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ORIGINAL RESEARCH

Fire frequency and bison presence have direct and indirect effects on below- and above- ground nesting bee communities in tallgrass prairies

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Abstract

Tallgrass prairies are important habitat for bee pollinators because they provide diverse floral and nesting resources throughout the growing season. Management strategies such as fire and grazing can maintain plant diversity within prairies; however, it is unclear how pollinators, respond to these management practices, and whether all groups of pollinators are affected similarly. In a two-year study, we examined the direct and indirect effects of fire frequency and bison grazing on above-ground (AG) and below-ground (BG) nesting bees through changes in both their floral and nesting resources. We found that overall bee abundance was greater in bison grazed sites but the effect was stronger in the second year of the study. Furthermore, we found that overall bee richness was greater in the second year of the study and that fire and grazing interacted to affect bee community composition. Using structural equation models, we found the mechanisms by which fire and grazing affected bee communities varied by bee nesting strategies. For example, fire and grazing increased the amount of bare ground, which in turn increased BG nesting bee abundance. However, bison-mediated changes in soil compaction increased AG nesting bee abundance and richness. Both fire and grazing impacted forb communities but these changes in floral resources did not translate to changes in bee communities. Because disturbance mediated changes in soil structure influenced both AG and BG bees, our research highlights the need to consider how disturbances influence nesting resources for bee pollinator conservation and habitat restoration.

Keywords Native bees · Grasslands · Prescribed burns · Conservation · Restoration

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Introduction

Insect pollinator biodiversity is in decline due to habitat loss and fragmentation (Calderone 2012; Powney et al. 2019; Williams et al. 2010). Native tallgrass prairies have been a long target of conservation and restoration efforts in the Midwest USA due to 90% of tallgrass prairie land cover being converted to agricultural land over the last century (Kremen et al. 2002; Samson and Knopf 1994). Land management practices such as fire and grazing have been used to promote biodiversity, but fire and grazing regimes may not yield similar results for species at all trophic levels. For instance, past studies have shown that plant, bee, and butterfly communities respond differently, and at times, in conflicting ways to fire and grazing management strategies (Davis et al. 2008; Griffin et al. 2021; Kruess and Tscharntke 2002). Therefore, in order to effectively manage the tallgrass prairie ecosystem, further research is needed to understand the effects of land management on different taxonomic groups within the tallgrass prairie habitat.

Tallgrass prairie is a disturbance-dependent habitat and is maintained through a combination of fire and grazing to impede woody encroachment and maintain a high floral diversity (Hartnett et al. 1996; Knapp et al. 1999). However, results vary on how often and to what intensity these two practices should be executed. Some studies determined that frequent fires increase plant heterogeneity and diversity, and therefore should similarly benefit pollinator richness and abundance (Burkle et al. 2019; Carbone et al. 2019; Moylett et al. 2020; Simanonok and Burkle 2019). However, other studies show that different fire rotations have no effect (Carbone et al. 2019; Moranz et al. 2012), or that frequent burns have negative impacts on pollinators and floral resources (Collins and Calabrese 2012; Welti and Joern 2018). These conflicting results suggest that fire management strategies that benefit the native plant community may not necessarily scale up to benefit other trophic levels such as pollinators.

The impact of grazing on bees is also variable (Collins and Calabrese 2012; van Klink et al. 2015; Welti and Joern 2018). Grazing can increase the amount of bare soil exposure (Elwell et al. 2016; Kimoto et al. 2012; van Klink et al. 2015), which is known to benefit bee nesting (Buckles and Harmon-Threatt 2019; Potts et al. 2005). However, some studies have found negative or neutral grazing effects on pollinators and that pollinator species might respond differently to grazing (Buckles and Harmon-Threatt 2019; Elwell et al. 2016; Kimoto et al. 2012; Minckley 2014; van Klink et al. 2015). For example, Kimoto et al. (2012) found that bumble bees altered their foraging behavior and had an overall negative response to grazing intensity by horse, sheep, and cattle, but smaller sweat bees were not affected by grazing intensity. These different findings indicate that variability in bee life histories might influence how they respond to disturbances, as pollinators change their foraging behaviors to avoid disturbance and adjust to changes in floral and nesting resource availability (Buckles and Harmon-Threatt 2019; Burkle et al. 2019; Moylett et al. 2020). Previous studies have focused on the impact of disturbances on above-ground floral resources, but fewer studies have investigated the importance of nesting resources, particularly for ground-nesting bees, which make up the majority of native bees in North America (Bruninga-Socolar et al. 2022; Cane 1991; Harmon-Threatt 2020). Given the variability in bee responses to disturbance, a more in-depth approach to understanding how fire and grazing impact of bees is needed.

