands having declined by 92% of their historic extent in the central tallgrass prairie, compared to 50% for northwestern Great Plains mixed-grass prairie (Comer et al. 2018). Using management practices that support bees in their remaining grassland habitats is critical for their persistence and benefits to these systems.

Disturbances including grazing, fire, and climatic variation regulate grassland structure and function. Grazing is an important factor shaping North American grasslands, and grazing management can influence pollinator habitat, including its effects on foraging and nesting habitat for bees (Welti and Joern 2018, Cutter et al. 2021, Bruninga-Socolar et al. 2022, Kral-O'Brien et al. 2023, Mitchell et al. 2023, Butters et al. 2025, Collins et al. 2025). Mammalian herbivores may modulate food availability for bees through their selective foraging. Bison and cattle preferentially graze on grasses, reducing their competitive advantage over forbs (Damhoureyeh and Hartnett 1997, Towne et al. 2005, Ratajczak et al. 2022), the main pollen and nectar source used by pollinators. However, bison and cattle often exhibit some differences as well: compared to cattle, bison tend to consume slightly less forbs, create wallows which represent unique microhabitats, and use space more heterogeneously, with high rates of grazing in some locations such as grazing lawns, and lower rates elsewhere (Raynor et al. 2016, Geremia et al. 2025). Although cattle can also graze heterogeneously when under specific management regimes like patch-burn or rotational grazing (Limb et al. 2011, Duquette et al. 2022, Spiess et al. 2024).

Large herbivores are charismatic megafauna with large ecological impacts (Galetti et al. 2018, Pringle et al. 2023). However, small native mammalian herbivores like prairie dogs also alter vegetation through their foraging, shaping plant communities with high abundances of

annual forbs (Fahnestock and Detling 2002, Winter et al. 2002, Beals et al. 2014). In some areas, the spatial extent of prairie dog colonies was very large, ranging from thousands to hundreds of thousands of acres (Knowles et al. 2002). As with bison, prairie dogs have declined across North America, further altering the potential habitat for native pollinators, (Miller et al. 2007).

Along with food resources, nesting resources and suitable microhabitats are critical for bee survival. Approximately 83% of bee species nest in the ground (Harmon-Threatt 2020). Female ground-nesting bees construct burrows in the soil, laying their eggs in underground compartments which they provision with nectar and pollen for their young (Danforth et al. 2019; Antoine and Forrest 2020). Nesting bees may favor bare ground, steeper slopes, and drier, sandier soils, but species-specific responses and the difficulty of direct observation make broad generalizations challenging (Sardiñas and Kremen 2014, Cope et al. 2019, Antoine and Forrest 2020, Gardein et al. 2022, Leone et al. 2022, Albrecht et al. 2023, Butters et al. 2025, Collins et al. 2025). Floral resource availability nearby to nesting sites is associated with increased bee nesting in some cases (Williams et al. 2024) but not others (Pane and Harmon-Threatt 2017). Assessing the importance of both above-ground (e.g., floral resources, vegetation height, bare ground) and below-ground resources (e.g., soil texture, soil compaction) adds complexity to attempts to understand bee nesting preferences (Butters et al. 2025, Collins et al. 2025).

Herbivores can alter nesting resources that are necessary for bee survival but are far less studied than floral resources. Herbivores affect numerous aspects of the landscapes they inhabit, from soils and nutrient cycling to plant community structure to fire regimes (Pringle et al. 2023, Duchardt et al. 2025, Rebh and Welti 2025). Large ungulates like cattle and bison can compact soils through trampling, prairie dogs alter soil conditions through burrowing, and both ungulates and prairie dogs can increase bare ground cover (Whicker and Detling 1988, Kimoto et al. 2012,

Beals et al. 2014). In addition, grazers change vegetation structure by creating patches of tall and short plants, and increase the amount of light reaching soil (Towne et al. 2005, Borer et al. 2014, Antoine and Forrest 2020, Pringle et al. 2023), which may affect bee nesting by altering soil temperature, moisture, and landmarks to identify nesting sites. Bison create grazing lawns of short, grass-dominated vegetation where they preferentially forage, and wallows, bare soil depressions used for dust baths (Hempson et al. 2016, Ozment et al. 2021, Horne et al. 2024). Grazers' urine contains essential elements like nitrogen and sodium, which are limiting nutrients for arthropods (Steinauer and Collins 1995, Welti et al. 2019). Pollinators preferentially forage on nectar with higher sodium levels, indicating that elevated sodium levels in plants due to grazer urine may be attractive for pollinators (Veen et al. 2008, Finkelstein et al. 2022). Through their strong modifications of vegetation and soil characteristics, grazers may influence bee nesting site quality and quantity.

Studies on bee nesting in soils are relatively scarce. In a recent review, only 33% of studies on bee nesting focused on ground-nesting bees despite ground-nesting being the strategy used by the majority of bee species (Orr et al. 2022). Additionally, studies focused on ground-nesting bees often lack direct measurements of nesting bee communities; instead inferring nesting based on methods in which flying or foraging bees are captured (e.g., hand-netting, bee bowls, pan traps; Butters et al. 2025, Collins et al. 2025). Whether bees forage and nest in the same places remains an open topic of investigation (Winfree et al. 2010), and direct measurements of bee nesting are needed to better understand bee nesting ecology (Orr et al. 2022). Direct measures of bee nesting may involve searching for bee nest entrances (Gardein et al. 2022, Tschanz et al. 2023, Albrecht et al. 2023) or using emergence traps, which are small tents that cover the soil surface and capture bees as they leave their nests (Sardiñas and Kremen

2014, Pane and Harmon-Threatt 2017, Cope et al. 2019, Ulyshen et al. 2021). Studies that directly investigate the effects of management practices on bee nesting in prairies are limited, although prescribed burning appears to be beneficial in promoting bee nesting sites, and ground-nesting Hymenopterans use bison-grazed areas for nesting, including wallows (Brokaw et al. 2023, Campbell et al. 2025).

This study investigates how grazing management and habitat characteristics mediated by grazing affect ground-nesting bee communities. In 2024 and 2025, we used emergence traps to sample ground-nesting bee species richness and abundance, and measured floral, vegetative, and soil characteristics in tall- and shortgrass prairies across the Great Plains. To better understand how a variety of grazing practices influence bee nesting, we assessed sites grazed by bison, cattle, and prairie dogs, contrasted with ungrazed sites. We hypothesized that **H1)** more floral resources, higher bare ground cover, and shorter vegetation would be found in bison-, cattle-, and prairie dog-grazed sites compared to ungrazed sites, and that more compacted soils would be found in cattle- and bison-grazed sites than prairie dog or ungrazed sites. We hypothesized that **H2)** nesting bee richness, abundance, and diversity would be higher in grazed sites than ungrazed sites, and that **H3)** nesting bee abundance would be associated with greater floral resource availability, more bare ground, shorter vegetation, higher soil sodium content, intermediate soil compaction, and sandier soils. In Montana, we also also measured the effects of bison grazing at low versus high intensities.

Methods

Study sites

This study took place in the Flint Hills of northeast Kansas, USA, at Konza Prairie Biological Station (hereafter Konza), and in northeast Montana, USA, at American Prairie Reserve, Fort Belknap Indian Reservation, and Charles M. Russell National Wildlife Refuge.

Konza (Riley Co., KS) is a tallgrass prairie site managed by The Nature Conservancy and Kansas State University that consists of bison-grazed, cattle-grazed, and ungrazed long-term research areas. Eastern Kansas experiences hot summers and high interannual climate variability characteristic of a continental climate, and annual rainfall is approximately 840 mm. The site is unglaciated, contributing to the formation of shallow soils rich in clay and silt. The topography is complex, consisting of flat uplands with rocky, shallow soils (<0.5 m depth) and lowlands with deeper soils (>1 m depth). Connecting these landforms are steep slopes, with soils that are complex and fall between these upland/lowland end-members, and flat, erosion-resistant benches, typically with shallow soils that resemble uplands. The tallgrass prairie vegetation is dominated by perennial tallgrasses (*Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum nutans*) and mid-height and shortgrasses (*Schizachyrium scoparium*, *Bouteloua curtipendula*, *B. gracilis*). Forbs (*Solidago* spp., *Asclepias* spp., *Vernonia baldwinii*) are also abundant. Woody shrubs and trees (*Cornus drummondii*, *Rhus glabra*, *Gleditsia triacanthos*) make up an increasing component of the site's vegetation. Native bees are abundant, particularly in the Halictidae (sweat bee) family.

At Konza, bison are stocked at 1 head per 10.9 acres, and cattle are stocked at one head per 10.8 acres. Bison removed approximately 25% of annual net primary production and cattle removed approximately 15% during the study period. Bison reintroduction to Konza took place

between 1987 and 1992, and cattle were introduced in 1992. Bison are present year-round and cow-calf cattle herds graze approximately May-October.

American Prairie (hereafter AP) is an NGO-managed mixed-grass prairie preserve with bison, cattle, ungrazed, and prairie dog town sites, and Charles M. Russell National Wildlife Refuge (hereafter CMR) is a Fish and Wildlife Service-managed site encompassing the Fort Peck Reservoir, south of the AP sites (Phillips Co., MT). Fort Belknap is a tribal reservation northwest of the previous two sites, and is home to the Nakoda and Aaniiih peoples, who graze bison and cattle on their land (Blaine Co., MT). Northeast Montana has a highly variable continental climate, with an average annual precipitation of 310 mm, and a growing season lasting approximately late May-early July (Fick and Hijmans 2017). Soils in the region are highly variable, with Harlake Clay predominating. Our study sites were characterized by rolling hills with nearby creeks. Mixed-grass prairie vegetation includes a mix of native and introduced grasses (native grasses: *Bouteloua gracilis*, *Hesperostipa comata*, *Nassella viridula*, *Pascopyrum smithii*; nonnative grass: *Agropyron cristatum*) and forbs (native forbs: *Opuntia polyacantha*, *Tetraneuris acaulis*, *Astragalus* spp.; nonnative forbs: *Medicago sativa*, *Melilotus officinalis*), as well as sagebrush (*Artemisia* spp.). The bee community is highly diverse, and efforts to document it thoroughly are ongoing (Dolan et al. 2017, Pritchard et al. 2025).

Stocking rates at American Prairie are approximately one head per 36.5 acres (cattle are managed as cow-calf pairs), and one bison per 62.5 acres. Fort Belknap has comparable cattle stocking rates, and higher bison stocking rates of approximately one bison per 13.5 acres. Cattle have been removed from sections of the Charles M. Russell NWR between 1976-2021.

Field sampling

We repeated data collection during two field seasons (May-August 2024 and 2025). Each year, we divided data collection into multiple weeklong "sampling rounds" in which one round of surveying was completed at a given site, for a total of 1-4 sampling rounds taking place at each site throughout the season. Study sites were located in areas with burn regimes consistent with common burning practices in each region—annually burned sites at Konza (Ratajczak et al. 2017) and infrequently burned sites in Montana.

We collected data at Konza for two weeks in May, one week in July, and one week in August each year. We returned to the same approximately one-acre locations for each sampling round, with two sampling areas each in cattle, bison, and ungrazed sites (six sampling sites total). To account for the hilly topography of Konza, during each sampling round all data collection was evenly split between the upland and sloped areas of each replicate. In 2025, the cattle sites we sampled previously in 2024 were not burned following their usual schedule to promote grassland bird habitat. We sampled in the same areas in these cattle sites in 2025 as we had in 2024 to stay consistent in sampling sites despite the management change, and because alternative options were limited.

We spent June at the Montana sites to capitalize on the short growing season in this high latitude, relatively dry region. Across American Prairie and the CMR we collected data in bison-grazed, cattle-grazed, prairie dog town, and ungrazed sites, and at Ft. Belknap we collected data in bison- and cattle-grazed sites, with two approximately one-acre sampling sites per grazing regime at AP/CMR (eight sampling sites total) and Ft. Belknap (four sampling sites total).

Each sampling round involved trapping ground-nesting bees and recording floral and other habitat data along transects. To measure the diversity and abundance of bees nesting in

sites under varied grazing management practices, we conducted bee-nesting surveys using emergence traps in each grazing treatment. Emergence traps are 60 x 60 x 60-cm miniature tents with an open base and a collection jar at the apex (bugdorm.com; we filled the collection jars ~1/8th full with 90% ethanol for trapping), and are a tool for capturing ground-nesting insects as they emerge from their burrows (Figure 1; Pane and Harmon-Threatt 2017). Cattle and bison tampered with the emergence traps at Konza and Ft. Belknap, but at low frequencies that did not majorly disrupt our sampling effort. At Konza, approximately 4% of deployed traps were disturbed over the course of the project, evenly across bison- and cattle-grazed areas. At Ft. Belknap, approximately 5% of deployed traps were disturbed, during one sampling night in one of the bison-grazed sampling sites. To account for this, reported values are per trap/night.

During each sampling round, we deployed 10 bee emergence traps per sampling site (totaling 20 per grazing regime) every 10 m along a haphazard transect and moved them approximately 10 m perpendicular to the transect line every 24 hours. To maximize the soil surface area sampled, the traps were moved two to three times per sampling round after their initial deployment before being taken down after the last 24-hour period. In 2024 we primarily conducted three 24-hour trapping periods per sample round, and in 2025, we increased to four 24-hour trapping periods per sample round when weather allowed. Each trap covered 0.36 m^2 of ground at a time. After catching similar numbers of bees when traps were deployed and moved during the nighttime and daytime in May 2024, we deployed and moved traps during the daytime for all subsequent sample rounds. Each time traps were moved, we removed any bees that had been collected and transferred them to labeled vials of 90% ethanol.

