

Pollinators in a changing world: climate change and grazing impacts on bee communities

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Abstract

Pollinators face many threats today including habitat loss and fragmentation, increased pesticide usage, and new pathogens. Climate change can accentuate these threats through increased temperatures, expanded arid areas, and more frequent and intense extreme weather events. Additionally, grasslands are among the world's most imperiled ecosystems, and bees in the prairies of Kansas face a variety of challenges. Kansas prairies vary based on their management from cattle grazing as well as along a longitudinal precipitation gradient. The objectives of this work are to 1) understand the effects of climate change on pollinators and identify knowledge gaps in this field and 2) determine the effects of grazing on prairie bee communities along a precipitation gradient in Kansas. To better understand how climate change impacts pollinators we conducted a systematic review of the literature and utilized a vote-counting approach to summarize the results. We found that climate change has an overall negative impact on pollinators which includes effects like, range reductions, phenological mismatch, and reduced pollinator health and fitness. Community level effects such as abundance, richness, and diversity showed mixed responses indicating that pollinator species respond differently to climate change. To identify the effects of grazing on prairie bee communities throughout Kansas, we sampled 30 prairie sites spread across the precipitation gradient found in the state during the summer of 2023. These sites were divided evenly amongst tallgrass, shortgrass, and mixedgrass prairies. Within each prairie type, five sites were grazed and five were ungrazed. We found that bees were most impacted by grazing in the shortgrass prairies of western Kansas where grazing had the greatest effect on bee abundance and community composition. We also found that region effects usually had a stronger effect on bee communities than grazing, and that these effects were often mediated through differences in floral abundance.

These findings offer insights into how a changing climate, and management practices can impact pollinators, while informing bee conservation efforts in Kansas and identifying knowledge gaps and directing future research to protect pollinators globally.

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Introduction

Today, pollinators face a variety of threats including habitat loss and fragmentation, increased pesticide usage, and the introduction of non-native pathogens (Potts et al. 2010). These threats are the result of a world that has undergone significant change in recent history as a result of human influence (Diaz et al. 2019). Perhaps the most widespread way that humans have altered our world is through a variety of activities that have increased greenhouse gas concentrations in our atmosphere, leading to increased temperatures and other climatic changes (Forster et al. 2024). These changes are wide-reaching and can impact pollinators in a variety of ways. Due to the multidimensionality of climate change and the diversity of pollinators, it is difficult to summarize the total impacts of climate change (Forster et al. 2024).

Bees, in particular, face a number of other threats and stressors besides climate change. Research has shown that various bee species have seen population declines in recent years. For example, *Bombus affinis* (Cresson, 1863), *B. franklini* (Frison, 1921) and seven Hawaiian *Hylaeus* Fabricius, 1793 species have been placed on the federal endangered species list in the United States. Additional bee species such as *Bombus pensylvanicus* (De Geer, 1773) and *B. fraternus* (Smith, 1854) are being considered for listing, while there are many more species whose current populations (and thus need for conservation action) are largely unknown. These declines are primarily a result of habitat loss and fragmentation as human development has expanded (Vié et al. 2009). Globally only 20-40% of land is considered to be under “low human influence” (Riggio et al. 2020, Williams et al. 2020) leaving only a fraction of the natural habitat available for bee species. In 2021, Olynyk et al. found that both local loss of prairie habitat, and edge effects from roads negatively impact bee abundance (Olynyk et al. 2021). Additionally, global pesticide usage has increased 80% between 1990 and 2017 (Tostado and Bollmohr 2022)

which further harms bee populations in and around developed and agricultural areas. One example of this effect is demonstrated by Woodcock et al. (2016) who showed that neonicotinoid usage contributed to increased local extinction rates over 18 years for wild bee foraging on the treated crop, as well as, to a lesser extent, bee species not known to utilize the crop (Woodcock et al. 2016). Finally, non-native pollinators have been introduced to many parts of the world, which can spread novel pathogens to native bees, as well as increase competition for food resources (Goulson 2003). Along with the widespread *Apis mellifera* Linnaeus, 1758, various other species, such as *Bombus terrestris* (Linnaeus, 1758), *Osmia cornifrons* (Radoszkowski, 1887), and *Megachile rotundata* (Fabricius, 1787), are found outside of their natural ranges (Bohart 1972, Dafni 1998, Bosch and Kemp 2002, Goulson 2003). Of the various threats facing pollinators, this project will focus on two: the effects of climate change, and land management impact for bee conservation.

Climate change impacts on pollinators

Climate change can accentuate threats to pollinators through both direct and indirect effects (Oliver and Morecroft 2014, Garcia et al. 2014). For example, rising temperatures and more frequent and intense weather events such as floods, droughts, and heat waves can cause direct mortality for pollinators (Nicholson and Egan 2020). Furthermore, because insects are ectotherms, they are particularly susceptible to changes in temperature caused by climate change. Additionally, climate changes may cause distribution or phenology changes in a pollinator and/or its floral host, leading to a spatial or temporal mismatch between the pollinator and its host plant, with detrimental effects for both organisms as the pollinator loses its food source, and the plant loses its pollination service (Hegland et al. 2009, Garcia et al. 2014). Several studies have shown that this also applies to pollen and nectar, with negative consequences for the pollinators that

depend on them (Rankin et al. 2020, Hemberger et al. 2023). This is especially important for species at the edge of their range who might more easily be forced into inhospitable conditions, and for species with narrow flight periods or narrow host plant specificity (monolectic) that lack the flexibility to quickly adapt to phenological changes (Minckley et al. 2013).

Although the effects of climate change and pollinator (and other insect) declines have been increasingly well documented in recent years, we still lack an in-depth understanding of the ways pollinators are impacted by a changing climate. Climate change is driven by increases in greenhouse gases, like carbon dioxide (CO₂), in the atmosphere (Forster et al. 2024). There has been a wealth of research on the direct impacts of increased CO₂ concentration on plants, which generally finds that it will increase plant growth rate but lower the nutritional density of plant tissues (Peñuelas and Estiarte 1998). Furthermore, heat waves have been shown to reduce nectar production (Hemberger et al. 2023) while droughts can decrease the nutritional quality of both nectar and pollen (Rankin et al. 2020). However, it is expected that these effects will vary based on flower species (Bernauer et al. 2024). Additionally, we know comparatively little about how climate effects scale up to impact pollinators and other aspects of climate change, namely seasonality and intensity of temperature and precipitation events.

Second, most pollinator research focuses on the largest and most charismatic pollinators such as bumble bees (*Bombus*) and large butterflies, thanks to their relatively easy observation and identification compared to smaller pollinators. Additionally, climate change is unlikely to impact all pollinators equally, the effects will vary based on species and geographic region. Multiple studies have shown that different pollinator species respond differently to a changing climate. For example, Fründ, et al. (2013) found that bees respond differently to warming winter temperatures depending on overwintering life stage. Specifically, they found that bee species

overwintering as adults generally showed decreased weight and earlier emergence with increasing temperature, whereas bee species overwintering in pre-imaginal stages showed weaker or even opposite responses (Frund et al. 2013).

Climate change impacts pollinators at a variety of scales, from individual mortality, to community composition changes, to ecosystem-wide shifts in pollination services (Vanbergen et al. 2013). As a result, there are a wide range of variables that can be measured to assess the impacts of climate change on pollinators. These range from individual measures such as body size, fecundity, and survival rate, to community and population measures such as abundance, richness, and diversity. Additionally, many measures link pollinators to their food plants and compare things like flight period to the phenology of flowering plants. There are also nearly limitless ways to quantify climate change from looking at changes to temperature, precipitation, or CO₂ concentration, and also from varying the spatial and temporal scales that these variables are measured at. Remote sensing can provide a wealth of this data, however it is important to maintain an ecological basis for why pollinators may be responding to a given climate variable. Despite the wealth of literature documenting the effects of climate change on pollinators, a review that synthesized these studies is lacking and needed to inform global bee conservation efforts.

Grazing impacts on bee pollinators

In addition to climate change, humans impact the environment through changes in land use. This includes activities ranging from urban development to agricultural intensification, and a variety of management practices. Land use changes are not inherently bad for any given ecosystem, but intense land use can make former habitats unsuitable for certain organisms (Cariveau and Winfree 2015, Hall et al. 2017, Hung et al. 2017, Prendergast et al. 2022). The

loss of habitat alone has an adverse effect on organisms, but highly developed landscapes can lead to fragmentation between remaining habitat patches, which can further strain populations through reduced dispersal and gene flow, and increased demographic stochasticity (Hung et al. 2017, Chase et al. 2020). This makes management of remaining habitat critical to conserving ecosystems.

Grasslands are among the most imperiled ecosystems in the world, putting grassland bees at great risk of habitat loss (Morrison 2006). Hoekstra et al. (2005) found that temperate grasslands and savannahs had some of the greatest losses of area to human land use with conversion rates exceeding 50% in North America, while less than 5% of this biome is protected from development. Kansas in, particular, historically had roughly one-third of the state covered with each of these prairie type with tallgrass in the east, shortgrass in the west, and mixed grass between them (Dixon et al. 2014). Much of this historic prairie area is now used as rangeland for cattle (and occasionally, bison). The management of these rangelands varies regionally and according to the system (Wilmer et al. 2018, Smart et al. 2021). Some examples of common management practices include prescribed fire, targeted pesticide application, and various grazing regimens/rotations (Roche et al. 2015, Wilmer et al. 2018). The presence of large grazing herbivores shapes the plant communities of a prairie (Hobbs 1996). It has been established that bison and cattle graze differently, with bison preferring to eat grasses and thus promoting more forbs, while cattle are less selective (Steuter and Hidinger 1999, Towne et al. 2005). There is, however, evidence that under moderate stocking rates, cattle are quite selective towards grasses and fairly similar to bison in terms of feeding preference (Helzer and Steuter 2005). These effects of grazing on grassland flora have been well studied, however the way in which these changes mediate impacts on pollinators is less commonly addressed (Herrero-Jáuregui and

Oosterheld 2018). Only a subset of this research occurs in North American prairies, and what has been done shows variable effects of grazing on bees and other pollinators (Rosenberger and Conforti 2020, Cutter et al. 2021). Additionally, Butters et al. (2025) demonstrated that floral community changes from grazing do not always equate to changes in bee communities, and that the grazing effects of soil compaction play a significant role in shaping bee communities (Butters et al. 2025). In addition to changes in plant communities, the presence of large grazing herbivores (cattle) can modify the landscape in various ways with consequences for bee communities. This includes changes to bare ground, soil compaction, and pesticide exposure, which can differentially impact bees based on life history traits such as nesting and sociality (van Klink et al. 2015, Obregon et al. 2024).

Further complicating the effects of grazing on prairie bee and plant communities, are the different prairie ecosystems in the Great Plains. Precipitation is the primary driver of prairie variation with highly variable effects on prairie bee and plant communities. In Kansas, there is a gradient of precipitation from the wetter east (~1000 mm annually) to the drier west (~400mm annually) which creates three distinct prairie types distributed along this gradient (“U.S. Climate Normals” 2021). Tallgrass prairies are the most commonly studied North American prairie type and the interaction between grazing and precipitation and/or prairie type has scarcely been studied (Buckles and Harmon-Threatt 2019, Rosenberger and Conforti 2020, Cutter et al. 2021, Leone et al. 2022). Additionally, climate change is making the Great Plains more arid overall and will continue to do so (Seager et al. 2018). As the climate becomes drier, eastern areas of the state will become more climatically similar to current western areas as the precipitation gradient shifts eastward. If water is limiting, bees (and other organisms) will have to move eastward, adapt to a changing climate, or face local extinction (Kazenel et al. 2024). In addition to these

climatic shifts, climate change also is increasing frequency and intensity of extreme weather events like droughts, floods, and heatwaves, and expanded arid areas (Nicholson and Egan 2020). These changes may be lethal to bees on their own or cause sublethal effects that worsen other stressors (Potts et al. 2010, Nicholson and Egan 2020).

Research objectives:

This project seeks to address the ways in which bees and other pollinators are impacted by human caused environmental change, specifically climate change and cattle grazing. Because of the diversity of pollinators and the wide variety of ways in which climate change might impact them, it is difficult to determine the net impact of climate change on pollinators. Climate change impacts many different facets of the environment and thus may affect pollinators in a variety of direct and indirect ways. An in-depth understanding of these interactions is critical to effectively evaluate risks and threats to pollinators, and to make well-educated decisions that best conserve their populations and diversity. The aim of this objective is to synthesize the literature to determine how climate change impacts pollinators (currently and predicting in the future), as well as identify what knowledge gaps. We particularly ask (1) which pollinator taxa have received the most and least research focus (2) which areas of the world does this research most often occur in, and (3) how climate change has, and is predicted to impact pollinators by determining the nature of the relationship (positive, negative, mixed, etc.) between specific pollinator response variables (abundance, diversity, distribution, phenology) and climate change measures (temperature, precipitation, CO₂ concentration). This also reveals which pollinator taxa and their responses, and dimensions of climate change have been explored the least and are in the greatest need of future research. To do this we conducted a systematic review of the literature and utilized a vote-counting approach to summarize the results.