The objective of this study is to determine the direct and indirect effects of fire and bison grazing on pollinator communities within tallgrass prairie using structural equation modeling (SEM). Using a SEM approach, we hypothesized that frequent fires and grazing would have direct negative effects on bees through increased mortality (paths a and b, respectively, Fig. 1). We also hypothesized that fire frequency and bison grazing would have indirect effects on bees through changes in bare ground cover (Potts et al. 2005), soil compaction (Sardiñas and Kremen 2014), and forb communities (Hopwood 2008). In particular, we hypothesized that frequent fires would increase the amount of bare ground (path c), reduce soil compaction (path d) and decrease forb species richness (path e). In contrast, the presence of grazers would increase bare ground (path f) and soil compaction (path g) through the physical disturbance of wallowing and walking. Finally, we hypothesized increased bison effects on forb communities (path h) as bison preferentially feed on grass thus allowing forbs competitive release and opportunities to thrive and grow (Hartnett et al. 1996).

Fire- and bison-mediated changes in the prairie habitat could affect pollinator communities in a number of indirect ways by affecting bee foraging and nesting behaviors, however, the magnitude and directionality of the effects would vary depending on the pollinator species or functional group. For example, soil composition, especially the presence of sand, has been shown to play an important role in the nesting requirements of ground-nesting bees, where soil types must be dense enough to maintain the integrity of the nest, yet be soft enough to excavate (Cane 1991; Harmon-Threatt 2020; Potts and Willmer 1997). Therefore, we hypothesized that greater sand amount in the soil would positively affect ground nesting bee communities (path k), and that greater soil compaction would have negative effects (path j). We also hypothesized that for ground nesting bees, access to nests would be important for nest establishment therefore increased bare ground cover associated with fire and grazing would increase bee abundance and richness (path i). In contrast, we hypothesized that increased ground cover (or less bare ground) would favor above-ground nesting bees as litter layer and stems would provide important nesting material or refuges for above-ground bees (Bruninga-Socolar et al. 2022; Grundel et al. 2010). We also hypothesized that the availability of floral resources will also affect bee communities and therefore predict a positive association between forb and pollinator communities (path l). Forb communities, in turn, are affected by bare ground cover (path m), soil compaction

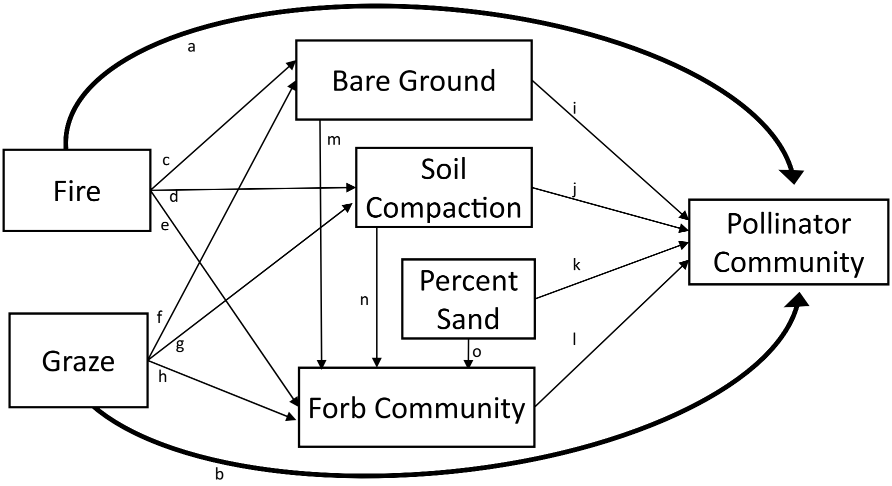

Fig. 1 Hypothesized mechanisms by which fire frequency and bison presence affect pollinator communities through their effects on the forb community (food resources) and soil characteristics (nesting resources)

(path n), and the amount of sand in the soil (path o). Because different members of the pollinator community may respond to land management strategies in varying ways (Bruninga-Socolar et al. 2022; Davis et al. 2008; Kruess and Tscharntke 2002), understanding mechanisms by which fire and grazing practices affect pollinators will allow land managers to better target conservation and restoration efforts to support both natural areas and pollinator communities.