To link bee nesting site choice to habitat variables, we recorded the species and number of inflorescences of forbs flowering along four 1x50-m transects during each sampling round.

We counted all angiosperms flowering within one meter to the left of the 50-m transect tape. At the 10, 20, 30, 40, and 50-m marks along each transect, we measured vegetation structure using a Robel pole, a technique in which a pole marked with 10-cm measurements marked is examined from four meters away at a height of one meter and the height at which vegetation fully obscures the pole is recorded (Robel et al. 1970). At the 10, 20, 30, 40, and 50-m marks on each transect we also estimated bare ground cover in a 1x1m area to the left of the transect tape. In 2024, we collected soil samples at the 0, 25, and 50-m marks along each transect once during the field season to measure soil bulk density, soil texture, and soil sodium (Na) concentration. Soil characteristics like texture, bulk density, and micronutrient content are not expected to vary substantially between consecutive years; therefore, soil samples were only collected once (Lin 2011).

Sample processing

After each field season, bees were identified to the lowest taxonomic level possible, primarily species, and verified by experts. Keys used for bees included Michener et al. (1994) and Dolan et al. (2017). Bee specimens will be deposited at the University of Kansas Entomology Collection after the study concludes.

Soil samples were dried at 60ºC for 48 hours, weighed to calculate soil bulk density, and sent to the Kansas State Research and Extension Soil Testing Lab (Manhattan, KS) for percent sand/silt/clay and sodium content measurements. Sodium cations were extracted with 1 M, pH 7.0 ammonium acetate (Warncke and Brown 1998), and analysis was performed by inductively coupled plasma spectrometry (Model 720-ES ICP Optical Emission Spectrometer, manufactured by Varian Australia Pty Ltd, Mulgrave, Victoria, Australia). Soil texture was assessed using

sodium hexametaphosphate as a dispersing agent, and the sand, silt, and clay fractions of each sample were estimated using the hydrometer method.

Statistical analysis

For flowering plant community metrics, we calculated floral richness, abundance, and Shannon's diversity index (-1*(p_i ln [p_i]), where the proportional abundance of species, p_i, was calculated on per-species abundance. For the nesting bee community, we calculated richness (number of bee species observed), abundance (number of individual bees), and Shannon's diversity index. We used the R package vegan to calculate Shannon's diversity (Oksanen et al. 2025). We used R version 4.4.3 for all analyses and the ggplot2 package to make graphics (Wickham 2016, R Core Team 2025). We did not attempt to compare our results statistically between the tall- and shortgrass prairie sites because of the strong contrasts in climate, ecology, and historic and current management practices between the regions. Instead, we performed all analyses separately for Konza and Montana.

To address H1, we assessed the responses of floral richness, abundance, and diversity, vegetation height, and bare ground cover to grazing regime using generalized linear mixed-effects modeling (package lme4, Bates et al. 2015). Sampling site was included as a random effect in each model to account for repeated sampling, and for floral richness and abundance, we used a Poisson distribution. We also assessed the effects of grazing regime on soil texture, bulk density, and Na content using [generalized linear mixed effects modeling for Konza] and generalized linear modeling for Montana as limited replication of soil data in Montana made using mixed-effects models inappropriate.

To address H2, we examined the responses of nesting bee species richness, abundance, and diversity to grazing regime using generalized linear mixed effects models (package

glmmTMB, Brooks et al. 2017). These models included the random effect of sampling site, and used a Poisson distribution for bee richness and abundance. We also calculated the density of bees nesting per square meter in each grazing regime.

To address H3, we investigated the relationship between ground-nesting bee abundance and above- and below-ground habitat characteristics. We assessed the correlations of above- and below-ground characteristics with nesting bees separately, as grazers may influence above-ground characteristics on faster timescales compared to belowground characteristics. The above-ground habitat model included the predictors floral richness, floral abundance, bare ground cover, and vegetation height. The below-ground habitat model included the predictors soil bulk density, soil sand content, and soil Na content. We set up each habitat model using two approaches, the first of which was generalized linear mixed effects modeling with nesting bee abundance as a response (package glmmTMB; random effect of sampling site in aboveground habitat model, and a Poisson distribution, Brooks et al. 2017). The second approach used generalized linear modeling with a negative binomial distribution and modeled nesting bee presence/absence as a response to the same two sets of above- and below-ground characteristics. We performed both approaches as both aimed to account for zero-inflation in the nesting bee data, and whether or not the model approaches' results aligned could help strengthen or add caution when interpreting our results. The two methods had qualitatively similar outcomes, and therefore we report the generalized linear mixed-effects modeling in our results (see Tables S1-S2 for negative binomial glm approach results).

One observation at Konza included an unusually high value for floral abundance (twice as large as the next largest value), and we tested the model investigating the response of ground-nesting bee abundance to aboveground habitat characteristics both with and without this

observation. The results did not change in significance with or without this observation, so we report results with it included, but removed it from one graphic depicting the relationship between bee abundance and floral richness for visual clarity.

To investigate whether above- and belowground habitat characteristics influenced nesting bee community composition, we performed direct ordinations using constrained analysis of principal components (capscale function, vegan package). We constructed one model focused on the effects of aboveground characteristics on the nesting bee community, including the predictors floral richness, floral abundance, bare ground cover, and vegetation height, and one model focused on the effects of belowground characteristics, with predictors soil bulk density, sand content, and soil Na content.

Results

Konza

We observed a total of 70 bees from 14 different species nesting at Konza (31 bees/10 species in 2024 and 39 bees/9 species in 2025), for an approximately 4.2% emergence trap success rate. The majority of nesting bees were in the family Halictidae, with the only non-Halictid sampled being an individual of *Bombus griseocollis*. We collected one individual of *Sphecodes pimpinellae*, which is a nest parasite of *Augochlorella*, one of the most abundant bee genera at Konza.

Montana

We observed a total of 39 bees from 11 species nesting in Montana throughout the study (36 bees/eight species in 2024, three bees/three species in 2025), for an approximately 3.8% emergence trap success rate. The majority of nesting bees were in the family Halictidae (~94.9%), with one individual each from Andrenidae (*Andrena* spp.) and Apidae (*Bombus*

rufocinctus). We collected three bees in the genus *Sphecodes*, which are nest parasites of other bees.

Foraging and nesting resources across grazing regimes

We hypothesized that floral resources, bare ground cover, and vegetation would vary between grazed and ungrazed areas, with greater floral resource availability, higher bare ground cover, and shorter vegetation found in bison-, cattle-, and prairie dog-grazed sites compared to ungrazed sites (H1). We also hypothesized that soil bulk density would be higher in cattle- and bison-grazed sites than prairie dog or ungrazed sites.

Konza

At Konza, floral richness, abundance, and diversity were higher in bison and cattle-grazed sites than ungrazed sites at Konza (Figure 2; Tables B1-B2). Vegetation height and bare ground cover did not vary with grazing regime (Table B3). In terms of soil characteristics, soil bulk density did not vary with grazing regime, although it trended higher in bison- and cattle-grazed sites than ungrazed (Table B4). Sand, silt, and clay content also did not vary with grazing regime (Table B4). Soil sodium content did not vary with grazing regimes, although it trended lower in cattle-grazed sites than bison-grazed or ungrazed sites (Table B4).

Montana

In Montana, high-intensity bison grazing (Ft. Belknap) was associated with higher floral richness than in the ungrazed sites (Figure 2; Table B5). The high-intensity bison grazing regime also had higher floral abundance than in the ungrazed sites, the low-intensity bison grazing regime, and both the Ft. Belknap and American Prairie/CMR cattle-grazed sites (Figure 2; Table B5). Prairie dog colonies had higher floral abundance than ungrazed sites and Ft. Belknap cattle sites (Figure 2; Table B5). Floral diversity did not vary significantly among grazing regimes, but trended

higher in both bison grazing intensities, particularly in the high-intensity bison sites (Figure 2; Table B6).

Vegetation height and bare ground cover did not vary with grazing regime, although they trended lower and higher respectively in prairie dog colony sites (Table B7). Soil bulk density and soil sand and silt content did not vary with grazing regime (Table B8). The cattle-grazed sites at Ft. Belknap were negatively associated with soil clay content in the overall model, but were not significantly different in post-hoc tests (Table B8). Soil Na content did not vary with grazing regime (Table B8), although it trended higher in ungrazed and prairie dog colony sites; notably, one transect in an ungrazed area on the Charles M. Russell NWR averaged a sodium content of >1100 ppm Na.

Bee nesting and grazing management

We hypothesized that nesting bee richness, abundance, and diversity would be higher in grazed sites than ungrazed sites (H2).

Konza

Nesting bee abundance was higher in bison-grazed sites than in cattle-grazed or ungrazed sites (Figure 3; Table B9). Diversity and species richness did not vary with grazing management (Figure 3; Tables B9-B10). Bee nesting density was highest in bison-grazed sites, averaging 0.66 $\pm$ .15 bees/m^2, and was lower in cattle-grazed sites (0.28 $\pm$ .10 bees/m^2) and ungrazed sites (0.28 $\pm$ .08 bees/m^2).

Montana

There were no differences in nesting bee species richness or abundance by grazing regime, although both trended higher in the high-intensity bison-grazing sites (Figure 3; Table B11). Nesting bee diversity was higher in the high-intensity bison-grazing sites (Ft. Belknap) than in

all other grazing regimes (Figure 3; Table B12). From highest to lowest, bee densities were 0.49 $\pm$ 0.17 bees/m^2 in high-intensity bison-grazed sites, 0.38 $\pm$ 0.38 bees/m^2 in American Prairie/CMR cattle-grazed sites, 0.28 $\pm$ 0.18 bees/m^2 in low-intensity bison-grazed sites, 0.21 $\pm$ 0.14 bees/m^2 in ungrazed sites, 0.17 $\pm$ 0.14 bees/m^2 in prairie dog colony sites, and 0.14 $\pm$ 0.08 bees/m^2 in the Ft. Belknap cattle-grazed sites. Notably, we collected zero bees nesting on American Prairie/CMR sites in 2025.

Bee nesting and habitat characteristics

We hypothesized that nesting bee abundance would be associated with greater floral resource availability, more bare ground, shorter vegetation, higher sodium content, intermediate soil compaction, and sandier soils, and that nesting bee community composition would vary with these habitat characteristics (H3).

Konza

Nesting bee abundance was positively associated with flowering species richness, bare ground cover, and vegetation height, while floral abundance was not associated with changes in nesting bee abundance (Figure 4; Table B13). The soil characteristics sand content, bulk density, and Na content were not associated with changes in nesting bee abundance (Figure S1; Table B13). The overall model assessing the effects of aboveground habitat characteristics on nesting bee community composition was not significant, but the bare ground term in the model had a significant negative effect (Figure 5; Table B14). Similarly, the model assessing the effects of belowground habitat characteristics on community composition was also not significant, but the soil bulk density term in the model had a significant positive effect (Table B14).

Montana

Nesting bee abundance was positively associated with flowering species richness, but not with floral abundance, bare ground cover, or vegetation height (Figure 4; Table B15). Soil characteristics of sand content, bulk density, and Na content were not associated with changes in nesting bee abundance (Figure S1; Table B15). The multivariate model assessing the effects of aboveground characteristics on nesting bee community composition was not significant, but the floral richness term in the model had a significant positive effect (Figure 5; Table B16). The multivariate model assessing the effects of belowground habitat characteristics on nesting bee community composition was not significant (Table B16).

Discussion

In this study, at both sites, bee nesting abundance increased with floral resources. Floral resource availability, but not other measured bee nesting habitat characteristics, were driven by grazing regimes. At Konza, nesting bees were most abundant in bison-grazed sites compared to cattle-grazed and ungrazed sites, while in Montana, nesting bee diversity was highest in the high-intensity bison grazing regime. In addition to floral resources at Konza, nesting bee abundance tended to increase with vegetation height and bare ground cover. Our study suggests that floral resource availability can be mediated by grazing, and that proximity to floral resources may inform bee nesting site selection.

Bee nesting and habitat characteristics

We investigated the relationship of belowground (soil texture, soil sodium content, and soil bulk density) and aboveground (floral resource availability, vegetation height, and bare ground cover) habitat characteristics with bee nesting, and found more evidence for associations between bee nesting and aboveground characteristics than belowground characteristics. Among studies directly measuring bee nesting, floral resource availability has been previously linked to

nesting bee abundance in some grasslands and agricultural landscapes (Buckles and Harmon-Threatt 2019, Cope et al. 2019, Williams et al. 2023; but see Pane and Harmon-Threatt 2017). Two non-exclusive causes of this pattern may be that bees select areas with greater floral resource availability for their nesting sites (Danforth et al. 2019), or that areas with higher densities of bee nesting sites maintain more flowering plant resources through this mutualistic interaction.