Additionally, it is valuable to understand how pollinators are reacting to environmental changes at a landscape or community scale (instead of global). Pollinators have a variety of life history traits which can also alter their responses to environmental change, making global trends difficult to interpret. Local studies could provide more applicable data to a given system since it would focus on local pollinators and environmental changes. With this objective, we aim to determine how bee communities are affected by grazing across the three prairie regions of Kansas. We hypothesized that bee communities in western Kansas would be the most species rich based on overall geographic patterns of bee diversity in North America (more specious in drier areas) (Orr et al. 2021, Turnley et al. 2025). Additionally, we predicted greater bee abundance in the wetter eastern portions of the state due to water being less of a limiting factor. Finally, we predicted that grazed prairies would support greater bee richness based on previous work in this system (Butters et al. 2025), and that this difference would primarily be mediated through greater access to floral resources in the grazed areas.

Objective 1: Climate change effects on pollinators

Methods

To address the first objective, we conducted a literature review of publications studying the effects of climate change on pollinators for studies published up until 2022. We started by searching Web of Science using search terms “pollinat*” and “climate change” in the “Topic” category which searches the title, abstract, and indexing of a given paper. The “pollinat*” search term was used to include any variations of the words “pollinator” and “pollination” (Fig. 1).

Once these publications were collected, we first determined if they were relevant to be included in this review. We made this decision based on whether the paper measured or predicted the impact that changing climate variables would have on pollinators. Many of the

papers deemed “not relevant” included plant-focused studies that only briefly measured pollination when giving background information (N=691), or pollinator-focused studies that alluded to potential climate change implications during the discussion, but did not measure any climate variables.

Of the remaining relevant studies, we categorized each by study type. Broadly, these categories were Observational, Experimental, Modelling, and Review. Review papers were excluded at this point since they did not report original data (N=86). Next, papers were grouped by the broad taxonomic category which included bees (Anthophila), wasps (other Hymenoptera, excluding Symphyta), flies (Diptera), butterflies/moths (Lepidoptera), beetles (Coleoptera), birds (Aves), and bats (Chiroptera), as well as a separate category for papers which recorded all floral visitors (studies not constrained by pollinator taxon). Papers were grouped by the continent in which the research took place: Asia, Africa, North America, South America, Europe, and Oceania (Australia and surrounding islands). Some studies also spanned multiple continents and were categorized as “global”.

Additionally, we counted the number of studies that examined climate predictor variables such as temperature, precipitation, and CO₂. We also recorded if the climate variable measured the frequency or intensity of extreme events (such as floods or heatwaves), and if an environmental gradient was used as a proxy for climate changes (such as temperature changes across an elevation gradient). Next, we categorized the pollinator response variables, including changes in species distribution, abundance, or phenology of pollinators, and we recorded the relationship direction between climate and pollinator variables. The relationship was described as either positive, negative, no effect, mixed effect or shift. “Positive” and “negative” effects reflect the direction of the relationship between an independent climate change variable and a pollinator

response variable. For example, if a paper found that rising temperatures (+) caused reduced pollinator abundance (-), then this would be classified as a “negative effect”. “No effect” was used for studies which found no significant effect of climate change on pollinators. “Mixed effect” was used to describe papers which demonstrated that pollinators respond differently to a climate change variable based on factors like their life history or geographic location. Finally, the “shift” category was used to describe changes in phenology or range that did not result in net changes in synchronicity with flowers, or range size, respectively. We found that these five categories were sufficient to describe the relationships between climate change variables and pollinators found among all reviewed literature.

Once categorized, we used a vote-counting approach and tallied the number of papers that fell into each category. We looked especially at the response directions and how they varied by pollinator response variable, pollinator taxon, and climate variable. We used the chi-square test to determine whether the distribution of these counts varied from an even distribution.

Study selection workflow

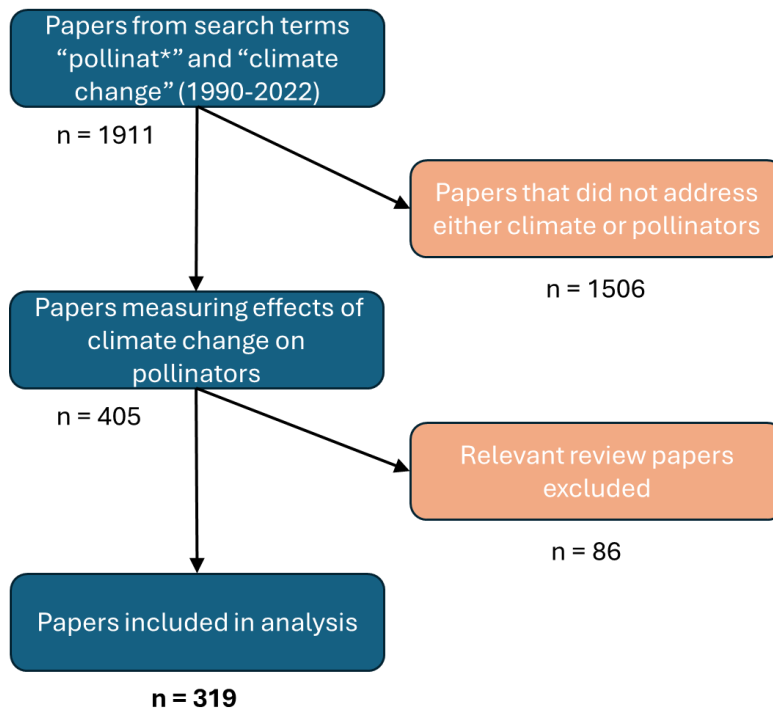


Figure 1. Workflow for finding and selecting papers relevant to the effects of climate change on pollinators. Publications were retrieved from a Web of Science search, then determined to be relevant if they measured the effects of a climate change variable on pollinators. Review papers were excluded from the final vote counting analysis.

Results

Our search terms returned 1,911 papers relating pollinators to climate change from 1991 through 2022. Of these papers, we determined that 319 measured or predicted the effects of climate change on pollinators and therefore were included in this review (see Supplemental A). The total number of relevant papers per year has increased exponentially with time beginning with 2 publications in 1998 and increasing to 79 publications in 2022 (Fig. 2). Observational studies made up 41.5% of all relevant studies, while modelling made up 31.7% and experimental contributed 26.8%. The global distribution of these publications is not even. Europe and North America had the greatest proportion of publications with 32.3% (103) and 29.8% (95), respectively (Fig. 3). The remaining continents each had far fewer publications with 11.6% (37) from South America, 8.8% (28) from Asia, 5.6% (18) from Oceania, and 2.8% (9) from Africa.

There were 8.5% (27) of those relevant publications occurring at the global scale, which were mostly modeling studies. For example, Giannini et al. (2013), predicted that pollinator ranges would shift towards higher latitudes in Mexico, Brazil, and Great Britain. This uneven geographic distribution of research indicates a need to prioritize understudied areas.

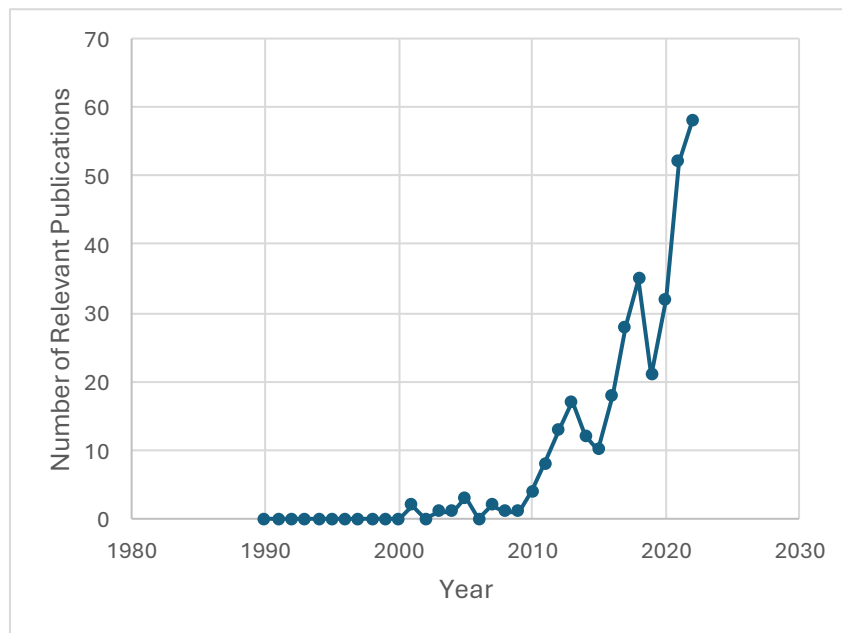


Figure 2. Number of publications per year measuring the effects of climate change on pollinators from 1990 through 2022.

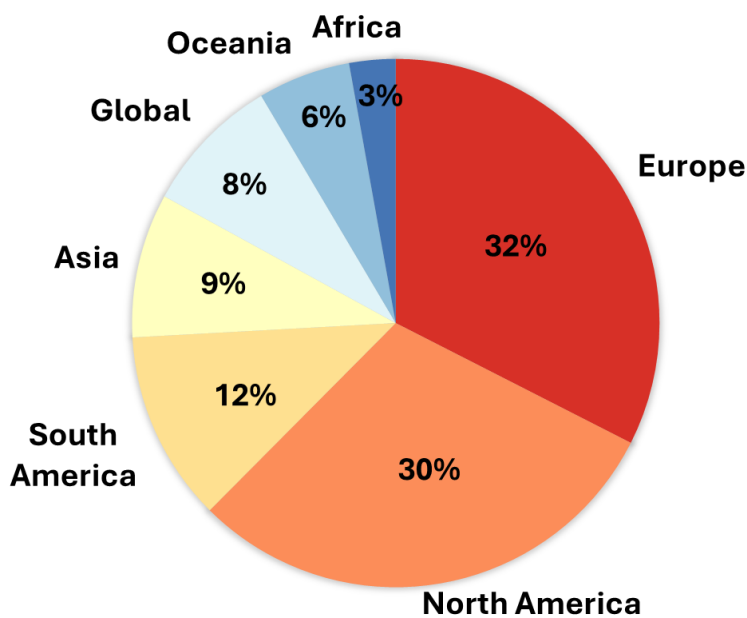


Figure 3. Percentage of relevant publications from each continent (out of 319 total). Papers that included multiple continents were placed into the “Global” category.

Pollinator taxa used in reviewed studies

The most studied pollinator taxon was bees with 56.8% (N=190) of studies focusing on them. Of these, roughly one third included a variety of bee genera (32.1%, N=61) and roughly one third (32.1%, N=61) focused only on *Bombus* (Fig. 4). The bee family Apidae was overrepresented compared to all other families with over half (57.4%, N=109) of bee studies addressing only apid bees (Kuppler et al. 2021). The next most common category was studies that used all floral visitors which made up 24.1% (N=60) of publications. Non-bee insect pollinators were far less studied of all papers with lepidopterans (5.4%), wasps (4.2%), flies (3.9%), and beetles (0.6%) included in the studies. Non-insect pollinators were also comparatively poorly represented with 3.0% of studies on birds and 2.1% on bats. Response directions for each taxon roughly mirrored the overall proportions with about half (49.4%) of the studies for each taxa finding a negative relationship and with mixed effects usually being the next largest group, making up a total of 21.1% of responses (Fig. 5, Table 1). Also it is noted that some papers studied multiple pollinator groups without including all floral visitors so raw counts total above 319 and percentages can be above 100%.

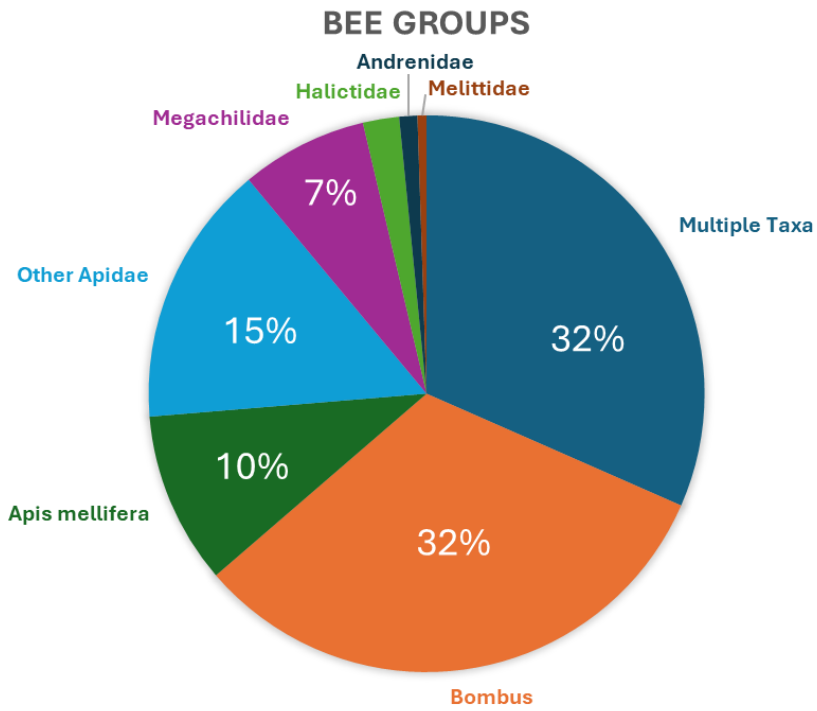


Figure 4. Percentage of relevant papers that focused on a particular bee group (out of 190 total). Papers were grouped by family except for *Bombus* and *Apis mellifera*, and papers incorporating a variety of bee groups. Those that included multiple taxa or whole bee communities were put into the “Multiple Taxa” category.