Materials and methods

Study site

We conducted our experiment at the Konza Prairie Biological Station (hereafter "KPBS"), located within the Flint Hills region of northeastern Kansas, USA near Manhattan, KS (39°05'N, 96°35'W, Fig. 2). KPBS is a long-term ecological research site owned and operated jointly by Kansas State University and The Nature Conservancy since 1977 and the surrounding landscape consists mostly of natural tallgrass prairie with some mixed wood lots, sections of riparian forest along with a few small agricultural fields. The property is divided into 50 watersheds, each receiving a fire regime treatment (ranging in fire rotation intervals of once every 1 to 4 years or once every 20 years) and grazing treatment (bison grazed, cattle grazed, and ungrazed control).

During the two-year study (2019–2020), we utilized a 2 × 3 factorial design with two bison treatments (grazed versus ungrazed treatments, N = 6 watersheds/graze treatment) crossed with a fire rotation treatment (burned annually, once every four years, or once every twenty years, N = 4 watersheds/fire treatment). Pollinator, soil, and plant

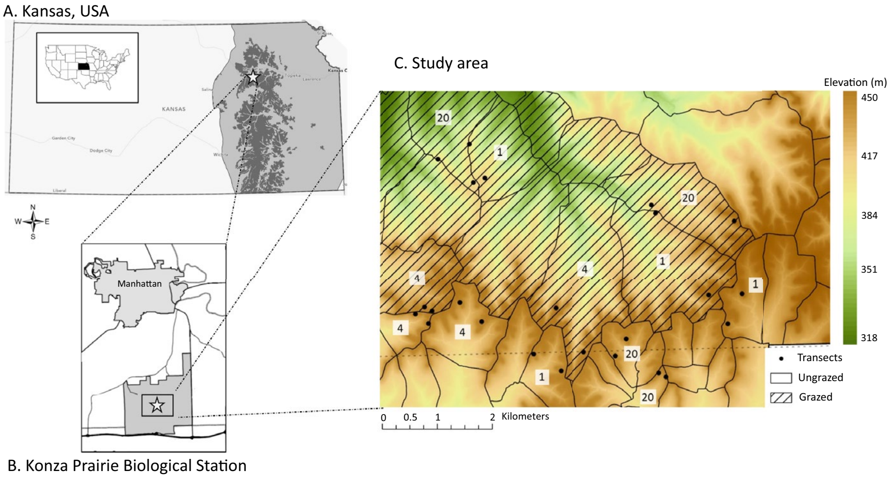

Fig. 2 Locations of transects within tallgrass prairies in Kansas. **A.** Light grey area is the historical range of tallgrass prairies and dark grey areas are the current distribution of tallgrass prairie. **B.** The Konza Prairie Biological Station is located south of Manhattan, KS. **C.** The study area is composed of grazed (hatches) and ungrazed (unhatched) watersheds that vary with fire rotation ("1", "4", "20" years between fire events). Transects for this study are shown as black dots within each watershed and were located in the upland portions of the experimental station

sampling was conducted along two permanent sampling transects located in each watershed, resulting in a total of 24 sampling locations. All transects were separated at least 270 m apart (min distance between transects = 270.1 m, max distance = 4027.8 m, median distance = 1970 m), which is larger than the foraging distances of most bees captured (Bennet et al. 2018; Wright et al. 2015). All transects were located on Florence soils located on hillslopes (uplands), are well drained, and deep.

Pollinator collection

During the summers of 2019 and 2020, we collected bees along 50 m × 5 m sampling transects using both hand collection and pan traps. Hand-collected specimens were captured during two 10-min observation periods at each transect (totaling 20 min/transect) using aerial nets (38 cm in diameter) and hand-held insect vacuums (Heavy Duty 18-V Hand-Held DC Vac/Aspirator built on Skil® hand-held vac platform from BioQuip©, Catalogue number: 2820GA). Bees were collected if they landed on flowers within the transect area. The captured specimens were placed in 100 mL plastic twist-cap sample vials (timer stopped during this time to account for handling time), placed on ice in the field, and then stored in a − 20 °C freezer until they were processed. We sampled bees over three sampling sessions (June, July, and August) and twice/sampling session (once at pan trap setup and once at pan-trap collection, see below for pan trap methods). This sampling design resulted in 120 h of timed observations per transect per year (10 min × 2 replicates/transect × 2 days/month × 3 months).