The habitat features driving bee nesting vary widely across studies. Patterns are likely species and habitat-specific, and dependent on the methods used. Studies often identify contrasting drivers of bee nesting: in one case, floral resource abundance and soil sand content were positively associated with bee nesting, while in another bare ground (but not floral resources or soil texture) predicted bee nesting (Butters et al. 2025, Collins et al. 2025). However, both studies used indirect measures of bee nesting, such as the occurrence of bees foraging or flying through sampling sites. Studies conducted in grasslands using direct measures of bee nesting tend to report more nesting in sites with higher bare ground cover, reduced vegetation height, and/or reduced litter (Tschanz et al. 2020, Gardein et al. 2022, Albrecht et al. 2023, Brokaw et al. 2023). Bee nesting abundance at Konza increased with greater bare ground, but also had a positive relationship with vegetation height, which seems contradictory. However, in a heterogeneous landscape, both larger bare ground patches and taller vegetation patches may co-occur. For instance, at Konza, areas with abundant forbs often had a tall, robust canopy, but more bare ground underneath than areas with a high abundance of rhizomatous grasses. We observed a limited impact of belowground characteristics on bee nesting, consistent with some studies on ground-nesting bees in agricultural contexts (Tschanz et al. 2020, Williams et al. 2023). It is also possible that our data on floral communities and other aboveground

characteristics had higher resolution than our data on belowground characteristics, as soil microhabitats may vary on a scale smaller than our sampling captured, limiting our ability to identify important belowground characteristics for bee nesting.

Bee nesting and grazing management

Pollinators coexisted with grazers, and in the case of bison, potentially promoted bee nesting density and bee diversity. This contrasts with the one study we are aware of that used emergence traps to measure bee nesting in cattle-grazed and ungrazed tallgrass prairies, which found grazed areas had fewer nesting bees (Buckles and Harmon-Threatt 2019). However, both our results and this study found that floral resource abundance and bare ground cover positively predicted bee nesting (Buckles and Harmon-Threatt 2019).

Despite bison- and cattle-grazed sites at Konza having comparable floral resources, and the positive association between floral resources and bee nesting we observed, bees nested at higher densities in Konza's bison-grazed compared to cattle-grazed sites. One potential factor is that in 2025, the cattle sites we used at Konza were not burned (a departure from their typical annual schedule), while the bison and ungrazed sites were burned as usual. Soil-nesting bees may prefer burned sites in grasslands and other fire-adapted ecosystems, possibly due to increased bare ground cover and/or floral resources available after burning (Ulyshen et al. 2021, Brokaw et al. 2023). However, the missed burn year in the Konza cattle sites did appear to benefit stem-nesting bees, as we collected more *Ceratina* individuals foraging in the unburned cattle sites in 2025 than any other grazing regime. Additionally, bison-grazed areas may have provided benefits for ground-nesting bees that cattle-grazed areas did not, potentially related to the specific identities of the floral resources available, or to the heterogeneity added by bison wallows and overall landscape use.

Methods considerations

The use of emergence traps allows for relatively high confidence that collected bees were nesting, rather than foraging or simply traveling through an area. However, they are time-consuming to use, costly, and frequently have low catch rates relative to the effort required. Success with emergence traps can range from almost zero bees caught to ~85% success rates, and varies with site conditions (Sardiñas and Kremen 2014, Anderson and Harmon-Threatt 2016). Our success rates were between 3-5% for both sites, which is low but comparable to previous work (Cope et al. 2019).

We primarily caught nesting bees in the family Halictidae, despite many bees of other taxa also being ground-nesters. This pattern has been noted in other studies on ground-nesting bees in North America (Sardiñas and Kremen 2014, Pane and Harmon-Threatt 2017). As of now it is difficult for us to determine to what degree this pattern reflects the high abundance of Halictidae bees in our study regions versus the potential that emergence trapping methods may be biased towards capturing Halictids.

Recent work at one of the sites used in our low-intensity bison-grazed sampling on American Prairie indicates that ground-nesting Hymenopterans, primarily wasps, can make up a large proportion of ground-nesting insects (Campbell et al. 2025). In both our study and Campbell et al.'s work, wasps made up a greater proportion of the insects collected via emergence traps than bees. Assessment of ground-nesting wasp communities using emergence traps may be a fruitful area for further study, and an opportunity to investigate parasitic interactions among ground-nesting insects.

Summary

Understanding how management can support multiple aspects of life histories is of particular importance for bees, as they respond more strongly to habitat conversion compared to other pollinator taxa (Spiesman and Inouye 2013). Nesting requirements in particular are understudied for ground-nesting bees (Orr et al. 2022). We used direct measurements of bee nesting to investigate the effects of a range of grazing management practices on nesting habitat for ground-nesting bees and nesting bee abundance, and found that nesting bee abundance is positively associated with floral resource richness across our northern and central Great Plains study sites. We observed that grazers do not have any clear negative impacts on bee nesting, and that bison grazing was associated with greater numbers of nesting bees than cattle grazing or no grazing at our Kansas tallgrass prairie site, and with greater diversity of nesting bees in our Montana short- to mixed-grass prairie sites. In the tallgrass prairie, heterogeneous vegetation with tall, florally rich patches and bare ground patches may be beneficial for ground-nesting bees, and grazing, particularly by bison, may help achieve these conditions. Our results suggest that managing for robust flowering plant communities benefits not only foraging bees, but additionally promotes bees nesting. Additionally, measuring soil characteristics in a way that captures fine-scale microhabitat variation, such as sampling soils in immediate proximity to identified bee nesting locations, may help elucidate the role of soil characteristics for nest site choice.

Figures

Figure 3.1. A transect of emergence traps, the collection method we used to directly measure bee nesting in sites under varying grazing practices in Kansas and Montana. Photo is from Konza (KS), May 2024.

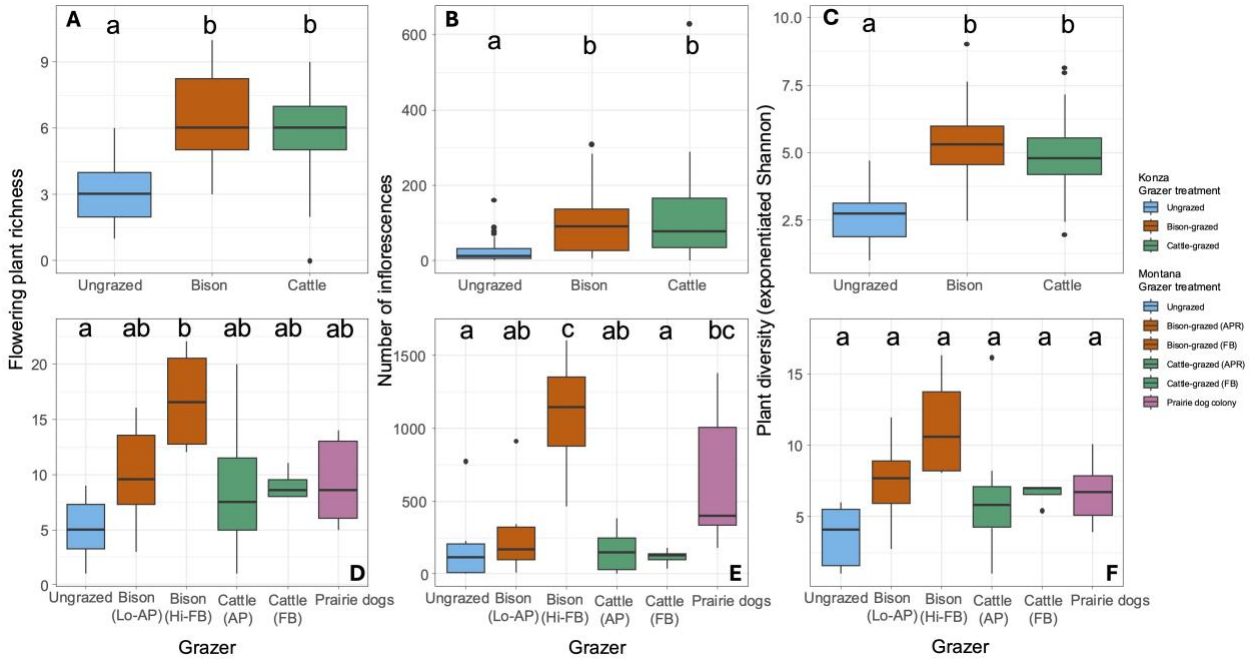

Figure 3.2. Boxplots illustrating floral resource availability by grazing regime. Boxes A-C show data from Konza, D-F show data from Montana. Boxes A and D show flowering plant richness by grazing regime, B and E show floral abundance (measured as the number of inflorescences) by grazing regime, and C and F show flowering plant diversity by grazing regime.

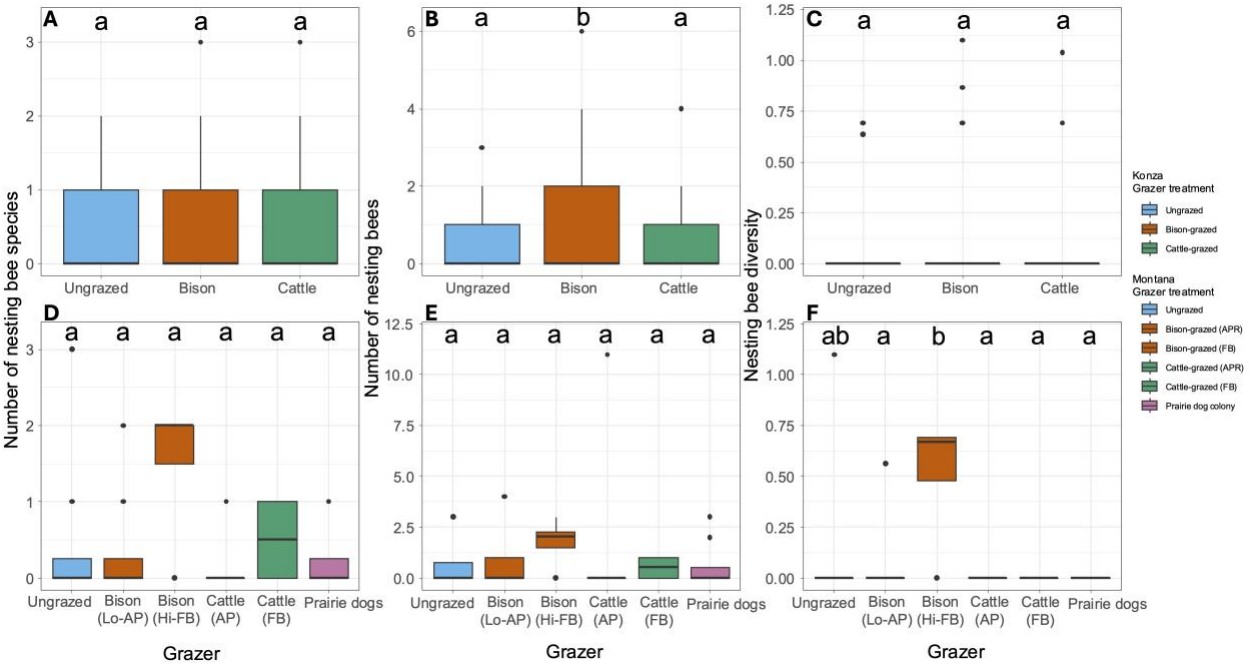

Figure 3.3. Boxplots illustrating nesting bee species richness, abundance, and diversity by grazing regime. Boxes A-C show data from Konza, D-F show data from Montana. Boxes A and D show nesting bee species richness by grazing regime, B and E show nesting bee abundance by grazing regime, and C and F show nesting bee diversity by grazing regime.

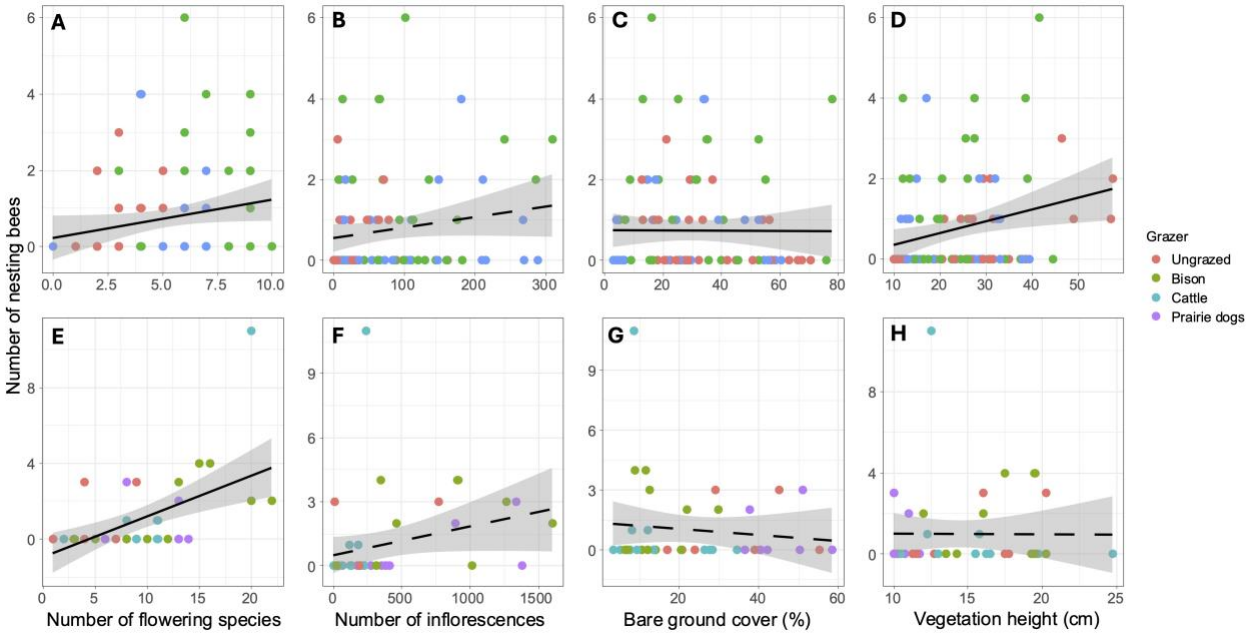

Figure 3.4. Plots illustrating the relationship between nesting bee abundance and the aboveground habitat characteristics floral species richness (A and E), floral abundance (B and F, measured as number of inflorescences), bare ground cover (C and G), and vegetation height (D and H, measured via Robel pole). Plots A-D show data from Konza, and E-H show data from Montana. Solid lines represent statistically significant relationships, and dashed lines represent nonsignificant relationships. Points on all plots are colored by grazing regime.