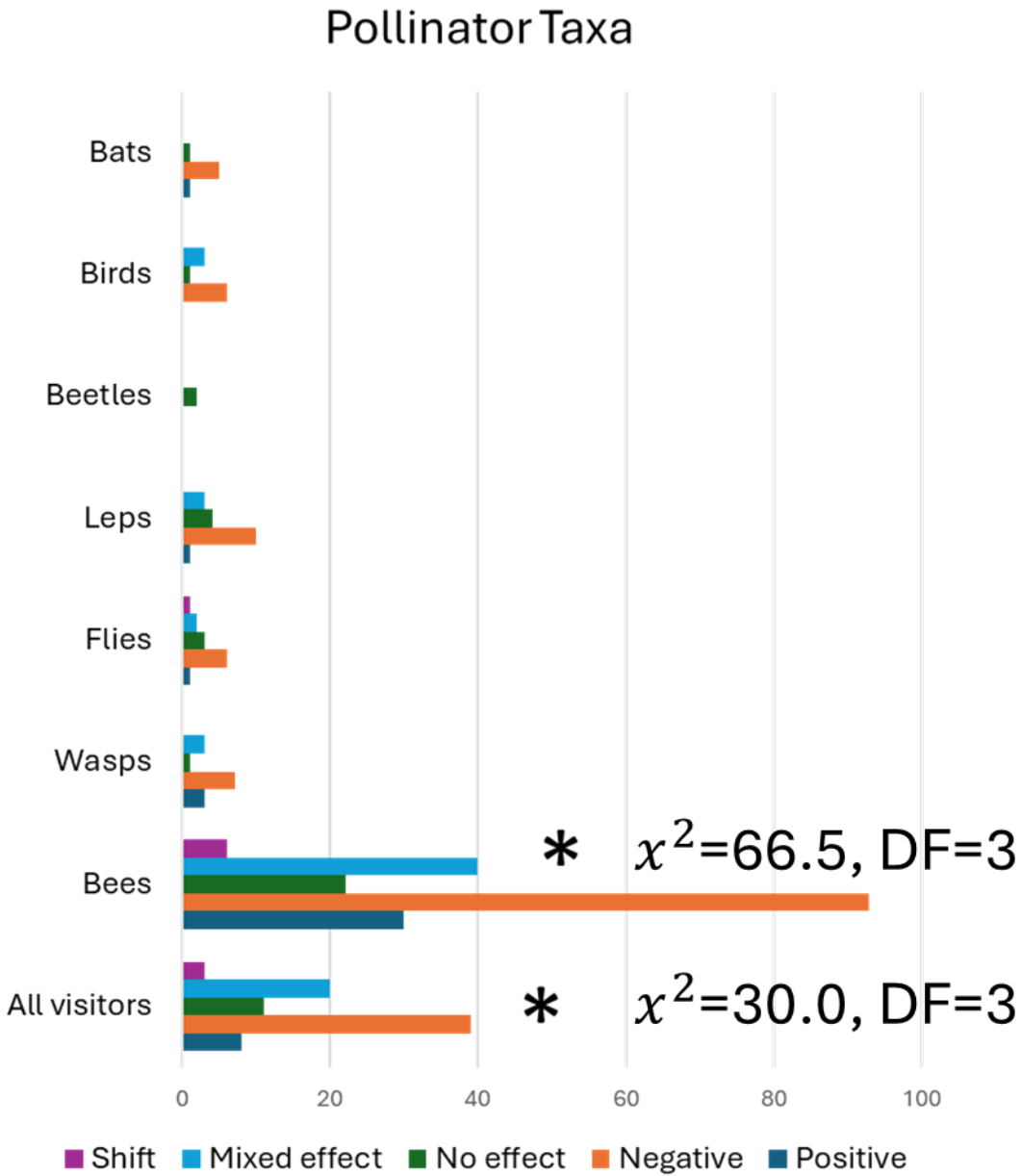


Figure 5. Response directions of pollinator and climate change relationships grouped by pollinator taxon. A chi-squared test was used on each group of pollinator response variables. An asterisk (*) represents a p-value of less than 0.01 (significant difference in frequency of effects within a taxon). Chi-squared and p values are calculated from data which omitted the “shift” category since it was by far the smallest category in each response variable. Chi-squared tests were not performed on other taxa groups since the number of observations were too small.

Climate predictor variables used in reviewed studies

Different climate variables were used throughout all the studies. Temperature variables were the most common with 161 studies (50.4%) using only temperature-related variables (Fig. 6). These variables included measures such as greater temperatures over seasonal and yearly scales (Freimuth et al. 2022), more frequent heat waves (Rasmont and Iserbyt 2012), and earlier spring onset (Kudo and Ida 2013). Conversely, only 21 studies (6.6%) used precipitation variables (Fig. 6), which included measures such as changes in precipitation timing and seasonality (Papanikolaou et al. 2017), soil moisture content, and more frequent floods and droughts (Rasmont and Iserbyt 2012). Negative relationships were the most common and accounted for 72 of the temperature studies (44.7%) and eight of the precipitation studies (38.1%). However, there were slightly more mixed-effect relationships among precipitation studies with 10 (47.6%). We found that 125 studies (39.2%) used both temperature and precipitation variables and showed a similar proportion of negative variables to the precipitation-only (73 studies or 58.4%). Many of these studies were modeling studies which often used a large suite of bioclimatic variables to predict future climate change effects. Only five total studies (1.6%) looked at the direct effects of increased CO₂ concentrations on pollinators and 36 studies (11.5%) assessed climate change effects as extreme events with increasing frequencies and severities. Droughts and heatwaves were the most common of these extreme weather events with 15 (41.7%) and 10 (27.8%) studies each, respectively.

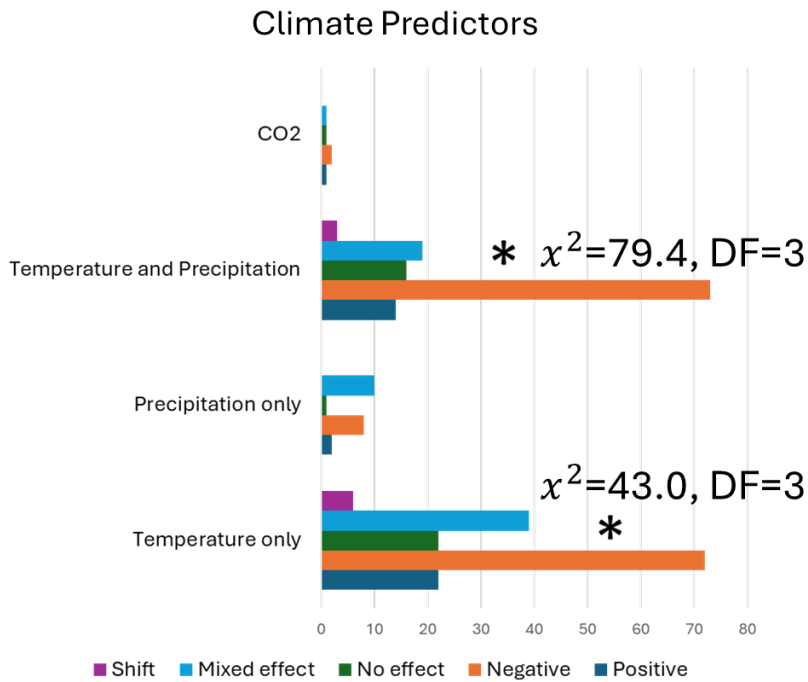


Figure 6. Response directions of pollinator and climate change relationships grouped by climate change predictor variables. A chi-squared test was used on each group of pollinator response variables that had enough samples available (“Temperature only” and “Temperature and Precipitation”). An asterisk (*) represents a p-value of less than 0.01 (significant difference in frequency of effects within a climate variable group). Chi-squared and p values are calculated from data that omitted the “shift” category since it was by far the smallest category in each response variable.

Climate change effects on pollinators

Pollinator responses to climate change were grouped into six categories as follows (in descending order of number of studies using each measure): range or distribution changes, pollinator health, floral visitation rates, abundance, richness or diversity, and phenology changes (Fig. 7, Table 2). Negative associations were the most common for each pollinator response and made up 47.6% of associations across all variables. Range and distribution changes had the greatest proportion of negative associations with 58.5% while richness and diversity had the lowest proportion with 35.8%. Mixed effects were the next most common association representing 23.3% of pollinator responses. Mixed effects were often a result of studies that included multiple pollinator species that responded differently to climate change.

Climate change effects on pollinator performance

Pollinator performance encompasses a wide variety of measures of fitness that pertain to an individual pollinator and includes body size (Oliveira et al. 2016), survival rate (Becker et al.

2018), and number of offspring (Harrower and Gilbert 2018). These measures made up 24.8% of relevant studies (N=79) and were mostly laboratory experiments that involved exposing pollinators to temperatures that are equivalent to those predicted under future climate change scenarios (Jevanandam et al. 2013). Negative responses were the most common, making up 44.3% of responses (35 out of 79) while mixed effects were also relatively high at 26.6% (21 out of 79 studies) (Fig. 7). These mixed effects were primarily due to different responses to climate change by different pollinator species (Radmacher and Strohm 2011, Myers et al. 2012, Frund et al. 2013, Forrest and Chisholm 2017, Farzan and Yang 2018).

Climate change effects on pollinator communities

Most field studies examined community-level responses to climate change. These community metrics can be placed into three broad categories: measures of abundance, richness or diversity, and floral visitation. “Floral visitation” is used to describe every pollinating visitor to a given plant and were unconstrained by pollinator taxon. This type of observation gives a measurement describing the frequency of floral visitation, often divided by pollinator species or broader grouping, which can be interpreted as an indirect measure of abundance, richness, or diversity.

Floral visitation rates were more commonly measured and made up 21.6% (N=69) of relevant papers (Fig. 7). Abundance and richness or diversity measures were used by nearly identical numbers of papers with 16.9% for abundance (N=54) and 16.6% for richness or diversity (N=53). Unsurprisingly, there are many papers that used both of these community measures (Hung et al. 2021, Maihoff et al. 2022). These measures had some of the highest rates of mixed effects results at 28.4% averaged across all three (Minckley et al. 2013). This is unsurprising since community measures include multiple species and thus incorporate the

variable responses of individual species to climate change. Although negative responses are the most common at a community level, some species may have a positive response to climate change, at least in the short term. Studies that showed positive responses to climate change frequently included non-native pollinator species.