Two arrays of pan traps were set up at each transect, one at each end of the transect, resulting in 48 trap arrays. Each pan trap array consisted of one blue, one yellow, and one white 18 oz. Solo™ cup, cable-tied into a triad around a stake and placed at the height of the surrounding vegetation. Pan traps were set with soapy water during the time of hand-collections and were collected 48 h later. Collected specimens were drained and then stored in 75% ethanol until they were washed, dried, and pinned for identification. Pan traps were placed out over three sampling sessions (June, July, and August), before and after timed observations outlined above, resulting in 144 pan-trap hours (48 h/month × 3 months).

Most specimens were identified to the species level. Three specimens were identified to the subgenus level and therefore not included in species richness analyses. Additionally, females of the species *Heriades leavitti* and *Heriades variolosa* (Hymenoptera: Megachilidae) cannot be reliably distinguished, and therefore specimens of these two species were identified down to the two possible species names. We caught a total of four female bees that were either *Heriades leavitti* or *Heridaes variolosa*. For species richness calculations, we assumed that only one of these two species was present so that an underestimation of species richness was provided rather than an overestimation. The species *Hylaeus modestus* (Hymenoptera: Colletidae) was identified to species and not subspecies.

We utilized published and unpublished keys to identify bee species (Arduser unpublished data, Portman and Arduser unpublished data, Williams et al. 2014). Bee species were identified by JB and verified by Michael Arduser at Saint Louis University, St. Louis, MO., and *Agapostemon* (Hymenoptera: Halictidae) specimens were verified using specimens from the Museum of Entomological and Prairie Arthropod Research, at Kansas State in Manhattan, KS. Specimens are currently stored within the Kim Insect Ecology lab and the Museum of Entomological and Prairie Arthropod Research at Kansas State University.

Soil sampling and habitat measurements

At the end of the 2019 and 2020 growing seasons, we evaluated bee nesting habitat by measuring the percentage of bare ground, soil compaction, and soil composition within each transect. Soil samples for composition analysis were only collected in 2019, as composition is not likely to change between the two experimental years. Soil compaction and bare ground were measured in both 2019 and 2020 because of yearly variation in both these ground/soil characteristics. All soil measurements and collections were replicated in three locations along the length of each transect. Bare ground was estimated by randomly placing a 1-m^2 quadrat at three points along our pollinator transects and we visually estimated the percentage of bare ground within the quadrat (estimated to the nearest 5%).

Immediately after the amount of bare ground was estimated within a quadrat, soil compaction was measured by taking three readings within each quadrat placement using a penetrometer (FieldScout SC 900 Soil Compaction Meter, Item 6110 FS, from Spectrum Technologies, Inc), measured in pounds per square inch (PSI). Three soil samples were then collected per quadrat using a soil core (2.5 cm in diameter and 30 cm in depth), and then combined and dried in a 60 °C oven for seven days. The soil composition was measured in the lab using the hydrometer method (Bouyoucos 1962; Robertson et al. 1999), to calculate the percentage of sand, silt, and clay within each soil sample. However, percent sand was used in the statistical analyses, as this soil property is most likely to influence bee nesting (Harmon-Threatt 2020; Potts and Willmer 1997).

Plant community data

We utilized long-term plant species data collected annually by KPBS (Hartnett et al. 2021). These data were collected along our same sampling transects in 2019 and 2020 (see Collins 1992) for more details on plant collection methods). In short, plant species richness was estimated every year within five 10 m^2 sampling plots established along each of the transects. The percent cover of each species within each plot was recorded. We extracted forb data from these datasets to characterize floral resources and converted the cover measurements into presence/absence data. We then summed the total occurrence of each species as forb species richness for each of our sampling transects.