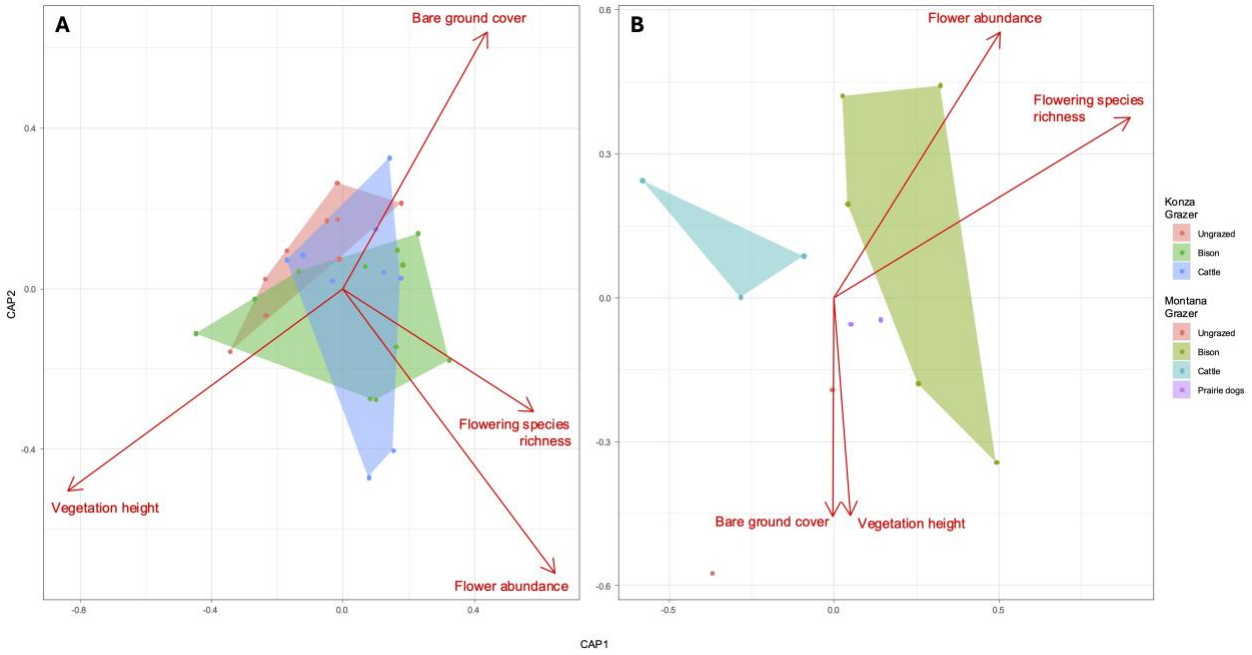

Figure 3.5. Plots illustrating the influence of aboveground habitat characteristics on nesting bee community composition. Plot A shows Konza data and B shows Montana data. Neither direct

ordination model is significant. Direct ordinations were conducted using constrained analysis of principal components. Points are colored by grazing regime.

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Chapter 4 - Conclusion

Floral species richness is key for both foraging pollinator species richness and ground-nesting bee abundance. Grazed areas were associated with increases (Konza) or trends towards increases (Montana) in floral richness and abundance compared to ungrazed areas. At Konza, both cattle and bison grazing were associated with increased floral resources, and in Montana, bison (especially at high stocking rates) were associated with increased floral resources. While floral richness was positively associated with both foraging pollinator richness and nesting bee abundance, floral abundance only trended towards positive relationships with foraging and nesting pollinators. In terms of bee nesting, at Konza, greater bare ground cover and greater vegetation height also were associated with nesting bee abundance, suggesting that heterogeneous habitats are preferable for ground-nesting bees. Across sites, below-ground characteristics (soil texture, bulk density, and sodium content) did not exhibit relationships with nesting bee abundance, indicating that aboveground features, particularly floral resources, are of high importance for bee nesting site selection.

Bees did not vary in size across grazing regimes, but bee species trended towards a negative relationship between average size and number of plant mutualists per species. This may indicate that larger bees use their greater dispersal capacity to fly to patches of single blooming plant species, while smaller bees that are more limited in dispersal take advantage of any resources available in the areas they are able to access. Further study on bee size and diet breadth may help clarify this relationship.

Observing plant-pollinator interactions allowed us to identify plant species that served both a broad range of pollinators, as well those that served particular specialist pollinator species. These observations can help inform restoration seed mix design. In Kansas, plant species serving

the highest number of pollinator species included (early season—May) *Asclepias viridis*, *Psoralidium tenuiflorum*, *Ceanothus americanus*, *Achillea millefolium*, and *Apocynum cannabinum*; and (late season—June-July) *Solidago canadensis*, *Dalea candida*, *A. verticillata*, *D. purpurea*, *Vernonia baldwinii*, and *Verbena stricta*. In Montana, plant species serving the highest number of pollinators included *Achillea millefolium*, *Opuntia polyacantha*, *Erigeron pumilus*, *Dieteria canescens*, *Sisymbrium altissimum*, *Melilotus officinalis*, *Astragalus agrestis*, and *Hymenoxys richardsonii*.

Overall, we conclude that floral richness is a critical aspect of both foraging and nesting pollinator habitat in Great Plains grasslands. We found neutral to positive impacts of grazers on pollinator habitat and communities. Grazing by a range of species and at varying intensities can be beneficial for pollinators, particularly when grazers promote floral resource availability through selective grazing. Continuing work should focus on how variation in a range of management practices, including various burn regimes, patch-burn grazing, rotational grazing, and varied grazing intensities influence pollinator foraging and nesting habitat. Additionally, investigating how community composition influences pollinator communities would be informative. Using a combination of direct and indirect measures of ground-nesting bee communities (e.g., assessing variation in where bees of ground-nesting taxa both nest and forage) would improve our knowledge of whether indirect measures of bee nesting like capturing foraging bees are useful in estimating their nesting preferences.

Appendix A - Chapter 2

Tables A1-A15

Response	Predictor	Estimate	Std. Error	z-value	P-value
Floral richness	Bison	0.778	0.123	6.310	**<0.001**
Floral richness	Cattle	0.693	0.125	5.545	**<0.001**
Floral abundance	Bison	1.293	0.217	5.948	**<0.001**
Floral abundance	Cattle	1.438	0.217	6.617	**<0.001**

Table A1. Model results (Konza) for generalized linear mixed-effects models examining relationships between grazing regime and flowering plant richness and abundance. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Floral diversity	Bison	0.722	0.103	2.974	7.108	**0.006**
Floral diversity	Cattle	0.648	0.103	3.045	6.335	**0.008**

Table A2. Model results (Konza) for generalized linear mixed-effects model examining the relationship between grazing regime and flowering plant diversity. Sampling site is included as a random effect in the model.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Floral richness	Bison (light-APR/CMR)	0.694	0.310	2.236	**0.025**
Floral richness	Bison (heavy-FB)	1.222	0.314	3.890	**<0.001**
Floral richness	Cattle (APR/CMR)	0.530	0.314	1.687	0.092
Floral richness	Cattle (FB)	0.609	0.334	1.824	0.068
Floral richness	Prairie dogs	0.618	0.312	1.980	**0.048**
Floral abundance	Bison (light-APR/CMR)	0.377	0.505	0.747	0.455
Floral abundance	Bison (heavy-FB)	2.093	0.505	4.147	**<0.001**

Floral abundance	Cattle (APR/CMR)	0.113	0.505	0.223	0.824
Floral abundance	Cattle (FB)	-0.214	0.507	-0.422	0.673
Floral abundance	Prairie dogs	1.546	0.505	3.063	**0.002**

Table A3. Model results (Montana) for generalized linear mixed-effects models examining relationships between grazing regime and flowering plant richness and abundance. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Floral diversity	Bison (light-APR/CMR)	0.846	0.506	5.763	1.673	0.147
Floral diversity	Bison (heavy-FB)	1.313	0.533	7.110	2.463	**0.043**
Floral diversity	Cattle (APR/CMR)	0.497	0.506	5.763	0.982	0.365
Floral diversity	Cattle (FB)	0.809	0.533	7.110	1.517	0.172
Floral diversity	Prairie dogs	0.7889	0.506	5.763	1.560	0.171

Table A4. Model results (Montana) for generalized linear mixed-effects model examining relationships between grazing regime and flowering plant diversity. Sampling site is included as a random effect in the model.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Pollinator richness	Floral richness	0.063	0.017	3.620	**<0.001**
Pollinator richness	Floral abundance	0	0	0.125	0.901

Table A5. Model results (Konza) for generalized linear mixed-effects model examining the relationship between floral resources and pollinator species richness. Sampling site is included as a random effect in the model.

Response	Predictor	df	Sum Squares	F-value	P-value
Pollinator community composition	Floral richness	1	0.929	2.946	**0.001**

Pollinator community composition	Floral abundance	1	0.430	1.365	0.129

Table A6. Model results (Konza) for constrained analysis of principal components (CAP) examining the relationship between floral resources and pollinator community composition.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Pollinator richness	Bison	0.177	0.094	1.879	0.060
Pollinator richness	Cattle	0.186	0.094	1.968	**0.049**
Pollinator abundance	Bison	0.091	0.095	0.955	0.340
Pollinator abundance	Cattle	0.231	0.094	2.457	**0.014**

Table A7. Model results (Konza) for generalized linear mixed-effects models examining the relationship between grazing regime and pollinator species richness and abundance. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Pollinator diversity	Bison	0.229	0.118	93.000	1.945	0.055
Pollinator diversity	Cattle	0.232	0.118	93.000	1.968	0.052

Table A8. Model results (Konza) for generalized linear mixed-effects model examining relationships between grazing regime and pollinator species diversity. Sampling site is included as a random effect in the model.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Pollinator richness	Floral richness	0.030	0.014	2.212	**0.027**
Pollinator richness	Floral abundance	0	0	1.460	0.144

Table A9. Model results (Montana) for generalized linear mixed-effects model examining the relationship between floral resources and pollinator species richness. Sampling site is included as a random effect in the model.

Response	Predictor	df	Sum Squares	F-value	P-value
Pollinator community composition	Floral richness	1	0.927	2.497	**0.003**

Pollinator community composition	Floral abundance	1	0.485	1.307	0.156

Table A10. Model results (Montana) for constrained analysis of principal components (CAP) examining the relationship between floral resources and pollinator community composition.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Pollinator richness	Bison (light-APR/CMR)	0.361	0.333	1.084	0.278
Pollinator richness	Bison (heavy-FB)	0.624	0.340	1.839	0.066
Pollinator richness	Cattle (APR/CMR)	0.080	0.337	0.237	0.813
Pollinator richness	Cattle (FB)	0.369	0.345	1.067	0.286
Pollinator richness	Prairie dogs	0.180	0.335	0.538	0.590
Pollinator abundance	Bison (light-APR/CMR)	0.895	0.477	1.875	0.061
Pollinator abundance	Bison (heavy-FB)	0.614	0.482	1.276	0.202
Pollinator abundance	Cattle (APR/CMR)	-0.085	0.482	-0.177	0.860
Pollinator abundance	Cattle (FB)	0.592	0.482	1.230	0.219
Pollinator abundance	Prairie dogs	0.393	0.479	0.819	0.413

Table A11. Model results (Montana) for generalized linear mixed-effects models examining the relationship between grazing regime and pollinator species richness and abundance. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Pollinator diversity	Bison (light-APR/CMR)	0.336	0.485	5.487	0.694	0.516
Pollinator diversity	Bison (heavy-FB)	0.965	0.528	7.668	1.828	0.107
Pollinator diversity	Cattle (APR/CMR)	0.385	0.485	5.487	0.795	0.460
Pollinator diversity	Cattle (FB)	0.638	0.528	7.668	1.210	0.262
Pollinator diversity	Prairie dogs	0.294	0.485	5.487	0.607	0.568

Table A12. Model results (Montana) for generalized linear mixed-effects model examining relationships between grazing regime and pollinator species diversity. Sampling site is included as a random effect in the model.

Site	Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Konza	ITD	Bison	-0.355	0.217	3.118	-1.639	0.196
Konza	ITD	Cattle	-0.798	0.214	2.936	-3.738	**0.035**
Montana	ITD	Bison (light-APR/CMR)	-0.088	0.588	6.296	-0.150	0.885
Montana	ITD	Bison (heavy-FB)	0.371	0.591	6.452	0.627	0.552
Montana	ITD	Cattle (APR/CMR)	-0.072	0.593	6.513	-0.121	0.907
Montana	ITD	Cattle (FB)	-0.011	0.587	6.280	-0.019	0.985
Montana	ITD	Prairie dogs	0.599	0.589	6.347	1.017	0.346

Table A13. Model results (Konza and Montana) for ANOVAs comparing average bee size (ITD; via community-weighted means) among grazing regimes. Sampling site is included as a random effect in all models.