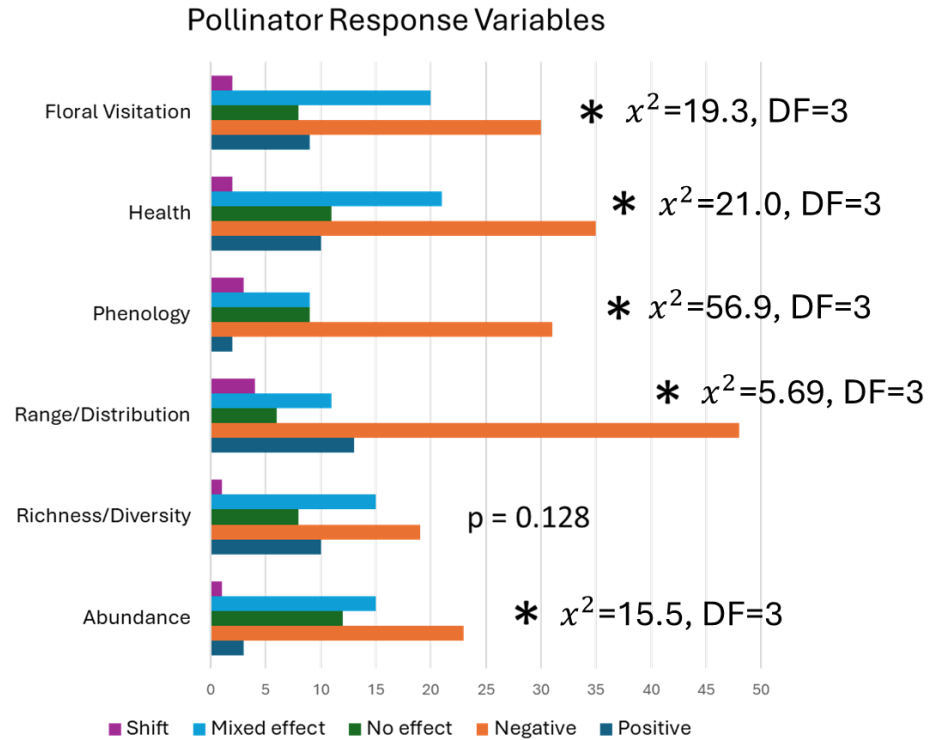
Climate change effects on spatial and temporal pollinator distributions

Due to the presence of ecological gradients, both spatially and temporally, species often respond to the effects of climate change by shifting their ecology in one of these aspects. In the case of spatial shift, this results in range or distribution changes, while temporal shifts are represented by changes in phenology. Range or distribution changes were the most commonly recorded pollinator response variable, making up 25.7% of included papers (N=82). Most of these papers used species distribution modeling or ecological niche modeling to predict how ranges and distributions of pollinators would change under future climate scenarios. These scenarios primarily came from the IPCC, which regularly releases emissions scenarios that range from best-case, to most-likely, to worst-case scenario, with expected temperature increases of 1.5°C, 2.7°C, and 4.4°C respectively. The most recent set of scenarios was released in 2021, and makes climate predictions out until 2100. These papers also had the greatest proportion of negative associations with 58.5% (48 out of 82). Negative associations in this case represent overall range decreases (Marshall et al. 2018, Nascimento et al. 2022). These decreases were usually combined with a shift towards higher latitudes (Milicic et al. 2018, Herrera et al. 2018) which were still recorded as a negative relationship if the range saw a net decrease in area. Conversely, 15.9% (13 out of 82) papers predicted range expansions for certain pollinator species under climate change (Franzen and Ockinger 2012, Kaloveloni et al. 2015, Silva et al.

2018, Parichehreh et al. 2022) which demonstrates, again, that there will likely be both winners and losers when it comes to climate change.

Conversely, phenology changes were one of the least studied pollinator response variables at 16.9% (N=54) of relevant papers. These included a mix of experimental (both laboratory and field) and observational techniques to determine the potential effects of climate change. Almost all phenology studies included a floral resource which they used to compare phenology changes of pollinators against so that they could determine if there was a phenological mismatch occurring between the two (i.e. a pollinator not flying at the times that its food plant is flowering). Greater degrees of mismatch were categorized as a negative relationship and were by far the most common (Gordo and Sanz 2005, Memmott et al. 2007, Olliff-Yang and Mesler 2018, Gallagher and Campbell 2021). There were, however, multiple instances of flowers and pollinators that had climate-induced phenology changes in the same way and thus remained synchronous (Bartomeus et al. 2011, Sevenello et al. 2020). Overall, when the phenology of pollinators did change, it usually advanced in the season due to higher global temperatures resulting in an earlier spring onset. This is further complicated by the fact that pollinators respond differently to climate change with examples of both lengthened (Dos Santos et al. 2015) and shortened (Duchenne et al. 2020) flight periods, or no change in phenology at all (Gillespie et al. 2016).

Figure 7. Response directions of pollinator and climate change relationships grouped by pollinator response variables. A chi-squared test was used on each group of pollinator response variables. Asterisks (*) represent a p-value of less than 0.01 (significant difference in frequency of effects within a pollinator response variable group). Chi-squared and p values were calculated from data which omitted the “shift” category since it was by far the smallest category in each response variable.



Objective 2: Grassland grazing effects on bee pollinators

Methods

Site selection

We surveyed bee communities at 30 prairie sites during the summer of 2023 to understand the impacts of grazing on bee communities, and how these impacts vary along the precipitation gradient in Kansas. We divided Kansas into three regions which represented the eastern, central, and western thirds of the state, and corresponded to tallgrass, mixedgrass, and shortgrass prairie respectively. Ten sites were selected within each region that were at least 2 kilometers away from each other (with one exception), to minimize potential overlap of individual bees (Gathmann and Tschardtke 2002, Greenleaf et al. 2007). Within each region, five

sites were grazed and five were ungrazed. These sites included properties managed by the state or federal government, nonprofit organizations, universities, and private landowners (Fig. 8).

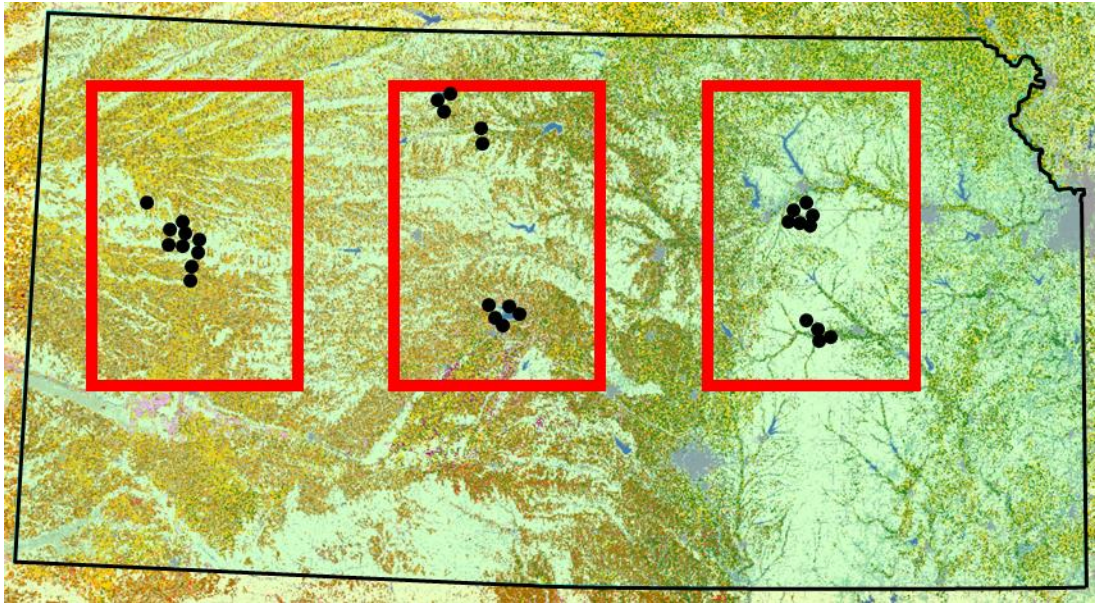
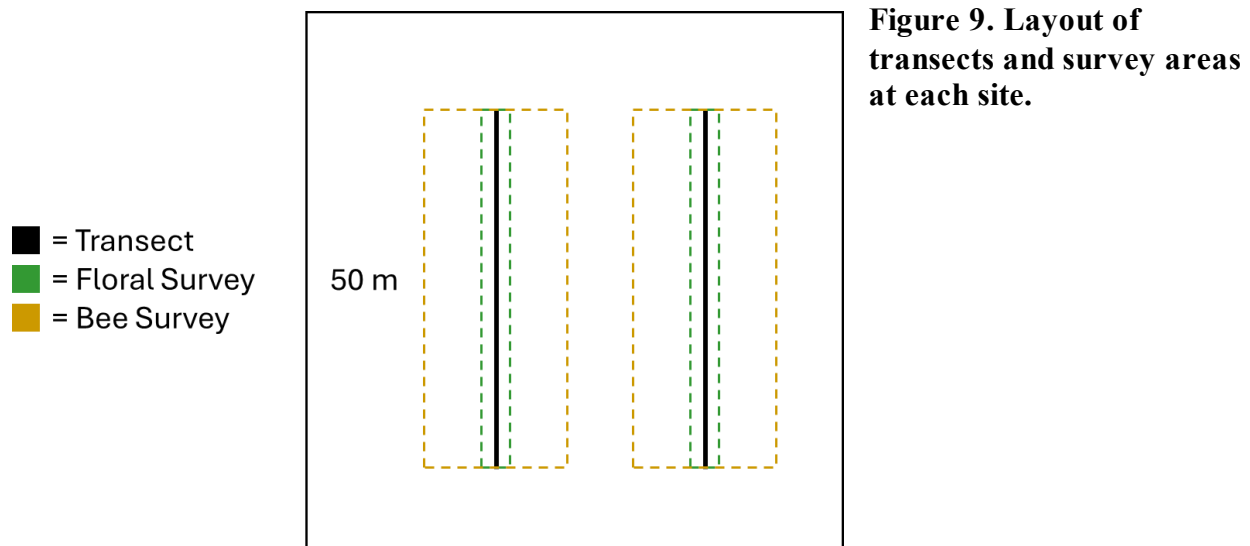


Figure 8. Landcover map of Kansas using the 2023 USDA Cropland Data Layer. Red boxes represent the approximate extents of the eastern, central, and western sampling regions. Black dots represent site locations.

Data collection

Each site was visited 6 times during the summer of 2023, twice each month during June, July, and August (with the exception of four sites that were visited during the last two days of May and lumped in with the June sampling). We established two parallel, 50 meter long transects that were 30 meters apart (Fig. 9). During each visit, these transects were surveyed for bees by walking within a 10-meter buffer on either side of the transect for 10 minutes per side, resulting in 40 person-minutes of bee collection per site visit. During this time, observers hand collected any bees seen visiting flowers using bee vacuums or aerial nets. To gain a more comprehensive sample of the bee community, sweep samples of 50 sweeps each which spanned the length of each transect were also collected. Bees were frozen until they were pinned for identification.

To minimize the effects of weather and maximize the number of bees caught, bee surveys were only conducted during daylight hours when the air temperature in the shade was between 70 and 90 degrees Fahrenheit and average wind speeds at vegetation level were below 15 miles per hour. These measurements were recorded at the beginning and end of each site visit using a Kestrel 2000 Weather Meter (Kestrel Instruments), along with the time and cloud cover. Precipitation data was obtained from Kansas Mesonet at monthly intervals during sampling (“Kansas Mesonet” 2024). We varied our sampling routes for sites to ensure that any given site was not exclusively visited during a specific time of day.



To evaluate the effects of floral communities on bee communities, flowering plant surveys were conducted at the same time as the bee surveys. The two visits to each site within a month were close together (usually within three days) and the floral communities changed very little in this time, making repeated surveys redundant. To survey flowering plants, a one-meter buffer was established on either side of both transects. We walked each transect looking for flowering plants within this buffer. Using a 0.5 x 0.5 meter quadrat, the number of quadrats

which contained a given species of plant was tallied. If multiple flowering plants of the same species were within the same quadrat, they were still only counted as a single quadrat which gives a time-efficient estimate of floral abundance. Floral richness included the species observed during this survey as well as other flowering plants noted within 10 meters of either transect. Only plants with open flowers (exposed reproductive structures) were counted, excluding grasses (Poaceae).

Data analysis

Bees were identified to genus using *The Bee Genera of North America* and unpublished keys from Mike Arduser. Species identifications were made using specific Discover Life keys (<https://www.discoverlife.org/>) and unpublished keys from Mike Arduser, as well as other taxon-specific publications (Timberlake 1954, Michener et al. 1994, LaBerge 2002, Griswold and Miller 2010, Dorchin et al. 2018, Sheffield et al. 2021, Portman et al. 2022, Sheffield 2023, Ascher and Pickering 2025). *Lasioglossum* Curtis, 1833 were identified by Dr. Joel Gardner at Washington State University. Species which we could not confidently identify to species were assigned a morphospecies identification (e.g. *Melissodes sp. 1*). Some species cannot be reliably distinguished morphologically (*Agapostemon texanus/angelicus* females, *Anthidiellum notatum/boreale*), these species were left identified to a single taxon to give a conservative value when calculating richness.

For these data analyses, all observations of bees and flowering plants at a site were summed across the survey period to give a single bee and flower community at each site. Precipitation also was summed across each month by site to give a total precipitation value over the season for each site. Temperatures from each visit to a site were averaged to give a mean temperature during sampling across all six site visits.

We used linear models to test how grazing, region, and their interactions affected the total abundance and richness of bees and flowers. We used a Permutational analysis of variance (PERMANOVA) to determine the effects of region, grazing, and their interactions on bee and floral community composition. We created a simple and a complex linear model for each response variable. The simple models included the categorical predictor variables of grazing and region, as well as an interaction term between the two. The complex models included these same variables with the addition of the continuous covariates average temperature, total season precipitation (June through August) and floral abundance (bee models only). Generalized Variance Inflation Factor ($\text{GVIF}^{1/(2 \cdot \text{df})}$) was used to check models for multicollinearity so that categorical and continuous variables could be compared. The values of $\text{GVIF}^{1/(2 \cdot \text{df})}$ for categorical variables are at maximum 2.02, indicating a low degree of multicollinearity (Table 13). The Akaike Information Criterion (AIC) was used to evaluate whether the simple or complex model was the best fit for each response variable. A lower AIC value represents a better fitting model. Models with a difference in AIC value (ΔAIC) of two or less are not considered to have a significant difference in fit. In this case the simple model is chosen since it has fewer terms and is thus more parsimonious.