Statistical analysis

Our unit of analysis was at the transect level so we combined bee data collected from pan traps and by hand collections at each transect across the three sampling sessions per year. For ease of interpretation, we converted fire rotation (number of years between fire events) to fire frequency (number of fires per year). Because the watersheds were added to the long-term experimental setup in different years (initial prescribed fires starting from 1972 to 1999), we selected a standardized time interval of fires from 1999 to 2019 (20-year period) for the fire frequency calculations. Therefore, one-, four-, and 20-year fire rotations resulted in fire frequencies that were low (0.04–0.06 fires/year), medium (0.24–0.3 fires/year), and high (1–1.05 fires/year), respectively. Both wildfires and prescribed fires were included in the fire frequency calculations. To examine the overall effects of fire and bison grazing on bees, we conducted a linear mixed model

(LMM) with bison grazing (presence/absence), fire frequencies, year (2019/2020) and their interactions as predictor variables, watershed as a random effect, and total bee abundance (log-transformed) and rarified bee richness as response variables. To examine how bee community composition changed with fire and grazing, we performed a PERMANOVA (Bray–Curtis dissimilarity index) with grazing treatment, fire frequency, and year as fixed effects and watershed as a random effect in our model. PERMANOVA were conducted in R v4.4.3, utilizing the vegan package (Oksanen et al. 2022). We tested for spatial autocorrelation using a Moran's I (Moran 1950) for AG and BG abundance and richness (distance method = Euclidean) using the spdep package (Bivand and Wong 2018) in R v.4.4.3. We found no significant spatial autocorrelation from the minimum distance 270 m to 3000 m (Table S5).

To understand the causal effects of fire and bison grazing on soil and habitat characteristics, and how these factors influence bee communities, we utilized piecewise structural equation modelling (SEM). First, we divided the captured pollinator specimens into three main groups (1) all bees combined, (2) aboveground nesters (AG) and (3) and belowground (BG) nesters using the nesting traits assigned to each species (Spiesman et al. 2019; Williams et al. 2010) and we ran separate SEMs for each group. Because soil conditions (compaction and bare ground cover) and floral richness was highly correlated across the two sampling years ($r = 0.74$, 0.64, and 0.89, respectively), we averaged habitat characteristics and bee response variables from both sampling years to yield one value per transect (our unit of analysis). For each bee group tested, we constructed a separate SEM and input all measured predictors (soil compaction, bare ground, percent sand, forb species richness, forb cover, fire frequency, and presence or absence of bison grazing) along with the bee abundance and richness data as response variables (all bees together, AG nesters only, and BG nesters only). We included watershed as a random effect in our SEM and each response and predictor variable relationship was tested for nonlinearity. We then utilized a backwards stepwise model selection approach to find the best fit model by removing non-significant relationships until the lowest Akaike's information criterion (AIC) and a p-value > 0.05 for each linear model was achieved (Shipley 2013). The interaction between bison presence and fire frequency was tested at the beginning of model building and its inclusion in the initial model did not improve model fit (compared to a model without an interaction, $\Delta\text{AIC} = 14.82$). SEMs were conducted in R v4.4.3, utilizing the piecewiseSEM package (Lefcheck 2016).

Results

Over the course of our 2-year study, we observed a total of 2115 bee individuals belonging to 57 species. Among these captured specimens, 171 bee specimens belonging to species with above-ground nesting behavior were captured, and 1944 below-ground nesting bee specimens were captured.

Overall bison presence and fire effects on bee groups

Results from the LMM indicated that bee abundance was affected by grazing and fire frequency through an interaction with year (Fig. 3, Table S2). In particular, grazing had a positive effect on bee abundance (50% increase compared to ungrazed transects) but only in the second year of the study (2020, graze × year interaction, $t = 2.043$. $P = 0.05$, Fig. 3a),

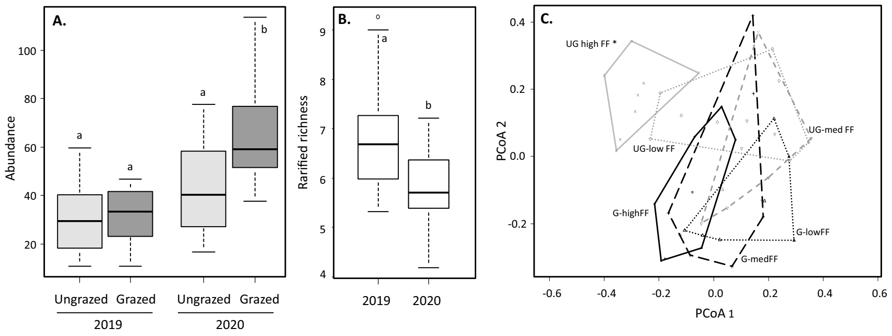

Fig. 3 The effects of bison presence, fire frequency (FF), and year on **A** bee abundance, **B** rarified species richness, and **C** and community composition. *UG* ungrazed treatments; *G* grazed treatments, *low FF* infrequent fires (every 20 years), *med FF* moderate fires (every 4 years), *high FF* annual fires. In **A** and **B**, boxplots with different letters indicate significant treatment differences. In **C**, asterisk indicate significant differences from other treatments