Site	Response	Predictor	Estimate	Std. Error	t-value	P-value
Konza	ITD	Floral richness	-0.186	0.109	-1.711	0.099
Konza	ITD	Floral abundance	-0.020	0.009	-2.141	**0.042**
Montana	ITD	Floral richness	-0.111	0.075	-1.473	0.158
Montana	ITD	Floral abundance	-0.026	0.018	-1.413	0.175

Table A14. Model results (Konza and Montana) for generalized linear models investigating how average bee size varies with flowering plant richness and abundance.

Site	Response	Predictor	Estimate	Std. Error	t-value	P-value
Konza	ITD	Number of plant mutualists	-0.030	0.032	-0.938	0.354
Montana	ITD	Number of plant mutualists	-0.066	0.059	-1.113	0.269

Table A15. Model results (Konza and Montana) for generalized linear models investigating how bee species' average sizes vary with the number of plant mutualists each bee species interacts with.

Tables S1-S4

Response	Predictor	Estimate	Std. Error	z-value	P-value
Bee richness	Bison	0.132	0.125	1.060	0.289
Bee richness	Cattle	0.196	0.123	1.592	0.111
Bee abundance	Bison	0.042	0.103	0.407	0.684
Bee abundance	Cattle	0.240	0.010	2.407	**0.016**

Table S1. Model results (Konza) for generalized linear mixed-effects models examining the relationship between grazing regime and bee species richness and abundance. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Bee diversity	Bison	0.179	0.147	93.000	1.217	0.227
Bee diversity	Cattle	0.208	0.147	93.000	1.417	0.160

Table S2. Model results (Konza) for generalized linear mixed-effects model examining relationships between grazing regime and pollinator species diversity. Sampling site is included as a random effect in the model.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Bee richness	Bison (light-APR/CMR)	-0.024	0.422	-0.058	0.954
Bee richness	Bison (heavy-FB)	0.537	0.426	1.260	0.208
Bee richness	Cattle (APR/CMR)	-0.110	0.424	-0.261	0.794
Bee richness	Cattle (FB)	0.445	0.430	1.036	0.300
Bee richness	Prairie dogs	-0.088	0.425	-0.208	0.835
Bee abundance	Bison (light-APR/CMR)	0.395	0.532	0.742	0.458
Bee abundance	Bison (heavy-FB)	0.735	0.536	1.370	0.171
Bee abundance	Cattle (APR/CMR)	-0.069	0.538	-0.128	0.898
Bee abundance	Cattle (FB)	1.190	0.531	2.240	**0.025**

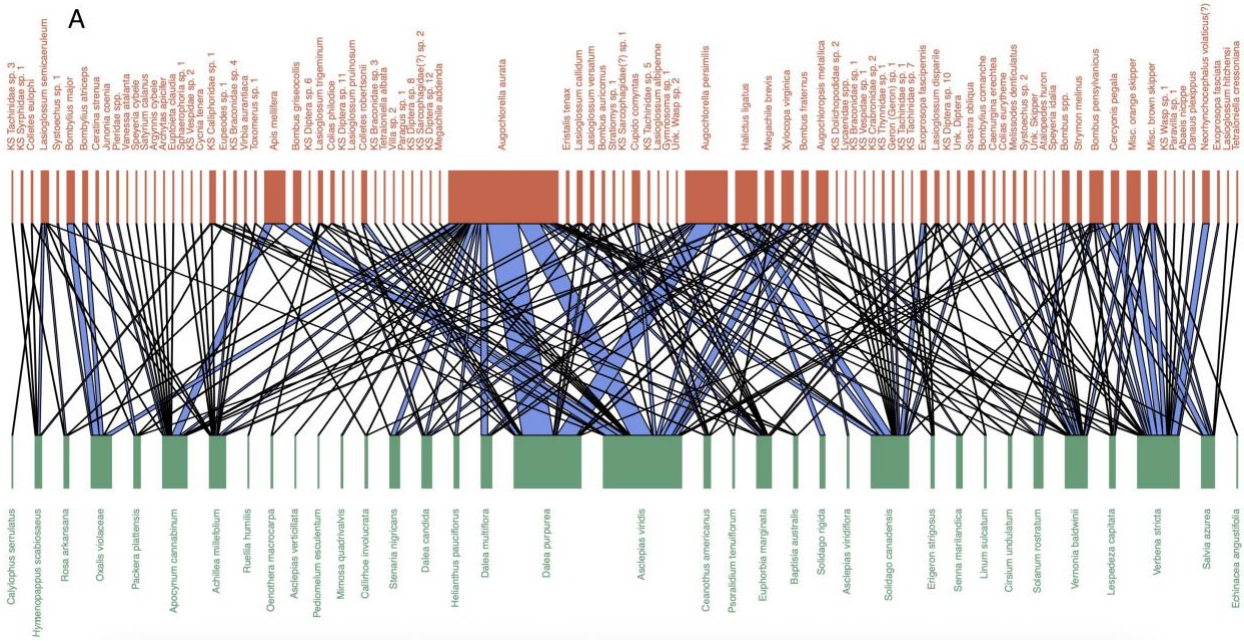
Bee abundance	Prairie dogs	0.181	0.534	0.339	0.735

Table S3. Model results (Montana) for generalized linear mixed-effects models examining the relationship between grazing regime and bee species richness and abundance. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Bee diversity	Bison (light-APR/CMR)	-0.107	0.573	5.727	-0.186	0.859
Bee diversity	Bison (heavy-FB)	0.617	0.601	6.904	1.027	0.339
Bee diversity	Cattle (APR/CMR)	-0.213	0.573	5.727	-0.372	0.723
Bee diversity	Cattle (FB)	0.329	0.601	6.904	0.547	0.602
Bee diversity	Prairie dogs	-0.059	0.573	5.727	-0.103	0.922

Table S4. Model results (Montana) for generalized linear mixed-effects model examining relationships between grazing regime and pollinator species diversity. Sampling site is included as a random effect in the model.

Figures S1-S3



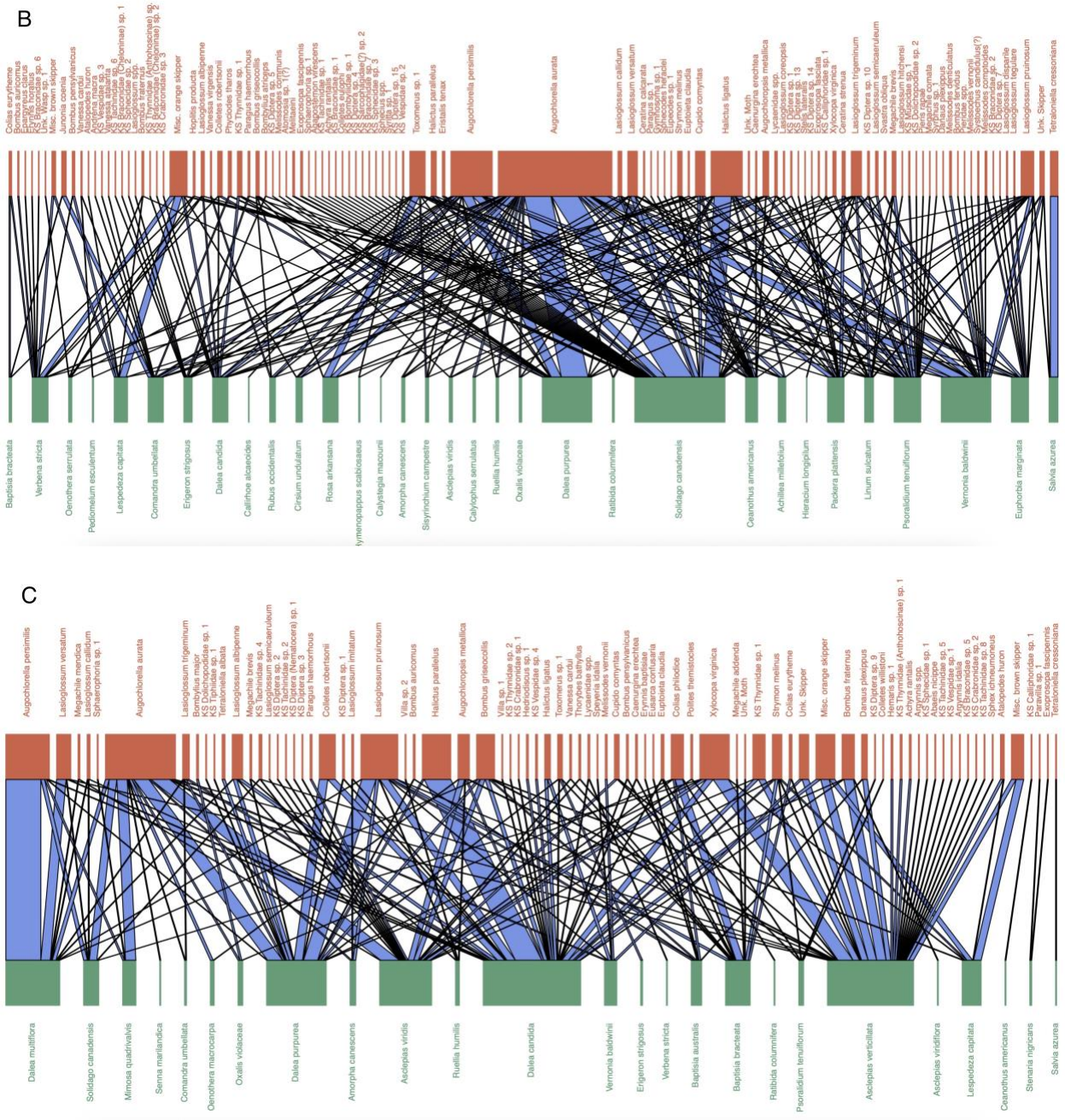
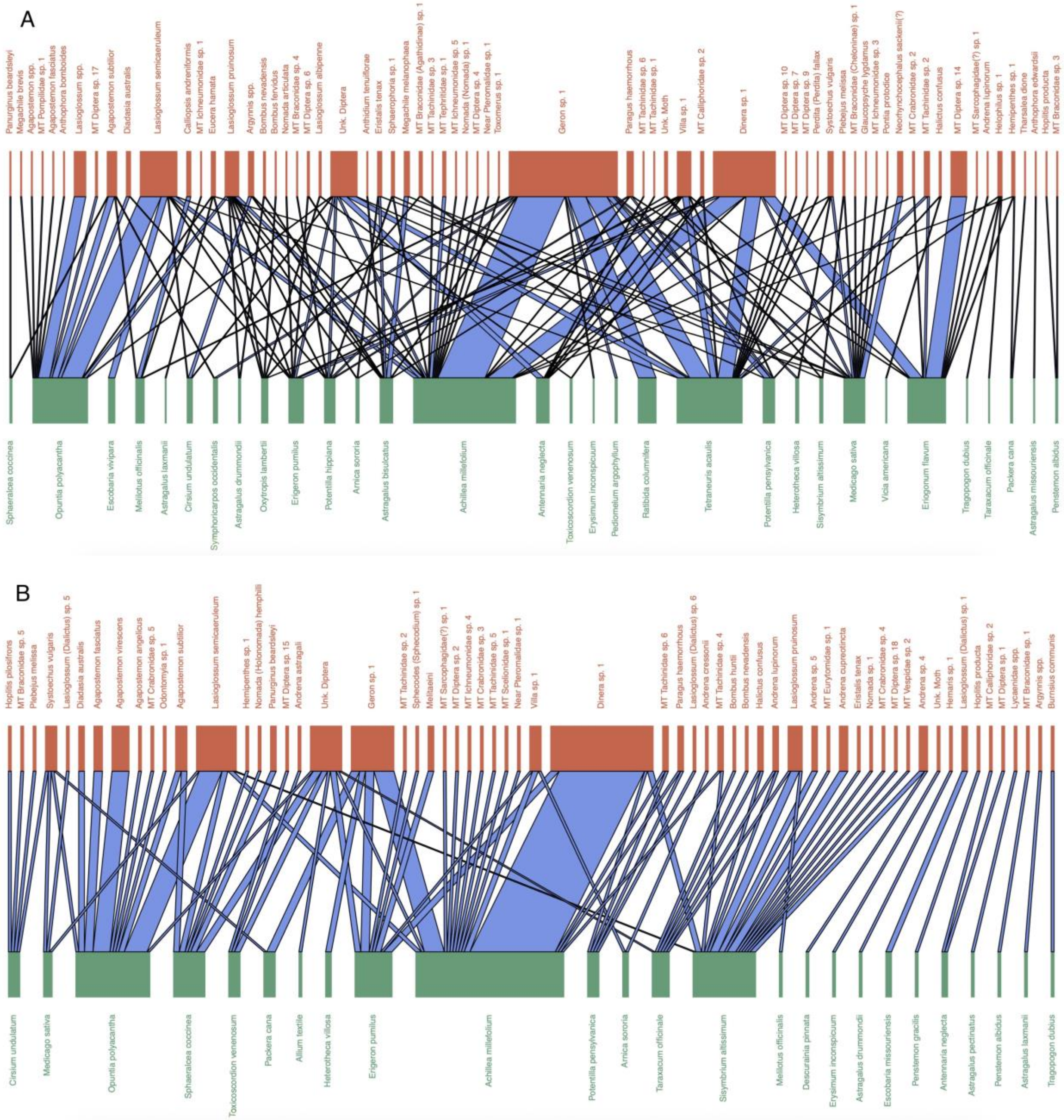
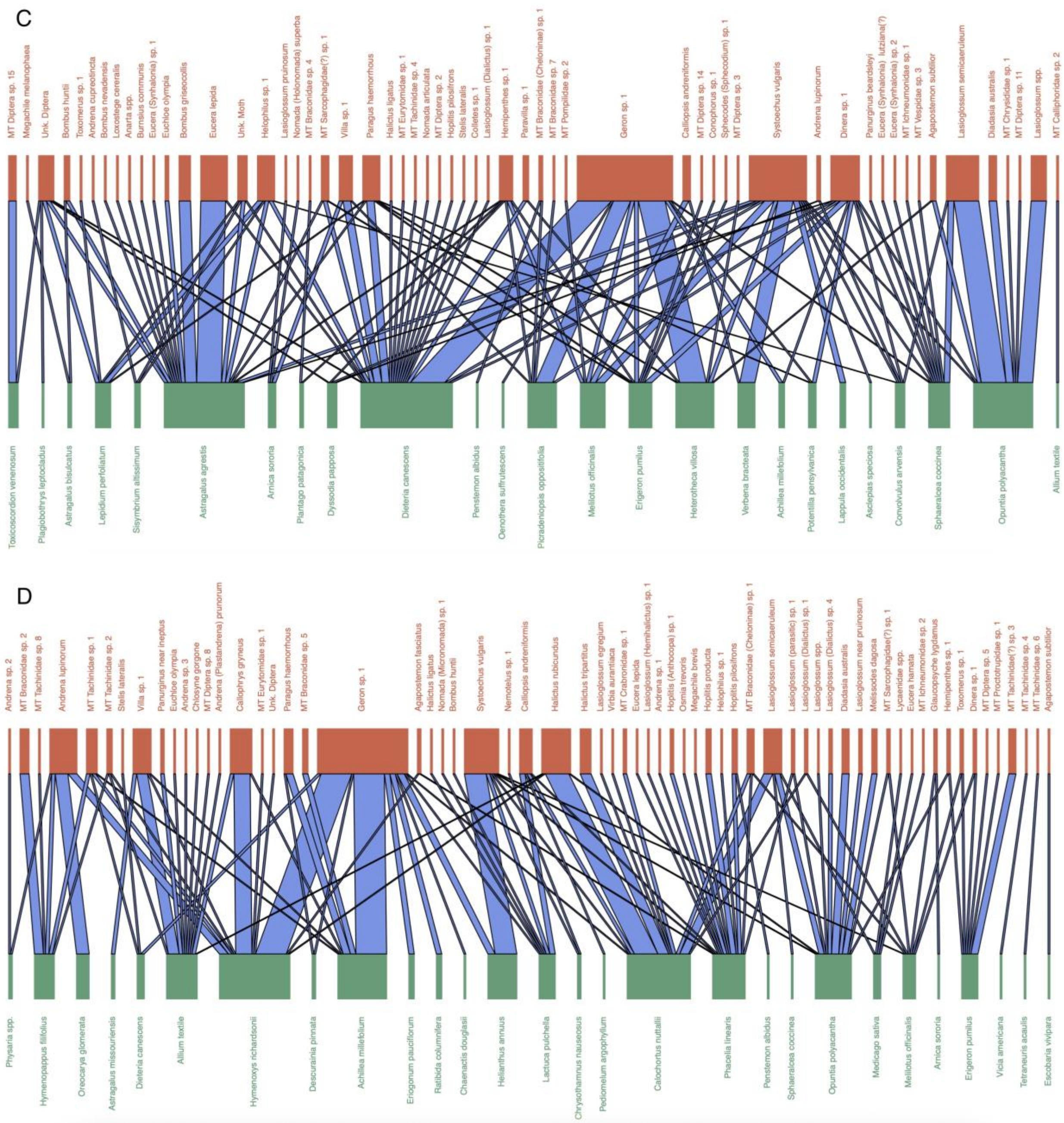