We performed an analysis of variance (ANOVA) on each linear model. A type III sum of squares was used first and was the final analysis if the interaction term was significant. If the interaction term was not significant, a type II sum of squares was used to give more analytical power. A Tukey's Honestly Significant Difference (HSD) test was used to quantify difference in groups by categorical variable.

Bees with different life history traits can have varying responses to land use changes, so we chose to split bees by nesting guild and into taxonomic and functional groups to measure the

impacts of grazing and precipitation (Williams et al. 2010, Cariveau and Winfree 2015). We categorized each bee species into aboveground or belowground nesting, excluding parasitic species to determine if grazing differentially influenced these two nesting guilds. Additionally, we divided our bees into 10 taxonomic and functional groups to measure the responses of specific groups. These groups are as follows: Andrenidae (*Andrena* Fabricius, 1775, *Calliopsis* Smith, 1853, *Perdita* Smith, 1853, *Protandrena* Cockerell, 1896, *Pseudopanurgus* Cockerell, 1897), eusocial Apidae (*Bombus* Latreille, 1802, *Apis* Linnaeus, 1758), carpenter bees (*Xylocopa* Latreille, 1802, *Ceratina* Latreille, 1802), longhorn bees (*Melissodes* Latreille, 1829, *Svastra* Holmberg, 1884, *Xenoglossodes* Ashmead, 1899), other Apidae (*Anthophora* Latreille, 1803, *Anthophorula* Cockerell, 1897, *Diadasia* Patton, 1879, *Epeolus* Latreille, 1802, *Triepeolus* Robertson, 1901, *Xeromelecta* Linsley, 1939), Colletidae (*Colletes* Latreille, 1802), green bees (*Agapostemon* Guérin-Méneville, 1844, *Augochlorella* Sandhouse, 1937, *Augochloropsis* Cockerell, 1897), *Lasioglossum*, other Halictidae (*Halictus* Latreille, 1804, *Nomia* Latreille, 1804, *Sphecodes* Latreille, 1804), and Megachilidae (*Anthidiellum* Cockerell, 1904, *Anthidium* Fabricius, 1804, *Ashmeadiella* Cockerell, 1897, *Coelioxys* Latreille, 1809, *Heriades* Spinola, 1808, *Hoplitis* Klug, 1807, *Lithurgopsis* Fox, 1902, *Megachile* Latreille, 1802, *Osima* Panzer, 1806). We used the `simper` function (`vegan`) to calculate the similarity percentage of each bee and plant species. This metric represents the contribution of each species toward Bray-Curtis similarity among sites. To further understand how specific species were contributing to differences in among grazed and ungrazed prairies in different regions, we performed a multi-level pattern analysis (`indicspecies::multipatt`) which tested for significant associations between a given species and a categorical group (grazing or region).

All analyses were performed in R v. 4.4.3 (2025-02-28) and used packages tidyverse, vegan, car, visreg, corrplot, BiodiversityR, agricolae, rms, labdsv, ggfortify, and indicpecies (Kindt and Coe 2005, Hothorn et al. 2008, Cáceres and Legendre 2009, Breheny and Burchett 2017, Horikoshi and Tang 2018, Fox and Weisberg 2019, Wickham et al. 2019, Shuangbin Xu et al. 2021, Behrendt 2023, Mendiburu 2023, Roberts 2023, Wei and Simko 2024, Harrell Frank 2025, Oksanen et al. 2025, R Core Team 2025).

Results

During the summer of 2023, from May 30th to August 17th, we collected 1736 bee specimens and observed 122 species of plants in flower. These bees represent 78 species belonging to 34 genera (Table 3). Bees in the family Halictidae made up 77.0% of all bees collected with the bulk of these coming from the genera *Lasioglossum* (583 individuals) and *Augochlorella* (550 individuals, Fig. 10A). The genera *Bombus* (119 individuals), *Melissodes* (74 individuals), and *Megachile* (71 individuals) were the next most abundant across all sites. Bee abundance varied throughout the season with an average of 8.20 bees caught per site in May and June (Fig. 10B). This increased to an average of 30.03 in July before decreasing to 19.63 in August. The July peak was largely influenced by the eastern region which had an average of 48.70 bees per site during July. This coincided with the flowering period of purple prairie clover (*Dalea purpurea*) and leadplant (*Amorpha canescens*). A Tukey's HSD test showed that May and June abundances were significantly different from both July ($P<0.001$) and August abundances ($P=0.031$).

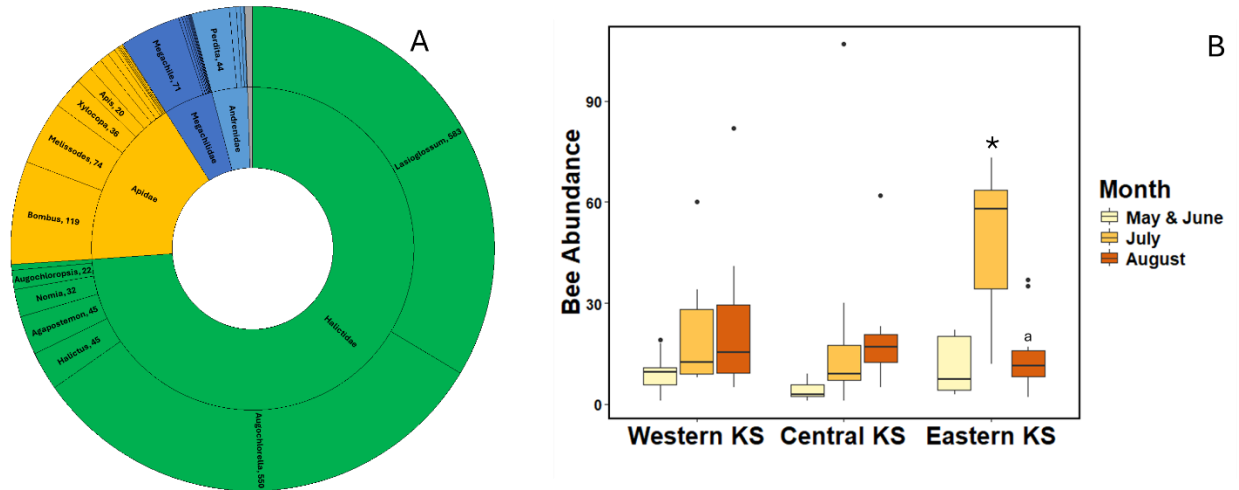


Figure 10. Bee abundance counts across all site visits, grouped by family (inner circle) and genus (outer circle) (A). Bee abundance by month and region (B). In B, an asterisk (*) represent significantly different bee abundances.

Bee community responses

We found a significant effect of grazing on bee abundance ($P=0.046$, Table 4A). A Tukey's HSD test showed that grazed sites had on average 1.7 times greater abundance than ungrazed sites (Table 4C, 4D). The difference in grazed and ungrazed sites was only significant in the western region with grazed sites having 2.6 times greater bee abundance ($P=0.027$, despite only a marginally significant interaction term ($P=0.079$, Fig. 11A, Table 4C, 4D). When the covariates of floral abundance, summer precipitation, and average summer temperature were added to the simple model (i.e., the complex model), the significant effects of grazing were replaced with only floral abundance ($P<0.001$) and average temperature ($P=0.027$, Table 4B). Floral abundance was positively correlated with bee abundance (beta coefficient = 0.590), while average temperature had a negative correlation (beta coefficient = -0.399). We also found a significant effect ($P=0.025$) of region where eastern sites had 1.7 times the average abundance of central sites (Fig. 11A, Table 4C, 4D). Of these two models, the complex (AIC=284.0, DF=10) was a better fit (delta AIC = 13.7) than the simple model (AIC=297.7, DF=7).

For bee richness, we found no significant effects of region or grazing on bee richness in our simple model (Table 5A). In the complex model, we found that region ($P=0.016$) and average temperature ($P=0.047$) had significant effects on bee richness (Table 5B). Average temperature had a negative impact on bee richness with a beta coefficient of -0.463 . Delta AIC between the simple ($AIC=163.78$, $DF=7$) and complex models ($AIC=162.55$, $DF=10$) is less than 2 (delta $AIC=1.23$) indicating they have the same model fit. We therefore considered the simple model the most parsimonious.

Our simple PERMANOVA found region to significantly affect bee community composition ($P<0.001$), and a marginally significant effect of grazing ($P=0.093$, Table 6A). Our complex PERMANOVA indicated that region ($P<0.001$) and floral abundance ($P=0.024$) have significant effects on bee community composition, while seasonal precipitation had a marginally significant effect ($P=0.061$, Table 6B). Additionally, bee communities in western Kansas varied the most between grazed and ungrazed sites, though only marginally significant ($P=0.072$, Fig. 11C). Our NMDS showed a similar distribution of sites and shows a strong correlation between axis 1 and seasonal precipitation ($P=0.008$), and a correlation between axis 2 and floral abundance ($P=0.002$, Fig. 11D, Table 6C).

The five species that contributed the greatest amount to dissimilarity among sites are *Lasioglossum semicaeruleum* (Cockerell, 1895), *Augochlorella aurata* (Smith, 1853), *Augochlorella persimilis* (Viereck, 1910), *Bombus pensylvanicus*, and *Megachile brevis* Say, 1837 (Table 7A). These species collectively contributed 54% of the dissimilarity in bee communities between sites. The multilevel pattern analysis showed that *Perdita albipennis* Cresson, 1868, *Agapostemon texanus/angelicus*, and *Melissodes sp.3* were all significantly associated with the western region. Two species were associated with the central region (*Nomia*

sp.1 and *Lasioglossum disparile*, Cresson, 1872). Six species were significantly associated with the eastern region: *Xylocopa virginica* (Linnaeus, 1771), *Augochlorella aurata* *Augochlorella persimilis*, *Augochloropsis metallica* (Fabricius, 1793), *Colletes sp.2*, and *Bombus auricomus* (Robertson, 1903). Several species were significantly associated with two regions. *Lasioglossum semicaeruleum* and *Melissodes sp.2* were significantly associated with the western and central regions, while *Lasioglossum callidum* (Sandhouse, 1924), *Lasioglossum trigeminum* Gibbs, 2011, and *Bombus griseocollis* (De Geer, 1773) were associated with the central and eastern regions. Only one species, *Halictus ligatus* Say, 1837, was significantly associated with grazed sites. (Table 7B).