and fire frequency had no effect on bee abundance (t =1.290, P= 0.20). Rarefied species richness varied by year (t =− 2.030, P= 0.050) where there were more bee species in the second year of the study compared to the first year (Fig. 3b). However, rarified species richness was not affected by the graze treatment (t =− 0.229, P= 0.820) or by fire frequency (t =0.727, P= 0.472, Table S2). We found a significant interaction between fire frequency and grazing on bee community composition where bees in ungrazed watersheds with high fire frequencies had dissimilar community composition compared to the other watersheds (F =1.61, df =2,36, P= 0.049, Fig. 3c). In particular, *Lasioglossum* and *Melissodes* were more abundant in high fire frequency watersheds compared to low and medium fire frequency watersheds and the effect was greater in ungrazed watersheds (*Lasioglossum* 3.2–8.8 times greater; *Melissodes* 1.9–6.8 times greater).

SEM: direct and indirect effects of fire and grazing on the overall bee community

To understand the mechanisms by which fire and bison grazing impacted pollinator communities, we utilized an SEM framework. Our best-fit model (Fisher's C= 58.77, P= 0.06, DF =44, Fig. 4) shows that grazing had no direct effects on overall bee richness or on overall bee abundance (paths removed from model selection process). Likewise, fire had no direct impact on bee abundance or richness (paths removed from model selection process). Instead, we found that fire and grazing indirectly affected bee communities through their effects on bare ground cover and soil compaction.

We found significant relationships between fire, grazing, and habitat characteristics (Fig. 4). As the fire frequency increased, the amount of bare ground significantly increased (β_c= 0.47, P= 0.05). Grazing had a similar relationship where grazing increased bare ground (β_f= 0.50, P= 0.04) but grazing also increased soil compaction (β_g= 0.58, P= 0.01). While the LMM results show that grazing and fire can influence forb cover and richness (Table S3), their effects were mediated through changes in the habitat characteristics. In particular, disturbance mediated changes in bare ground and soil compaction had negative effects on forb richness (β_m= − 0.23, P= 0.03) and forb cover (β_n= − 0.58, P= 0.003), respectively. Forb richness was positively affected by the amount of sand (β_o=

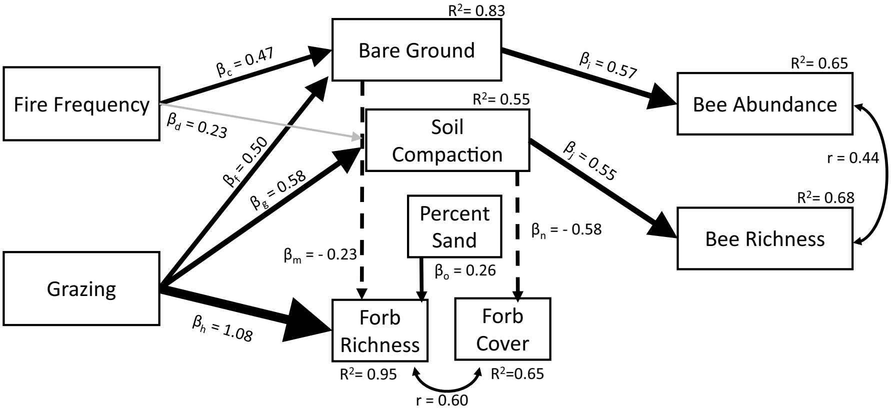

Fig. 4 Structural equation model results showing the direct and indirect effects of bison grazing and fire effects on overall bee abundance and rarified species richness. Solid arrows indicate positive relationships while dashed arrows indicate negative relationships. Grey arrows indicate non-significant relationships but relationships retained in the final model. Arrow width corresponds to the strength of the effect, where thicker arrows indicate stronger effects. Single headed arrows represent causal relationships where βs represent path coefficients. Double headed arrows represent correlations

0.26, P= 0.001), and positively affected by grazing where grazed sites had 26.8 more plant species compared to ungrazed sites (β_h= 1.08, $P < 0.001$).