Figure S1. Plant-pollinator networks from 2024-2025 across Konza bison (S1A), cattle (S1B), and ungrazed (S1C) sites. The species in red at the top of the graph are pollinator species, and those on the bottom in green are plant species. Each blue line indicates interactions observed between plant and pollinator species, and the width of the line indicates the relative frequency of interactions observed (thicker blue lines indicate more commonly observed interactions).


A
Panurginus beardsleyi
Megachile brevis
Agapostemon spp.
MT Pompilidae sp. 1
Agapostemon fasciatus
Anthophora bomboides
Lasioglossum spp.
MT Diptera sp. 17
Agapostemon subtilior
Diadasia australis
Lasioglossum semicaeruleum
Calliopsis andreniformis
MT Ichneumonidae sp. 1
Eucera hamata
Lasioglossum pruinosum
Argynnis spp.
Bombus nevadensis
Bombus fervidus
Nomada articulata
MT Braconidae sp. 4
MT Diptera sp. 6
Lasioglossum albipenne
Unk. Diptera
Anthidium tenuiflorae
Eristalis tenax
Sphaerophoria sp. 1
Megachile melanophaea
MT Braconidae (Agathidinae) sp. 1
MT Tachinidae sp. 3
MT Tephritidae sp. 1
MT Ichneumonidae sp. 5
Nomada (Nomada) sp. 1
MT Diptera sp. 4
Near Pteromalidae sp. 1
Toxomerus sp. 1
Geron sp. 1
Paragus haemorrhous
MT Tachinidae sp. 6
MT Tachinidae sp. 1
Unk. Moth
Villa sp. 1
MT Calliphoridae sp. 2
Dinera sp. 1
MT Diptera sp. 10
MT Diptera sp. 7
MT Diptera sp. 9
Perdita (Perdita) fallax
Systoechus vulgaris
Plebejus melissa
MT Braconidae (Cheloninae) sp. 1
Glaucopsyche lygdamus
MT Ichneumonidae sp. 3
Pontia protodice
Neorhynchocephalus sackenii(?)
MT Crabronidae sp. 2
MT Tachinidae sp. 2
Halictus confusus
MT Diptera sp. 14
MT Sarcophagidae(?) sp. 1
Andrena lupinorum
Heliophilus sp. 1
Hemipenthes sp. 1
Tharsalea dione
Anthophora edwardsii
Hoplitis producta
MT Braconidae sp. 3
Sphaeralcea coccinea
Opuntia polyacantha
Escobaria vivipara
Melilotus officinalis
Astragalus laxmanii
Cirsium undulatum
Symphoricarpos occidentalis
Astragalus drummondii
Oxytropis lambertii
Erigeron pumilus
Potentilla hippiana
Arnica sororia
Astragalus bisulcatus
Achillea millefolium
Antennaria neglecta
Toxicoscordion venenosum
Erysimum inconspicuum
Pediomelum argophyllum
Ratibida columnifera
Tetraneuris acaulis
Potentilla pensylvanica
Heterotheca villosa
Sisymbrium altissimum
Medicago sativa
Vicia americana
Eriogonum flavum
Tragopogon dubius
Taraxacum officinale
Packera cana
Astragalus missouriensis
Penstemon albidus
B
Hoplitis pilosifrons
MT Braconidae sp. 5
Plebejus melissa
Systoechus vulgaris
Lasioglossum (Dialictus) sp. 5
Diadasia australis
Agapostemon fasciatus
Agapostemon virescens
Agapostemon angelicus
MT Crabronidae sp. 5
Odontomyia sp. 1
Agapostemon subtilior
Lasioglossum semicaeruleum
Hemipenthes sp. 1
Nomada (Holonomada) hemphilli
Panurginus beardsleyi
MT Diptera sp. 15
Andrena astragali
Unk. Diptera
Geron sp. 1
MT Tachinidae sp. 2
Sphecodes (Sphecodium) sp. 1
Meliteini
MT Sarcophagidae(?) sp. 1
MT Diptera sp. 2
MT Ichneumonidae sp. 4
MT Crabronidae sp. 3
MT Tachinidae sp. 5
MT Scelionidae sp. 1
Near Pteromalidae sp. 1
Villa sp. 1
Dinera sp. 1
MT Tachinidae sp. 6
Paragus haemorrhous
Lasioglossum (Dialictus) sp. 6
Andrena cressonii
MT Tachinidae sp. 4
Bombus huntii
Bombus nevadensis
Halictus confusus
Andrena lupinorum
Lasioglossum pruinosum
Andrena sp. 5
MT Eurytomidae sp. 1
Andrena cupreotincta
Eristalis tenax
Nomada sp. 1
MT Crabronidae sp. 4
MT Diptera sp. 18
MT Vespidae sp. 2
Andrena sp. 4
Unk. Moth
Hemaris sp. 1
Lasioglossum (Dialictus) sp. 1
Hoplitis producta
MT Calliphoridae sp. 2
MT Diptera sp. 1
Lycaenidae spp.
MT Braconidae sp. 1
Argynnis spp.
Bumsius communis
Cirsium undulatum
Medicago sativa
Opuntia polyacantha
Sphaeralcea coccinea
Toxicoscordion venenosum
Packera cana
Allium textile
Heterotheca villosa
Erigeron pumilus
Achillea millefolium
Potentilla pensylvanica
Arnica sororia
Taraxacum officinale
Sisymbrium altissimum
Melilotus officinalis
Descurainia pinnata
Erysimum inconspicuum
Astragalus drummondii
Escobaria missouriensis
Penstemon gracilis
Antennaria neglecta
Astragalus pectinatus
Penstemon albidus
Astragalus laxmanii
Tragopogon dubius


C
MT Diptera sp. 15
Megachile melanophaea
Unk. Diptera
Bombus huntii
Toxomerus sp. 1
Andrena cupreotincta
Bombus nevadensis
Loxostege cereralis
Anarta spp.
Burnsius communis
Eucera (Synhalonia) sp. 1
Euchloe olympia
Bombus griseocollis
Eucera lepida
Unk. Moth
Helophilus sp. 1
Lasioglossum pruinosum
Nomada (Holonomada) superba
MT Braconidae sp. 4
MT Sarcophagidae(?) sp. 1
Villa sp. 1
Paragus haemorrhous
Halictus ligatus
MT Eurytomidae sp. 1
MT Tachinidae sp. 4
Nomada articulata
MT Diptera sp. 2
Hoplitis pilosifrons
Stelis lateralis
Colletes sp. 1
Lasioglossum (Dialictus) sp. 1
Hemipenthes sp. 1
Paravilla sp. 1
MT Braconidae (Cheloninae) sp. 1
MT Braconidae sp. 7
MT Pompilidae sp. 2
Geron sp. 1
Calliopsis andreniformis
MT Diptera sp. 14
Conophorus sp. 1
Sphecodes (Sphecodium) sp. 1
MT Diptera sp. 3
Systoechus vulgaris
Andrena lupinorum
Dinera sp. 1
Panurginus beardsleyi
Eucera (Synhalonia) lutziana(?)
Eucera (Synhalonia) sp. 2
MT Ichneumonidae sp. 1
MT Vespidae sp. 3
Agapostemon subtilior
Lasioglossum semicaeruleum
Diadasia australis
MT Chrysididae sp. 1
MT Diptera sp. 11
Lasioglossum spp.
MT Calliphoridae sp. 2
Toxicoscordion venenosum
Plagiobothrys leptocladus
Astragalus bisulcatus
Lepidium perfoliatum
Sisymbrium altissimum
Astragalus agrestis
Arnica sororia
Plantago patagonica
Dyssodia papposa
Dieteria canescens
Penstemon albidus
Oenothera suffrutescens
Picradeniopsis oppositifolia
Melilotus officinalis
Erigeron pumilus
Heterotheca villosa
Verbena bracteata
Achillea millefolium
Potentilla pensylvanica
Lappula occidentalis
Asclepias speciosa
Convolvulus arvensis
Sphaeralcea coccinea
Opuntia polyacantha
Allium textile
D
Andrena sp. 2
MT Braconidae sp. 2
MT Tachinidae sp. 8
Andrena lupinorum
MT Tachinidae sp. 1
MT Tachinidae sp. 2
Stelis lateralis
Villa sp. 1
Panurginus near ineptus
Euchloe olympia
Andrena sp. 3
Chlosyne gorgone
MT Diptera sp. 8
Andrena (Plastandrena) prunorum
Callophrys gryneus
MT Eurytomidae sp. 1
Unk. Diptera
Paragus haemorrhous
MT Braconidae sp. 5
Geron sp. 1
Agapostemon fasciatus
Halictus ligatus
Nomada (Micronomada) sp. 1
Bombus huntii
Systoechus vulgaris
Nemotelus sp. 1
Calliopsis andreniformis
Halictus rubicundus
Halictus tripartitus
Lasioglossum egregium
Virbia aurantiaca
MT Crabronidae sp. 1
Eucera lepida
Lasioglossum (Hemihalictus) sp. 1
Andrena sp. 1
Hoplitis (Anthocopa) sp. 1
Osmia trevoris
Megachile brevis
Hoplitis producta
Helophilus sp. 1
Hoplitis pilosifrons
MT Braconidae (Cheloninae) sp. 1
Lasioglossum semicaeruleum
Lasioglossum (parasitic) sp. 1
Lasioglossum (Dialictus) sp. 1
Lasioglossum spp.
Lasioglossum (Dialictus) sp. 4
Diadasia australis
Lasioglossum near pruinosum
Melissodes dagosa
MT Sarcophagidae(?) sp. 1
Lycaenidae spp.
Eucera hamata
MT Ichneumonidae sp. 2
Glaucopsyche lygdamus
Hemipenthes sp. 1
Toxomerus sp. 1
Dinera sp. 1
MT Diptera sp. 5
MT Proctotrupidae sp. 1
MT Tachinidae(?) sp. 3
MT Tachinidae sp. 4
MT Tachinidae sp. 6
Agapostemon subtilior
Physaria spp.
Hymenopappus filifolius
Oreocarya glomerata
Astragalus missouriensis
Dieteria canescens
Allium textile
Hymenoxys richardsonii
Descurainia pinnata
Achillea millefolium
Eriogonum pauciflorum
Ratibida columnifera
Chaenactis douglasii
Helianthus annuus
Lactuca pulchella
Chrysothamnus nauseosus
Pediomelum argophyllum
Calochortus nuttallii
Phacelia linearis
Penstemon albidus
Sphaeralcea coccinea
Opuntia polyacantha
Medicago sativa
Melilotus officinalis
Arnica sororia
Erigeron pumilus
Vicia americana
Tetraneuris acaulis
Escobaria vivipara