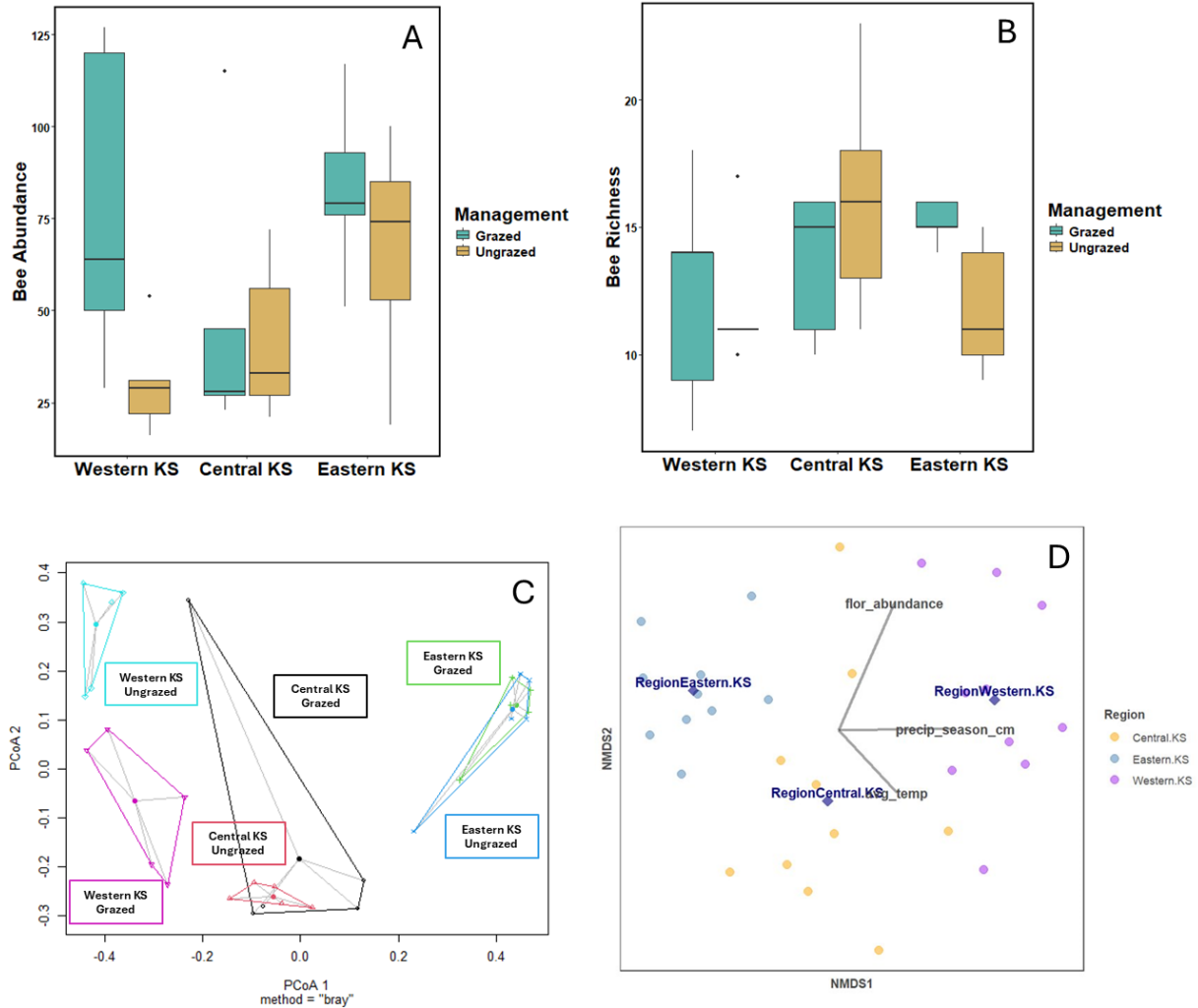


Figure 11. The effects of region and grazing on bee abundance (A) and rarefied richness (B). PCoA showing the effects of region on bee community composition (C). NMDS showing correlated covariates (D).

Aboveground nesting bee species made up only 11.3% of all non-parasitic bees and did not show any significant differences among groups or correlations with covariates ($P > 0.05$). Conversely, belowground bees made up 88.7% and followed most of the same patterns as full bee community abundance. We found that the abundance of bees in the family Andrenidae varied significantly by region ($P = 0.020$, Table 8) in simple and complex models, with abundances in western Kansas 3.9 times and 5.4 times greater than in the central or eastern regions, respectively (Fig. 12A). We found carpenter bees to have the greatest abundance in

eastern Kansas ($P < 0.001$) with an average 11.7 times that of the central region (Fig. 12A). No carpenter bees were observed at western sites. Longhorn bees were most abundant in the west ($P = 0.036$), averaging 5.3 times more abundant than in the east (Fig. 12A). Green sweat bees were the most abundant group throughout this study with eastern sites averaging 9.3 and 17.1 times greater abundance than central or western sites, respectively ($P < 0.001$, Fig. 12A). The genus *Lasioglossum* was the next most abundant and showed the opposite regional distribution from green bees, with the western region having 5.7 times as many as the east (Fig. 12A). This high western abundance was primarily a result of the grazed sites, which had 4.4 times the number of *Lasioglossum* of ungrazed sites (Fig. 12B). A complex model showed that this difference was explained by significantly greater floral abundances in the grazed western sites compared to ungrazed sites ($P < 0.001$). None of the other bee groups showed any significant differences in abundance based on region or grazing ($P > 0.05$, Table 8).

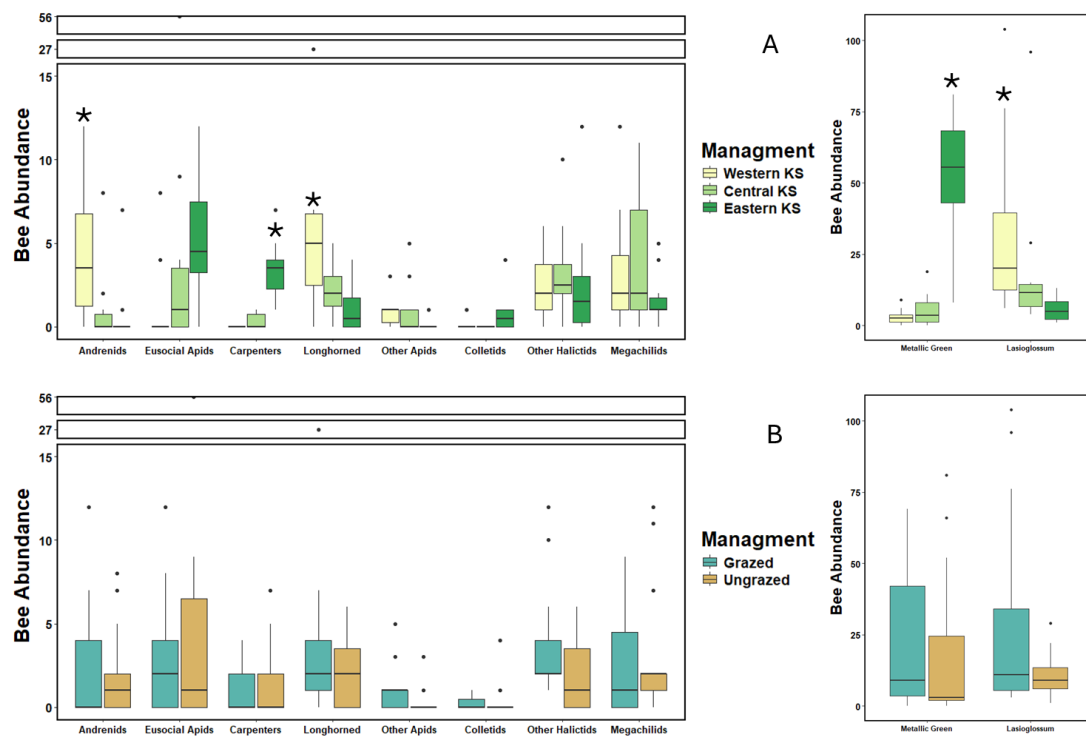


Figure 12. Bee group abundances by region (A), and management (B). An asterisk (*) represents significantly different bee abundances.

Floral community responses

We found region to be significant for floral abundance ($P=0.027$, Table 9A). The western region had the greatest floral abundance with an average of 325.2 floral quadrats per site (Table 9C). Central and eastern regions had considerably fewer flowers with averages of 184.9 and 141.1, respectively (Fig. 13A, Table 9D). The complex model added the covariates of total summer precipitation, and average summer temperature and found only a marginally significant effect of region ($P=0.083$, Table 9B). The simple model had an AIC of 382.2 (DF=7) and the complex model had an AIC of 396.2 (DF=9), which shows the simple model to be the best fit (delta AIC=14.0).

We found a significant effect of region on floral richness ($P=0.008$, Table 10A). The western region had the greatest floral richness, averaging 16.2 species per site, followed by the eastern region at 14.1 and the central region at 10.6 (Fig. 13B, Table 10C). An AIC was calculated which showed that the simple (AIC=170.78, DF=7) and complex (AIC=170.99, DF=9) models were similarly fit, (delta AIC=0.21) so the simple model is the most parsimonious.

Our PERMANOVA indicates that region, and total summer precipitation have a significant effect on floral community composition (Fig. 13C). The five plant species that contributed the most to dissimilarity among sites include *Pediomelum tenuiflorum*, *Croton sp.*, *Achillea millefolium*, *Convolvulus arvensis*, and *Helianthus annuus*. Our multilevel pattern analysis showed that the following 11 plant species were significantly associated with the western region: *Helianthus annuus*, *Croton sp.*, *Euphorbia marginata*, *Sphaeralcea coccinea*,

Solanum rostratum, *Thelesperma megapotamicum*, *Xanthisma spinulosum*, *Oenothera suffrutescens*, *Lygodesmia juncea*, *Chaetopappa ericoides*, and *Plantago patagonica*. Only one species was significantly associated with the central region was *Achillea millefolium*. Eight plant species were associated with the eastern region: *Asclepias viridis*, *Ruellia humilis*, *Dalea purpurea*, *Vernonia baldwinii*, *Mimosa quadrivalvis*, *Verbena stricta*, *Linum sulcatum*, and *Amorpha canescens*. *Physalis longifolia* and *Euphorbia davidii* were significantly associated with the western and central regions, while *Erigeron strigosus* was associated with central and eastern regions.

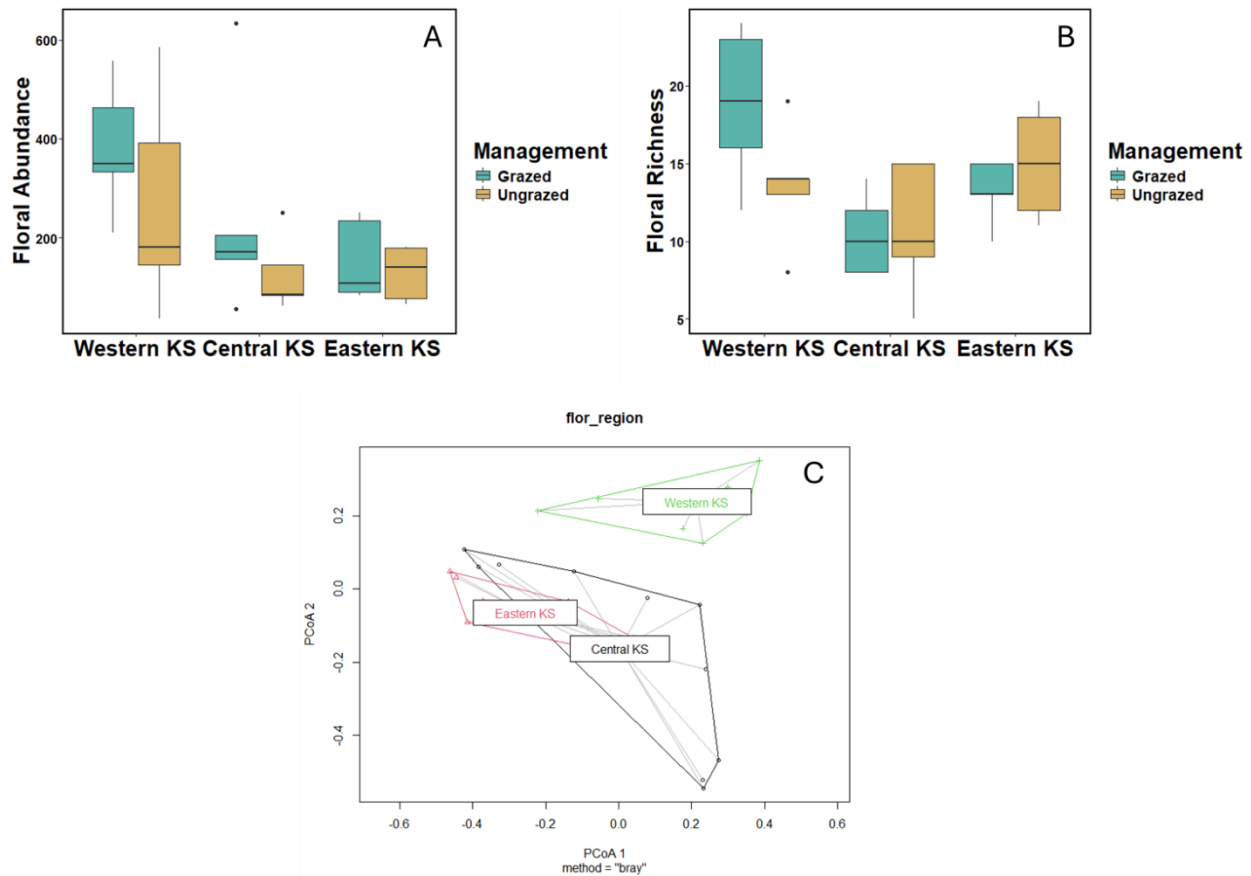


Figure 13. The effects of region and grazing on floral abundance (A) and richness (B). The effects of region on floral community composition (C).

Discussion

Pollinator decline is a complex, global issue with wide-reaching consequences, and a myriad of causes. This work focused on two of these causes: climate change and land use changes (specifically grazing management). Our literature review supports the notion that climate change is impacting pollinators in a variety of ways and at multiple scales, with negative outcomes occurring the most frequently. Additionally, our field study showed that while grazing per se did not significantly impact bees in Kansas, floral abundance (which can be impacted by grazing) was positively correlated with bee abundance. We also found that bee abundance and community composition varied by prairie region across a precipitation gradient.