Bison and fire-mediated changes in bare ground cover and soil compaction positively affected bee abundance (β_i= 0.57, P= 0.007) and bee richness (β_j= 0.55, P= 0.006), respectively, but none of the other bison and fire mediated changes in plant characteristics influenced overall bee abundance and bee species richness. We observed positive correlations between bee abundance and richness (Pearson correlation, r= 0.44, P= 0.01), and forb cover and richness (Pearson correlation, r= 0.60, P= 0.001).

Differential responses of bee nesting traits to fire and grazing

We found that fire- and bison mediated changes in soil and plant characteristics differentially affected above-ground (AG) and belowground (BG) bee communities (Fig. 5a. AG: Fisher's C= 44.40, P= 0.37, DF =42 Fig. 5b. BG: Fisher's C= 45.95, P= 0.31, DF =42). While the vast majority of collected specimens were BG species (91.8% which is in line with previous studies (Harmon-Threatt 2020)), their abundance and richness responses differed from the overall bee abundance and richness results above. In particular, BG abundance was positively affected by bare ground (β_{i-ab}= 0.61, P= 0.004, Fig. 5b). In contrast, changes in soil compaction had positive effects on AG species richness (β_{j-ab}= 0.51, P= 0.02, Fig. 5a) and abundance ($\beta_{i\text{-rich}}$= 0.42, P= 0.05, Fig. 5a).

Discussion

We hypothesized that fire and bison grazing would have direct effects on bee communities and indirect effects mediated through their impact on pollinator nesting and floral resources (soil and plant community characteristics, respectively). While previous work has focused

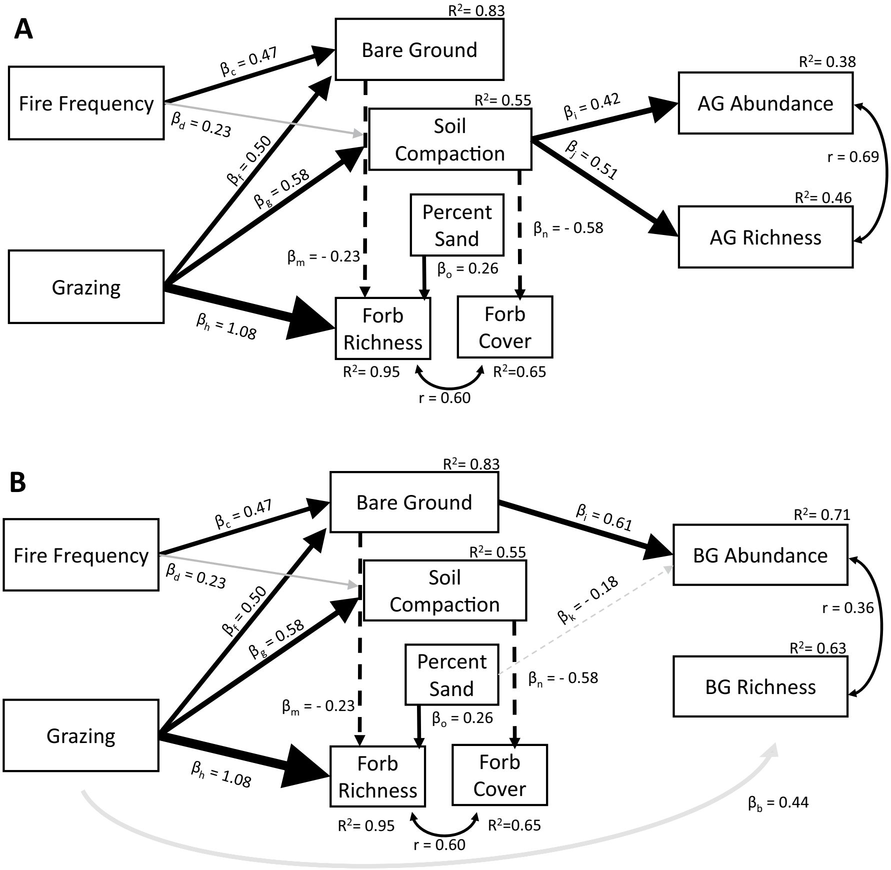

Fig. 5 Structural equation model results showing the direct and indirect effects of bison grazing and fire rotation interval on **A.** above-ground (AG) and **B.** below-ground (BG) nesting bee abundance and rarified species richness. Solid arrows indicate positive relationships while dashed arrows indicate negative relationships. Grey arrows indicate non-significant relationships but relationships retained in the final model. Arrow width corresponds to the strength of the effect, where thicker arrows indicate stronger effects. βs represent path coefficients. Single headed arrows represent causal relationships where βs represent path coefficients. Double headed arrows represent correlations