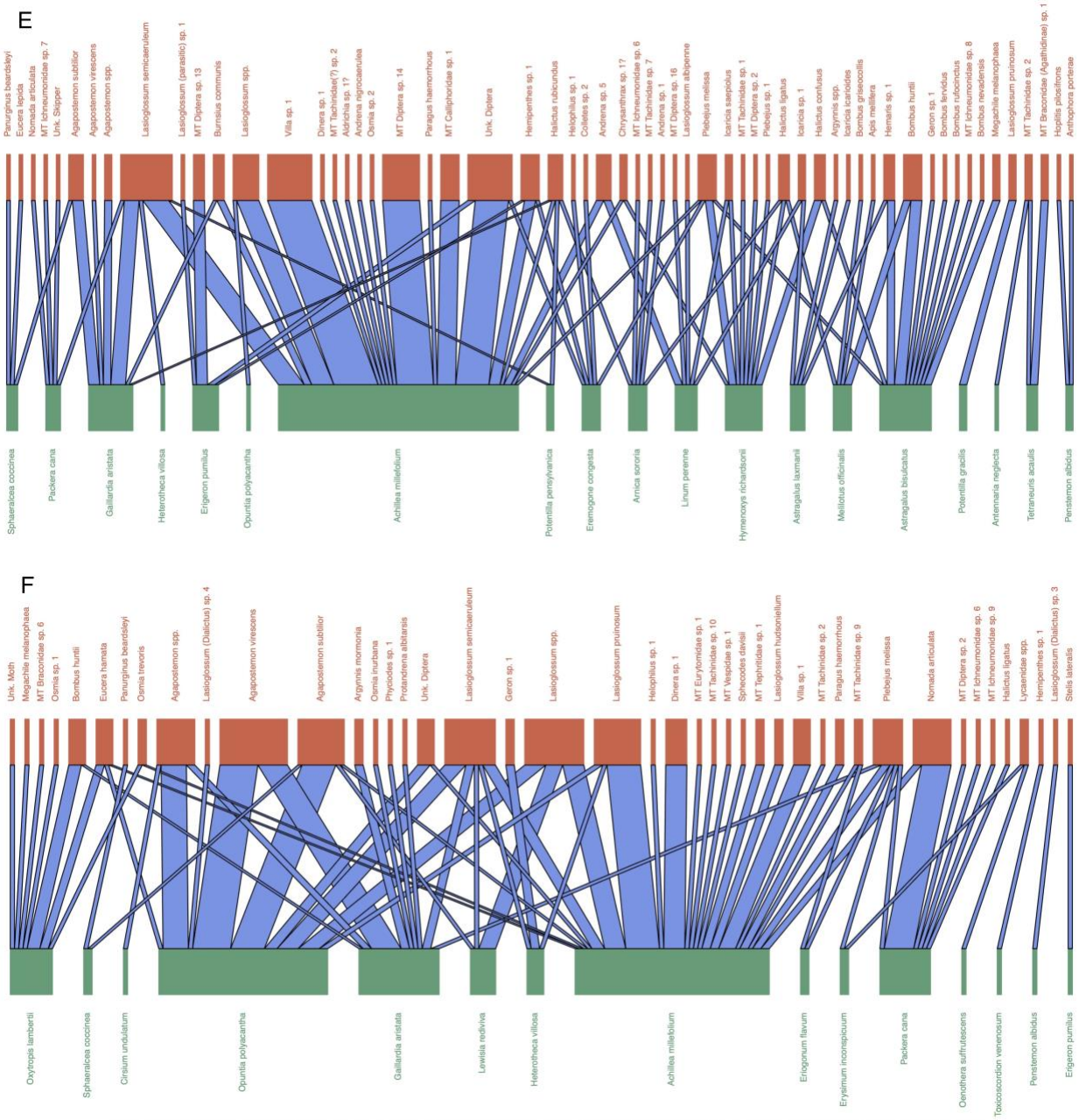


Figure S2. Plant-pollinator networks from 2024-2025 across Montana sites. Plot S2A shows APR bison-grazed sites, S2B shows APR cattle-grazed sites, S2C shows prairie dog colony sites, S2D shows APR/CMR ungrazed sites, S2E shows FB bison-grazed sites, and S2F shows FB cattle-grazed sites. The species in red at the top of the graph are pollinator species, and those on the bottom in green are plant species. Each blue line indicates interactions observed between plant and pollinator species, and the width of the line indicates the relative frequency of interactions observed (thicker blue lines indicate more commonly observed interactions).

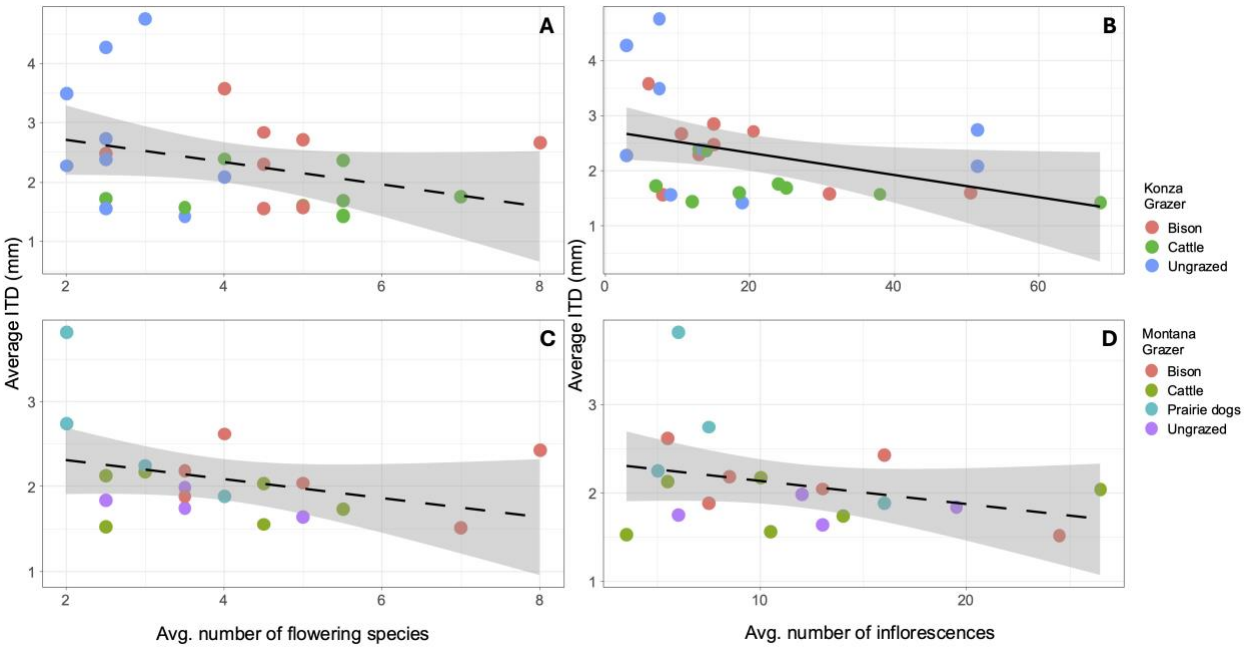


Figure S3. Plots showing the relationships among average bee size and average floral species richness and floral abundance. Points are color-coded by grazing regime; solid lines indicate statistically significant relationships and dashed lines indicate non-significant relationships. Plots A-B show Konza data, and plots C-D show Montana data.

Appendix B - Chapter 3

Tables B1-B16

Response	Predictor	Estimate	Std. Error	z-value	P-value
Floral richness	Bison	0.778	0.123	6.310	**<0.001**
Floral richness	Cattle	0.693	0.125	5.545	**<0.001**
Floral abundance	Bison	1.293	0.217	5.948	**<0.001**
Floral abundance	Cattle	1.438	0.217	6.617	**<0.001**

Table B1. Model results (Konza) for generalized linear mixed-effects models examining relationships between grazing regime and flowering plant richness and abundance. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Floral diversity	Bison	0.722	0.103	2.974	7.108	**0.006**
Floral diversity	Cattle	0.648	0.103	3.045	6.335	**0.008**

Table B2. Model results (Konza) for generalized linear mixed-effects model examining the relationship between grazing regime and flowering plant diversity. Sampling site is included as a random effect in the model.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Veg. height	Bison	-2.078	4.171	3.000	-0.498	0.653
Veg. height	Cattle	-3.328	4.171	3.000	-0.798	0.483
Bare ground	Bison	-9.062	5.447	3.000	-1.664	0.195
Bare ground	Cattle	-12.906	5.447	3.000	-2.370	0.099

Table B3. Model results (Konza) for generalized linear mixed-effects modeling examining the relationship between grazing regime and aboveground habitat characteristics (vegetation height and bare ground cover). Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Soil bulk density	Bison	0.086	0.069	9.000	1.250	0.243

Soil bulk density	Cattle	0.035	0.069	9.000	0.511	0.622
Soil sand content	Bison	1.000	1.907	3.000	0.524	0.636
Soil sand content	Cattle	3.125	1.907	3.000	1.639	0.200
Soil silt content	Bison	-3.375	2.745	9.000	-1.230	0.250
Soil silt content	Cattle	0.875	2.745	9.000	0.319	0.757
Soil clay content	Bison	2.375	2.584	9.000	0.919	0.382
Soil clay content	Cattle	-4.000	2.584	9.000	-1.548	0.156
Soil Na content	Bison	0.188	3.213	3.000	0.058	0.957
Soil Na content	Cattle	-6.825	3.213	3.000	-2.124	0.124

Table B4. Model results (Konza) for generalized linear mixed-effects modeling examining the relationship between grazing regime and belowground habitat characteristics (soil bulk density, soil sand, silt, and clay content, and sodium content). Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Floral richness	Bison (light-APR/CMR)	0.694	0.310	2.236	**0.025**
Floral richness	Bison (heavy-FB)	1.222	0.314	3.890	**<0.001**
Floral richness	Cattle (APR/CMR)	0.530	0.314	1.687	0.092
Floral richness	Cattle (FB)	0.609	0.334	1.824	0.068
Floral richness	Prairie dogs	0.618	0.312	1.980	**0.048**
Floral abundance	Bison (light-APR/CMR)	0.377	0.505	0.747	0.455
Floral abundance	Bison (heavy-FB)	2.093	0.505	4.147	**<0.001**
Floral abundance	Cattle (APR/CMR)	0.113	0.505	0.223	0.824
Floral abundance	Cattle (FB)	-0.214	0.507	-0.422	0.673
Floral abundance	Prairie dogs	1.546	0.505	3.063	**0.002**

Table B5. Model results (Montana) for generalized linear mixed-effects models examining relationships between grazing regime and flowering plant richness and abundance. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Floral diversity	Bison (light-APR/CMR)	0.846	0.506	5.763	1.673	0.147
Floral diversity	Bison (heavy-FB)	1.313	0.533	7.110	2.463	**0.043**
Floral diversity	Cattle (APR/CMR)	0.497	0.506	5.763	0.982	0.365
Floral diversity	Cattle (FB)	0.809	0.533	7.110	1.517	0.172
Floral diversity	Prairie dogs	0.7889	0.506	5.763	1.560	0.171

Table B6. Model results (Montana) for generalized linear mixed-effects model examining relationships between grazing regime and flowering plant diversity. Sampling site is included as a random effect in the model.