Objective 1: Climate change effects on pollinators

We found that the global distribution of research on the effects of climate change on pollinators is uneven. More research is needed to ensure the protection of pollinators in understudied areas like Asia, Africa, and Oceania. Bees, particularly *Bombus* and other apid bees, are overrepresented in the literature compared to other important pollinators. Non-insect pollinators like bats and birds are in particular need of additional research. Studies on the impacts of rising temperatures are common and mostly negative, but studies looking at precipitation are rarer and more often show mixed results. Additional work is needed to understand the effects of changing precipitation regimes on pollinators. There is a large number of studies that examine the combined effects of precipitation and temperature variables, however, these may lack a mechanistic understanding of how they influence each other or be biased towards modeling studies that use a suite of remotely sensed climate variables. Additionally, the direct effects of elevated CO₂ levels on pollinators rarely have been studied and require further attention. Overall, pollinators have mostly negative relationships with climate change regardless of the response

variable. Community level response variables such as abundance, richness or diversity, and floral visitation show a higher proportion of mixed effects compared to other measures. This indicates that some species within pollinator communities have positive responses to climate change. Studies that quantify the frequency of these positive responses and why these positive responses exist is needed.

We have identified a variety of knowledge gaps in our understanding of the effects of climate change on pollinators. We recommend that future research should prioritize addressing several of these key gaps. Bees have historically received the greatest attention when it comes to pollinator research (because of their active gathering and transport of pollen), however pollinators from other taxa contribute important pollination services for a variety of plants (especially bats and birds in tropical areas that harbor the greatest biodiversity). Non-bee pollinators are important pollinators in a variety of crop systems (Larson et al. 2001, Rader et al. 2013, 2016). Additionally, tropical areas have received less research attention compared to the global North. These areas contain a greater biodiversity and thus understanding the impacts of climate change in the tropics is critical to maximizing our ability to protect global biodiversity (Fine 2015, Barlow et al. 2018). Furthermore, most research focuses on the impacts of changes to temperature and precipitation, while little research addresses the direct impacts of increased CO₂ levels in pollinators. Research on the effects of greater CO₂ concentrations due to climate change has been focused most on ocean acidification and direct effects on plant growth and nutrition (Xu et al. 2015, 2016, Hughes et al. 2017, Dusenke et al. 2019, Falkenberg et al. 2020). Thus, it is important to understand how CO₂ could be impacting global pollinator communities, especially since our second objective, and other literature, have shown that plant-mediated effects are common (Pincebourde et al. 2017, Kessler and Chautá 2020). There is evidence that

CO₂ is an important cue for nectar-feeding insects, especially nocturnal moths, however this relationship has not been thoroughly investigated in the context of climate change (Guerenstein and Hildebrand 2008). Pollinator populations and communities are often the targets of field studies due to the nature of sampling for most (insect) pollinators by trapping or capturing a large number of difficult-to-track specimens. As a result, few studies address measures of individual health or fitness in pollinators in the field (but see Crone et al. 2024), although many laboratory studies address this. We recommend that creative ways to measure the effects of climate change at the individual pollinator level (such as experimental microcosms, or trap nests which can be monitored) should be encouraged to better understand the mechanisms behind documented population and community changes, and to more effectively conserve pollinators. Future work should aim to fill in the knowledge gaps we have identified, as well as determine ways to protect pollinators from the adverse effects of climate change.

Objective 2: Grassland grazing effects on bee pollinators

We hypothesized that grazing would have a positive impact on bee abundance due to increased floral resources available in grazed plant communities. Our complex model was the best fit and found bee abundance was significantly explained by floral abundance but not through grazing per se. This indicates that while bee abundance varies by grazing treatment and region, the effect is primarily mediated through the availability of floral resources. Therefore, management that augments floral resources matter the most, suggesting that other management practices like prescribed fires, or restoration would benefit bees if they increase floral abundance. This result matches our findings on floral abundance, which was greatest in the west by 1.9 and 2.5 times compared to the central and eastern regions, respectively. The floral abundance was again greatest in western sites (when a single outlier was removed from the central region), with

grazed sites containing 1.4 times as many flowers as ungrazed sites. Additionally, this suggests that the effects of increased floral resources have a stronger positive effect on bees than direct effects of grazing.

Bee richness did not vary by grazing treatment or region, but was negatively associated with higher temperatures. We found that Kansas bee communities are often dominated by a few, highly abundant species with two genera, *Lasioglossum* and *Augochlorella*, making up 67.9% of all individuals. In the east, *Augochlorella aurata* and *Augochlorella persimilis* were by far the most abundant species, while several species of *Lasioglossum* contributed most of the bee abundance for many central and western sites. These most abundant species typically were found to be those contributing the most to dissimilarity between sites overall, which is an expected result from this analysis. The more interesting result comes from the multilevel pattern analysis which showed which species were significantly associated with specific region and grazing categories. In addition to the most abundant species, we also saw several bee species which were not highly abundant but were highly specialized to a given region such as *Perdita albipennis* in the west. Future work to understand how abundant and rare species contribute to pollination services would provide a detailed understanding of how to best conserve this critical ecosystem service in Kansas prairies.

Although the result that flowers are good for bees is not unexpected, this study does establish that this trend holds true in different prairie environments (and precipitation regimes). The fact that bee abundance was negatively related to temperature may be cause for concern that under climate change, Kansas bees will face declines. This result may be the result of decreased activity during hotter periods instead of actual population declines, but under a warming climate, these pauses in foraging will become more frequent with negative impacts on bees.

Conclusion

Altogether, our results show that temperature and precipitation have negative effects on bee communities. In our literature review, we have found that climate change most frequently has a negative effect on pollinators, measured by a variety of response variables which range from individual measures to population and community metrics. There are, however, significant gaps in our knowledge on this topic, and further research should focus on non-bee pollinators and in tropical regions and should prioritize a mechanistic understanding of the effects. Similarly, in our field study, we found that bee abundance and richness were lower at warmer and drier sites, indicating a warming climate and increased aridity are detrimental to Kansas bees. Furthermore, we found that management practices such as grazing could augment bee communities but only if they increase floral resources. Management practices such as fire, haying could offer similar benefits to bees in other grassland systems.

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Appendix A - Tables

Table 1. Pollinator response directions grouped by pollinator taxon. Note that some papers studied multiple pollinator groups without including all floral visitors so raw counts total to 335 instead of 319.

Pollinator response direction by taxon								
	All visitors	Bees	Wasps	Flies	Butterflies & Moths	Beetles	Birds	Bats
Positive	8	30	3	1	1	0	0	1
Negative	39	93	7	6	10	0	6	5
No effect	11	21	1	3	4	2	1	1
Mixed effect	20	40	3	2	3	0	3	0
Shift	3	6	0	1	0	0	0	0
Totals	81	190	14	13	18	2	10	7

Table 2. Pollinator response directions grouped by pollinator response variable measured. Note that some papers used multiple types of pollinator response variables so raw counts total to 391 instead of 319. Also note that some papers used multiple types of pollinator response variables so raw counts total above 319 and percentages can be above 100%.

Pollinator response direction by response variable							
	Abundance	Richness/ Diversity	Range/ Distribution	Phenology	Health	Floral Visitation	Totals
Positive	3	10	13	2	10	9	47
Negative	23	19	48	31	35	30	186
No effect	12	8	6	9	11	8	54
Mixed effect	15	15	11	9	21	20	91
Shift	1	1	4	3	2	2	13
Totals	54	53	82	54	79	69	391

Table 3. Bee Species List. List of bee species collected during the summer of 2023 grouped by family, then alphabetically. Morphospecies identifications are denoted by a number (i.e. *Melissodes sp.1*).

Andrenidae	Apidae	Colletidae	Halictidae	Megachilidae
<i>Andrena sp.1</i>	<i>Anthophora sp.1</i>	<i>Colletes sp.1</i>	<i>Agapostemon fasciatus</i>	<i>Anthidiellum notatum/boreale</i>
<i>Andrena sp.2</i>	<i>Anthophorula sp.1</i>	<i>Colletes sp.2</i>	<i>Agapostemon texanus/angelicus</i>	<i>Anthidium porterae</i>
<i>Calliopsis andreniformis</i>	<i>Apis mellifera</i>		<i>Agapostemon virescens</i>	<i>Ashmeadiella buconis</i>
<i>Perdita albipennis</i>	<i>Bombus auricomus</i>		<i>Agapostemon sp.1</i>	<i>Coelioxys bisoncornuus</i>
<i>Perdita ignota</i>	<i>Bombus fraternus</i>		<i>Augochlorella aurata</i>	<i>Heriades variolosa</i>
<i>Protandrena bandcrofti</i>	<i>Bombus griseocollis</i>		<i>Augochlorella persimilis</i>	<i>Hoplitis pilosifrons</i>
<i>Protandrena cockerelli</i>	<i>Bombus impatiens</i>		<i>Augochloropsis metallica</i>	<i>Lithurgopsis apicalis</i>
<i>Pseudopanurgus sp.1</i>	<i>Bombus pensylvanicus</i>		<i>Halictus ligatus</i>	<i>Megachile brevis</i>
	<i>Ceratina sp.1</i>		<i>Halictus parallelus</i>	<i>Megachile exilis</i>
	<i>Diadastia sp.1</i>		<i>Halictus rubicundus</i>	<i>Megachile fortis</i>
	<i>Diadastia sp.2</i>		<i>Lasiglossum albipenne</i>	<i>Megachile mendica</i>
	<i>Epeolus/Triepeolus sp.1</i>		<i>Lasiglossum callidum</i>	<i>Megachile montivaga</i>
	<i>Epeolus/Triepeolus sp.2</i>		<i>Lasiglossum cinctipes</i>	<i>Megachile parallela</i>
	<i>Melissodes sp.1</i>		<i>Lasiglossum coactus</i>	<i>Megachile rugifrons</i>
	<i>Melissodes sp.2</i>		<i>Lasiglossum disparile</i>	<i>Megachile sp.1</i>
	<i>Melissodes sp.3</i>		<i>Lasiglossum ellisiae</i>	<i>Osmia sp.1</i>
	<i>Melissodes sp.4</i>		<i>Lasiglossum hitchensi</i>	
	<i>Svastra obliqua</i>		<i>Lasiglossum hudsoniellum</i>	
	<i>Xenoglossodes albata</i>		<i>Lasiglossum imitatum</i>	
	<i>Xenoglossodes paenalbata</i>		<i>Lasiglossum oceanicum</i>	
	<i>Xeromelecta sp.1</i>		<i>Lasiglossum packeri</i>	
	<i>Xylocopa virginica</i>		<i>Lasiglossum pictum</i>	
			<i>Lasiglossum pilosum</i>	
			<i>Lasiglossum pruinosum</i>	
			<i>Lasiglossum semicaeruleum</i>	
			<i>Lasiglossum trigeminum</i>	
			<i>Lasiglossum versatum</i>	
			<i>Nomia sp.1</i>	
			<i>Sphecodes sp.1</i>	

Table 4. Simple (A) and complex (B) bee abundance ANOVA tables. Mean and standard errors of bee abundance by category (C). Tukey's HSD test significant results (D).

A Simple Bee Abundance Type II Anova results lm(Bee_abundance~Region+Grazing+Region:Grazing)			
	Region	Grazing	Region:Grazing
P	0.10251	0.04649	0.30481
F	2.5084	4.4069	1.2489
df	2	1	2
Sum of Squares	4701.7	4130.1	2340.9

B Complex Bee Abundance Type II Anova results lm(Bee_abundance~Region+Grazing+Region:Grazing+ Floral_abundance+Precipitation+Temperature)						
	Region	Grazing	Region:Grazing	Floral Abundance	Season Precipitation	Average Temperature
P	0.283886	0.200240	0.079108	0.001137	0.403992	0.026797
F	1.3378	1.7489	2.8697	14.1772	0.7254	5.6702
df	2	1	2	1	1	1
Sum of Squares	1485.5	971.0	3186.5	7871.1	402.7	3148.1

C Bee Abundance Mean (SE)			
	West	Central	East
Grazed	78.0 (19.4)	47.6 (17.3)	83.2 (10.8)
Ungrazed	30.4 (6.5)	41.8 (9.6)	66.2 (14.1)

D Tukey's HSD Test Significant Results					
Model	Pairwise	Difference	Lower	Upper	P-value
Simple	Grazed vs. Ungrazed	23.46667	0.3952734	46.53806	0.0464926
Complex	Grazed vs. Ungrazed	23.46667	5.573985	41.35935	0.0126165
Complex	Eastern vs. Central	30.0	3.439442	56.560558	0.0250920
Complex	Western Ungrazed vs. Eastern Grazed	-53.684507	-100.30622	-7.062799	0.0180816
Complex	Western Grazed vs. Western Ungrazed	-51.004284	-97.62599	-4.382576	0.0267896

Table 5. Simple (A) and complex (B) bee richness ANOVA tables. Means and standard errors of bee richness by category (C).

A Simple Bee Richness Type II Anova results lm(Bee_abundance~Region+Grazing+Region:Grazing)			
	Region	Grazing	Region:Grazing
P	0.2056	0.7416	0.1461
F	1.6909	0.1113	2.0866
df	2	1	2
Sum of Squares	36.467	1.200	45.000

B Complex Bee Richness Type II Anova results lm(Bee_abundance~Region+Grazing+Region:Grazing+ Floral_abundance+Precipitation+Temperature)						
	Region	Grazing	Region:Grazing	Floral Abundance	Season Precipitation	Average Temperature
P	0.01603	0.65209	0.41567	0.46140	0.08567	0.04733
F	5.0648	0.2092	0.9156	0.5630	3.2527	4.4387
df	2	1	2	1	1	1
Sum of Squares	98.098	2.026	17.734	5.452	31.500	42.985

C Bee Richness Means (SE)			
	West	Central	East
Grazed	12.4 (2.0)	13.6 (1.3)	15.2 (0.4)
Ungrazed	12.0 (1.3)	16.2 (2.1)	11.8 (1.2)

Table 6. Simple (A) and complex (B) community composition PERMANOVA tables. NMDS axes (C).

A Simple Bee Community PERMANOVA results adonis2(Bee_community~Region+Grazing+Region:Grazing)			
	Region	Grazing	Region:Grazing
P	0.0001	0.0926	0.2396
F	9.2088	1.6724	1.2031
R ²	0.39611	0.03597	0.05175
Sum of Squares	4.0296	0.3659	0.5264
DF	2	1	2

C NMDS			
	Floral Abundance	Season Precipitation	Average Temperature
NMDS1	0.44827	0.99989	0.73064
NMDS2	0.89390	0.01467	-0.68276
r ²	0.3825	0.3338	0.1557
P	0.002	0.008	0.100

B Complex Bee Richness Type II Anova results adonis2(Bee_community~Region+Grazing+Region:Grazing+ Floral_abundance+Precipitation+Temperature)						
	Region	Grazing	Region:Grazing	Floral Abundance	Season Precipitation	Average Temperature
P	0.0001	0.0719	0.1928	0.0241	0.0609	0.2890
F	10.0937	1.8331	1.2732	2.3362	1.9144	1.1469
R ²	0.39611	0.03597	0.04996	0.04584	0.03756	0.02250
Sum of Squares	4.0296	0.3659	0.5083	0.4663	0.3821	0.2289
DF	2	1	2	1	1	1

Table 7. Top five bee species contributing to site dissimilarity (A). Multilevel pattern analysis results (B).

A				B			
Similarity Percentage				Multilevel Pattern Analysis			
Species	Average Contribution to Dissimilarity	SD	Cumulative Sum	Group	Species	Indicator Value	P
<i>Lastoglossum semicaeruleum</i>	0.15312	0.17043	0.187	West	<i>Perdita albipennis</i>	0.937	0.005
<i>Augochlorella aurata</i>	0.14360	0.13540	0.363		<i>Agapostemon texanus/angelicus</i>	0.818	0.005
<i>Augochlorella persimilis</i>	0.07971	0.09447	0.460		<i>Melissodes.sp.3</i>	0.658	0.050
<i>Bombus pensylvanicus</i>	0.04068	0.10905	0.510	Central	<i>Nomia.sp.1</i>	0.754	0.005
<i>Megachile brevis</i>	0.02615	0.03870	0.542		<i>Lastoglossum disparile</i>	0.744	0.005
					<i>Xylocopa virginica</i>	0.957	0.005
				East	<i>Augochlorella aurata</i>	0.940	0.005
					<i>Augochlorella persimilis</i>	0.939	0.005
					<i>Augochloropsis metallica</i>	0.757	0.010
					<i>Colletes.sp.2</i>	0.707	0.010
					<i>Bombus auricomus</i>	0.632	0.010
				West and Central	<i>Lastoglossum.semicaeruleum</i>	0.922	0.005
					<i>Melissodes.sp.2</i>	0.806	0.005
				Central and East	<i>Lastoglossum callidum</i>	0.775	0.005
					<i>Lastoglossum trigeminum</i>	0.775	0.010
					<i>Bombus griseocollis</i>	0.742	0.015
				Grazed	<i>Halictus ligatus</i>	0.75	0.005

Table 8. Grouped bee abundance simple ANOVA results.

Simple Bee Group Abundance Type II Anova results lm(Bee_abundance~Region+Grazing+Region:Grazing)					
		P	F	df	Sum of Squares
Andrenidae	Region	0.02024	4.6082	2	75.267
	Grazing	0.61395	0.2612	1	2.133
	Region:Grazing	0.17661	1.8653	2	30.467
Eusocial Apidae	Region	0.4085	0.9294	2	194.87
	Grazing	0.3722	0.8270	1	86.70
	Region:Grazing	0.2851	1.3231	2	277.40
Carpenter	Region	8.205e-08	34.7385	2	75.267
	Grazing	0.4896	0.4923	1	0.533
	Region:Grazing	0.3994	0.9538	2	2.067
Longhorn	Region	0.0363	3.8194	2	152.27
	Grazing	0.2031	1.7124	1	34.13
	Region:Grazing	0.2365	1.5318	2	61.07
Other Apidae	Region	0.1610	1.9730	2	4.8667
	Grazing	0.1132	2.7027	1	3.3333
	Region:Grazing	0.7073	0.3514	2	0.8667
Colletidae	Region	0.05604	3.2571	2	3.8000
	Grazing	0.81310	0.0571	1	0.0333
	Region:Grazing	0.67471	0.4000	2	0.4667
Metallic Green	Region	7.705e-09	44.9227	2	15715.5
	Grazing	0.3785	0.8051	1	140.8
	Region:Grazing	0.8601	0.1517	2	53.1
Other Halictidae	Region	0.7623	0.2745	2	4.200
	Grazing	0.0990	2.9455	1	22.533
	Region:Grazing	0.3166	1.2070	2	18.467
Megachilidae	Region	0.3346	1.1462	2	25.867
	Grazing	0.7472	0.1064	1	1.200
	Region:Grazing	0.2880	1.3117	2	29.600

Table 9. Simple (A) and complex (B) floral abundance ANOVA tables. Means and standard errors of floral abundance by category (C). Tukey's HSD test significant results (D).

A Simple Floral Abundance Type II Anova results lm(Floral_abundance~Region+Grazing+Region:Grazing)			
	Region	Grazing	Region:Grazing
P	0.02675	0.12277	0.72661
F	4.2270	2.5587	0.3237
DF	2	1	2
Sum of Squares	184984	55987	14164

B Complex Floral Abundance Type II Anova results lm(Floral_abundance~Region+Grazing+Region:Grazing+Precipitation+Temperature)					
	Region	Grazing	Region:Grazing	Season Precipitation	Average Temperature
P	0.08338	0.15716	0.79928	0.97221	0.91122
F	2.7872	2.1452	0.2263	0.0012	0.0127
DF	2	1	2	1	1
Sum of Squares	132921	51151	10794	30	303

C Floral Abundance Mean (SE)			
	West	Central	East
Grazed	382.6 (59.1)	244.6 (100.2)	153.6 (36.8)
Ungrazed	267.8 (97.9)	125.2 (34.4)	128.6 (24.5)

D Tukey's HSD Test Significant Results					
Model	Pairwise	Difference	Lower	Upper	P-value
Simple	Western vs. Eastern	184.1	18.89695	349.303	0.0269155
Complex	Western vs. Eastern	184.1	10.62355	357.5765	0.0361772

Table 10. Simple (A) and complex (B) floral richness ANOVA tables. Means and standard errors of floral richness by category (C). Tukey's HSD test significant results (D).

A Simple Floral Richness Type II Anova results lm(Floral_abundance~Region+Grazing+Region:Grazing)			
	Region	Grazing	Region:Grazing
P	0.008365	0.465195	0.101612
F	5.8776	0.5508	2.5190
df	2	1	2
Sum of Squares	160.07	7.50	68.60

C Floral Richness Means (SE)			
	West	Central	East
Grazed	18.8 (2.2)	10.4 (1.7)	13.2 (0.9)
Ungrazed	13.6 (1.7)	10.8 (1.9)	15.0 (1.6)

B Complex Floral Richness Type II Anova results lm(Floral_abundance~Region+Grazing+Region:Grazing+ Precipitation+Temperature)					
	Region	Grazing	Region:Grazing	Season Precipitation	Average Temperature
P	0.01080	0.44031	0.26776	0.10598	0.03924
F	5.6025	0.6176	1.2928	2.8417	3.7651
df	2	1	1	1	2
Sum of Squares	146.689	8.086	16.925	37.202	98.581

D Tukey's HSD Test Significant Results					
Model	Pairwise	Difference	Lower	Upper	P-value
Simple	Western vs. Central	5.6	1.4788457	9.721154	0.0065275
Simple	Western Grazed vs. Central Grazed	8.4	1.184022	15.615978	0.0160055
Simple	Central Ungrazed vs. Western Grazed	-8.0	-15.21597	-0.784022	0.0237401
Complex	Western vs. Central	5.6	1.5352024	9.664798	0.0060455
Complex	Western Grazed vs. Central Grazed	8.4583324	1.329793	15.586871	0.0139744
Complex	Central Ungrazed vs. Western Grazed	-8.3318478	-15.460387	-1.203309	0.0158352

Table 11. Simple (A) and complex (B) floral community composition PERMANOVA tables.

A Simple Floral Community PERMANOVA results adonis2(Floral_community~Region+Grazing+Region:Grazing)					
	Region	Grazing	Region:Grazing		
P	0.0001	0.7421	0.2918		
F	3.4058	0.7635	1.1078		
R²	0.20158	0.02259	0.06557		
Sum of Squares	2.3924	0.2682	0.7782		
df	2	1	2		
B Complex Floral Richness Type II Anova results adonis2(Floral_community~Region+Grazing+Region:Grazing+ Floral_abundance+Precipitation+Temperature)					
	Region	Grazing	Region:Grazing	Season Precipitation	Average Temperature
P	0.0001	0.6554	0.1321	0.0010	0.4481
F	3.6627	0.8211	1.2836	2.6371	0.9891
R²	0.20158	0.02259	0.07064	0.07257	0.02722
Sum of Squares	2.3924	0.2682	0.8384	0.8612	0.3230
df	2	1	2	1	1

Table 12. Top five floral species contributing to site dissimilarity (A). Multilevel pattern analysis results (B).

A				B			
Similarity Percentage				Multilevel Pattern Analysis			
Species	Average Contribution to Dissimilarity	SD	Cumulative Sum	Group	Species	Indicator Value	P
<i>Pedimentum tenuiflorum</i>	0.14822	0.15808	0.166	West	<i>Helianthus annuus</i>	0.949	0.005
<i>Croton sp.</i>	0.07831	0.13929	0.254		<i>Croton sp.</i>	0.939	0.005
<i>Achillea millefolium</i>	0.07650	0.14497	0.339		<i>Euphorbia marginata</i>	0.920	0.005
<i>Convolvulus arvensis</i>	0.07633	0.20362	0.425		<i>Sphaeralcea coccinea</i>	0.894	0.005
<i>Helianthus annuus</i>	0.05006	0.10936	0.481		<i>Solanum rostratum</i>	0.794	0.005
					<i>Thelesperma megapotamicum</i>	0.766	0.005
					<i>Xanthisma spinulosum</i>	0.707	0.010
					<i>Oenothera suffrutescens</i>	0.699	0.015
					<i>Lygodesmia juncea</i>	0.632	0.035
					<i>Chaetopappa ericoides</i>	0.632	0.035
				Central	<i>Plantago patagonica</i>	0.632	0.030
					<i>Achillea millefolium</i>	0.752	0.015
					<i>Asclepias viridis</i>	0.837	0.005
				East	<i>Ruellia humilis</i>	0.837	0.005
					<i>Dalea purpurea</i>	0.775	0.005
					<i>Vernonia baldwinii</i>	0.750	0.005
					<i>Mimosa quadrivalvis</i>	0.744	0.005
					<i>Verbena stricta</i>	0.655	0.040
					<i>Linum sulcatum</i>	0.632	0.015
				West and Central	<i>Amorpha canescens</i>	0.632	0.030
					<i>Euphorbia davidii</i>	0.707	0.03
				Central and East	<i>Asclepias verticillata</i>	0.671	0.035

Table 13. GVIF $^{(1/(2*Df))}$ values for linear models.

GVIF $^{(1/(2*Df))}$ Values for all Models						
	Region	Grazing	Region:Grazing	Floral Abundance	Season Precipitation	Average Temperature
Bee (simple)	1.414214	1.732051	1.681793	NA	NA	NA
Bee (complex)	2.018273	1.926070	1.805549	1.219606	1.929487	1.305608
Floral (simple)	1.414214	1.732051	1.681793	NA	NA	NA
Floral (complex)	1.946770	1.869724	1.796378	NA	1.929433	1.305231

Appendix B - List of publications included in literature review

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