Response	Predictor	Estimate	Std. Error	df	t-value	P-value
Veg. height	Bison (light-APR/CMR)	3.156	2.463	5.548	1.281	0.251
Veg. height	Bison (heavy-FB)	-2.781	2.643	7.321	-1.052	0.326
Veg. height	Cattle (APR/CMR)	0.875	2.463	5.548	0.355	0.736
Veg. height	Cattle (FB)	-0.719	2.643	7.321	-0.272	0.793
Veg. height	Prairie dogs	-4.375	2.463	5.548	-1.776	0.130
Bare ground	Bison (light-APR/CMR)	-20.375	10.229	5.931	-1.992	0.094
Bare ground	Bison (heavy-FB)	-9.687	10.386	6.301	-0.933	0.385
Bare ground	Cattle (APR/CMR)	-12.719	10.229	5.931	-1.243	0.261
Bare ground	Cattle (FB)	-21.187	10.386	6.301	-2.040	0.085
Bare ground	Prairie dogs	13.750	10.229	5.931	1.344	0.228

Table B7. Model results (Montana) for generalized linear mixed-effects modeling examining the relationship between grazing regime and aboveground habitat characteristics (vegetation height and bare ground cover). Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	t-value	P-value

Soil bulk density	Bison (light-APR/CMR)	-0.312	0.144	-2.162	0.074
Soil bulk density	Bison (heavy-FB)	-0.084	0.144	-0.583	0.581
Soil bulk density	Cattle (APR/CMR)	-0.048	0.144	-0.330	0.753
Soil bulk density	Cattle (FB)	-0.149	0.144	-1.035	0.341
Soil bulk density	Prairie dogs	-0.137	0.144	-0.946	0.381
Soil sand content	Bison (light-APR/CMR)	21.750	15.239	1.427	0.203
Soil sand content	Bison (heavy-FB)	9.250	15.239	0.607	0.566
Soil sand content	Cattle (APR/CMR)	7.625	15.239	0.500	0.635
Soil sand content	Cattle (FB)	31.250	15.239	2.051	0.086
Soil sand content	Prairie dogs	4.125	15.239	0.271	0.796
Soil silt content	Bison (light-APR/CMR)	-3.375	8.184	-0.412	0.694
Soil silt content	Bison (heavy-FB)	2.250	8.184	0.275	0.793
Soil silt content	Cattle (APR/CMR)	4.250	8.184	0.519	0.622
Soil silt content	Cattle (FB)	-8.875	8.184	-1.084	0.320
Soil silt content	Prairie dogs	2.375	8.184	0.290	0.781
Soil clay content	Bison (light-APR/CMR)	-18.375	8.721	-2.107	0.080
Soil clay content	Bison (heavy-FB)	-11.500	8.721	-1.319	0.235
Soil clay content	Cattle (APR/CMR)	-11.875	8.721	-1.362	0.222
Soil clay content	Cattle (FB)	-22.375	8.721	-2.566	**0.043**
Soil clay content	Prairie dogs	-6.500	8.721	-0.745	0.484
Soil Na content	Bison (light-APR/CMR)	-233.89	192.42	-1.216	0.270
Soil Na content	Bison (heavy-FB)	-205.55	192.42	-1.068	0.326
Soil Na content	Cattle (APR/CMR)	-177.10	192.42	-0.920	0.393

Soil Na content	Cattle (FB)	-242.69	192.42	-1.261	0.254
Soil Na content	Prairie dogs	21.35	192.42	0.111	0.915

Table B8. Model results (Montana) for generalized linear modeling examining the relationship between grazing regime and belowground habitat characteristics (soil bulk density, soil sand, silt, and clay content, and sodium content).

Response	Predictor	Estimate	Std. Error	z-value	P-value
Bee richness	Bison	0.337	0.338	0.995	0.320
Bee richness	Cattle	0.000	0.365	0.000	1.000
Bee abundance	Bison	0.865	0.298	2.902	**0.004**
Bee abundance	Cattle	0.000	0.354	0.000	1.000

Table B9. Model results (Konza) for generalized linear mixed-effects models examining the relationship between grazing regime and nesting bee species richness and abundance. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Bee diversity	Bison	0.063	0.068	0.935	0.350
Bee diversity	Cattle	0.013	0.068	0.186	0.852

Table B10. Model results (Konza) for generalized linear mixed-effects model examining relationships between grazing regime and nesting bee species diversity. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Bee richness	Bison (light-APR/CMR)	-0.288	0.764	-0.377	0.706
Bee richness	Bison (heavy-FB)	1.099	0.646	1.702	0.089
Bee richness	Cattle (APR/CMR)	-1.386	1.118	-1.240	0.215
Bee richness	Cattle (FB)	0.000	0.866	0.000	1.000
Bee richness	Prairie dogs	-0.693	0.866	-0.800	0.424
Bee abundance	Bison (light-APR/CMR)	0.239	1.036	0.230	0.818
Bee abundance	Bison (heavy-FB)	1.105	1.035	1.068	0.286
Bee abundance	Cattle (APR/CMR)	0.491	1.021	0.481	0.630
Bee abundance	Cattle (FB)	-0.240	1.195	-0.201	0.841
Bee abundance	Prairie dogs	0.047	1.062	0.044	0.965

Table B11. Model results (Montana) for generalized linear mixed-effects models examining the relationship between grazing regime and nesting bee species richness and abundance. Sampling site is included as a random effect in all models.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Bee diversity	Bison (light-APR/CMR)	-0.067	0.102	-0.665	0.512
Bee diversity	Bison (heavy-FB)	0.368	0.125	2.939	**0.003**
Bee diversity	Cattle (APR/CMR)	-0.137	0.102	-1.342	0.180
Bee diversity	Cattle (FB)	-0.137	0.125	-1.096	0.273
Bee diversity	Prairie dogs	-0.137	0.102	-1.342	0.180

Table B12. Model results (Montana) for generalized linear mixed-effects model examining relationships between grazing regime and nesting bee species diversity. Sampling site is included as a random effect in the model.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Nesting bee abundance	Floral richness	0.188	0.071	2.649	**0.008**
Nesting bee abundance	Floral abundance	0.000	0.001	0.233	0.816
Nesting bee abundance	Bare ground cover	0.027	0.008	3.219	**0.001**
Nesting bee abundance	Veg. height	0.057	0.013	4.518	**<0.0001**
Nesting bee abundance	Soil sand content	0.036	0.114	0.317	0.751
Nesting bee abundance	Soil bulk density	-1.035	2.178	-0.475	0.635
Nesting bee abundance	Soil Na content	-0.061	0.060	-1.021	0.307

Table B13. Model results (Konza) for generalized linear mixed-effects models examining A) the relationship between aboveground habitat characteristics and nesting bee abundance (first four terms) and B) the relationship between belowground habitat characteristics and nesting bee abundance (last three terms). Sampling site is included as a random effect in all models.

Response	Predictor	df	Sum Squares	F-value	P-value
Nesting bee community composition	Floral richness	1	0.553	1.678	0.116

Nesting bee community composition	Floral abundance	1	0.552	1.675	0.108
Nesting bee community composition	Bare ground cover	1	0.740	2.246	**0.042**
Nesting bee community composition	Veg. height	1	0.175	0.530	0.832
Nesting bee community composition	Soil sand content	1	0.249	0.746	0.646
Nesting bee community composition	Soil bulk density	1	0.893	2.680	**0.021**
Nesting bee community composition	Soil Na content	1	0.457	1.372	0.200

Table B14. Model results (Konza) for constrained analysis of principal components (CAP) examining A) the relationship between aboveground habitat characteristics and nesting bee community composition (first four terms) and B) the relationship between belowground habitat characteristics and nesting bee community composition (last three terms).

Response	Predictor	Estimate	Std. Error	z-value	P-value
Nesting bee abundance	Floral richness	0.277	0.068	4.042	**<0.0001**
Nesting bee abundance	Floral abundance	0.001	0.000	1.817	0.069
Nesting bee abundance	Bare ground cover	0.007	0.025	0.285	0.776
Nesting bee abundance	Veg. height	0.030	0.074	0.399	0.690
Nesting bee abundance	Soil sand content	-0.009	0.044	-0.198	0.843
Nesting bee abundance	Soil bulk density	-2.331	2.771	-0.841	0.400
Nesting bee abundance	Soil Na content	0.000	0.004	0.137	0.891

Table B15. Model results (Montana) for generalized linear mixed-effects models examining A) the relationship between aboveground habitat characteristics and nesting bee abundance (first four terms) and B) the relationship between belowground habitat characteristics and nesting bee abundance (last three terms). Sampling site is included as a random effect in all models.

Response	Predictor	df	Sum Squares	F-value	P-value

Nesting bee community composition	Floral richness	1	0.790	2.674	**0.023**
Nesting bee community composition	Floral abundance	1	0.219	0.740	0.709
Nesting bee community composition	Bare ground cover	1	0.411	1.392	0.178
Nesting bee community composition	Veg. height	1	0.168	0.569	0.853
Nesting bee community composition	Soil sand content	1	0.335	1.010	0.369
Nesting bee community composition	Soil bulk density	1	0.507	1.528	0.130
Nesting bee community composition	Soil Na content	1	0.161	0.487	0.871

Table B16. Model results (Montana) for constrained analysis of principal components (CAP) examining A) the relationship between aboveground habitat characteristics and nesting bee community composition (first four terms) and B) the relationship between belowground habitat characteristics and nesting bee community composition (last three terms).

Tables S1-S2

Response	Predictor	Estimate	Std. Error	z-value	P-value
Nesting bee presence	Floral richness	0.350	0.130	2.705	**0.007**
Nesting bee presence	Floral abundance	-0.001	0.003	-0.356	0.722
Nesting bee presence	Bare ground cover	0.040	0.017	2.372	**0.018**
Nesting bee presence	Veg. height	0.087	0.028	3.100	**0.002**
Nesting bee presence	Soil sand content	0.187	0.134	1.396	0.163
Nesting bee presence	Soil bulk density	3.550	2.930	1.211	0.226
Nesting bee presence	Soil Na content	0.038	0.063	0.602	0.547

Table S1. Model results (Konza) for generalized linear models examining A) the relationship between aboveground habitat characteristics and nesting bee presence/absence (first four terms) and B) the relationship between belowground habitat characteristics and nesting bee presence/absence (last three terms). Both models use a negative binomial distribution.

Response	Predictor	Estimate	Std. Error	z-value	P-value
Nesting bee presence	Floral richness	0.242	0.117	2.066	**0.039**
Nesting bee presence	Floral abundance	0.002	0.001	1.794	0.073
Nesting bee presence	Bare ground cover	-0.004	0.034	-0.116	0.908
Nesting bee presence	Veg. height	0.064	0.114	0.563	0.573
Nesting bee presence	Soil sand content	0.021	0.047	0.462	0.644
Nesting bee presence	Soil bulk density	-0.369	2.530	-0.146	0.884
Nesting bee presence	Soil Na content	0.002	0.004	0.598	0.550

Table S2. Model results (Montana) for generalized linear models examining A) the relationship between aboveground habitat characteristics and nesting bee presence/absence (first four terms) and B) the relationship between belowground habitat characteristics and nesting bee presence/absence (last three terms). Both models use a negative binomial distribution.

Figure S1

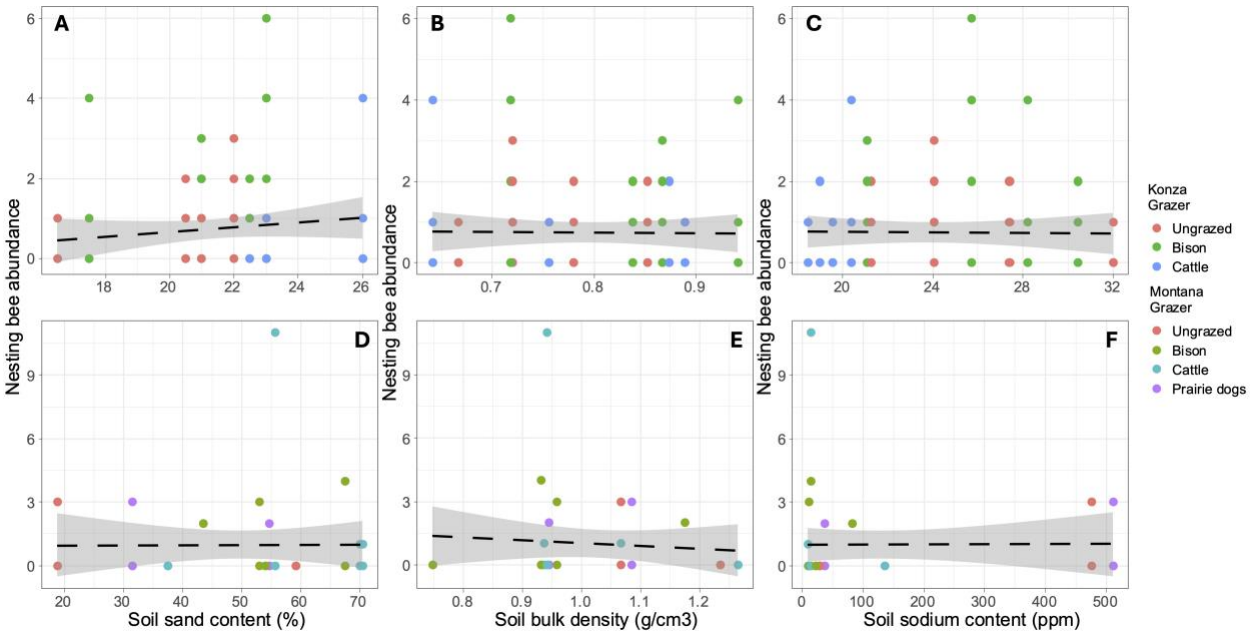


Figure S1. Plots illustrating the relationship between nesting bee abundance and the belowground habitat characteristics soil sand content (A and D), soil bulk density (B and E), and soil sodium content (C and F). Plots A-C show data from Konza, and E-F show data from Montana. Dashed lines represent nonsignificant relationships. Points on all plots are colored by grazing regime.