on disturbance effects on floral resources, our study shows that fire and grazing can affect nesting resources, which in turn have impacts on bee communities. Specifically, we found that frequent fires had overall positive effects on total bee abundance (total effect =0.27, Table S4) and bison presence had overall positive effects on both total bee abundance (total effect =0.29) and total bee richness (total effect =0.32, Table S4). The effects of fire and grazing also varied by year and interacted to affect bee community composition (Table S2). In particular, small sweat bees (*Lasioglossum*) and long-horned bees (*Melissodes*) were more common in frequently burned sites, especially sites that were ungrazed. For all bees, disturbance-mediated changes to the nesting habitat affected bee abundance and richness, and our results support previous work that suggest restoration practices should focus on augmenting nesting resources, not just floral resources (Bruninga-Socolar et al. 2022; Harmon-Threatt 2020). However, the mechanism by which bees responded to nesting resources varied by nesting group: BG nesters responded to bare ground cover while AG nesters responded to soil compaction. Because different land management strategies aimed at augmenting plant diversity (e.g., prescribed fire, bison and cattle grazing, mechanical or chemical control to reduce woody and invasive plants, seeding native plants) can have different effects on nesting habitat characteristics, these strategies can have different outcomes for bee communities. Therefore, if bee conservation is a management goal, then management strategies aimed at increasing bare ground cover should be targeted to augment BG nesters (the most common nesting group) while management practices that increase soil compaction should be considered for AG bees.

Effects of fire and grazing on plant, soil, and ground characteristics

We found that ground habitat characteristics were affected by both fire frequency and grazing disturbances. Sites experiencing frequent fires had barer ground as biomass loss through fires increased bare ground exposure (Moranz et al. 2012). Bison presence also increased the amount of bare ground and soil compaction through repeated visits to preferred areas throughout the year (Trager et al. 2004; Vinton et al. 1993) leading to higher levels of soil compaction or hardening (Knapp et al. 1999). Forb communities were directly and indirectly affected by disturbance type. In particular, in the presence of bison, we found a two-fold increase in forb species richness compared to ungrazed areas (Table S3). These results differ from other studies that show high intensity grazing can reduce forb species richness and overall plant performance (Hickman and Hartnett 2002; Kimoto et al. 2012). These differences can be explained by the types of grazers in our research sites where bison preferentially graze on the dominant C4 grasses over forbs unlike other ungulates such as horses, sheep, and cattle (Collins and Calabrese 2012; O'Keefe and Nippert 2017). Frequent fires affected plant cover but only through its interaction with bison grazing. Specifically, forb cover was about 2.5-fold greater in areas with infrequent fires but only in ungrazed areas (Table S3). These results suggest multiple disturbance types can have non-additive effects on plant communities.

Disturbance mediated changes in habitat characteristics on bee communities

Fire- and bison-mediated changes to nesting resources affected both BG and AG bees; however, AG and BG bees were affected by different habitat characteristics. In particular, BG abundance was affected by changes to bare ground cover which aligns with previous studies that document the importance of nesting resources for BG communities (Harmon-Threatt 2020; Potts et al. 2005; Sardiñas and Kremen 2014). Increased bare ground cover allows for warmer nest temperatures (through access to direct sunlight) and makes nest entrances easier for bees to locate (Potts et al. 2005; Sardiñas and Kremen 2014). Therefore, access to the soil through bare ground cover is an important feature for BG abundance in the tallgrass habitat.

In contrast to BG bees, we found that AG abundance and richness were only affected by soil compaction. We are uncertain about the mechanisms by which compact soils might directly benefit AG bees therefore our results may be due to unmeasured indirect effects. For example, if changes in plant quality occur with increased soil compaction, then AG nesting bees such as mason and leaf cutter bees that prefer to nest in dead wood and stems may benefit from sites with compact soils, if soil compaction increases plant mortality (Hamza and Anderson 2005; Kozlowski 1999). Furthermore, because AG bees compete with BG bees for food resources, the reduction in BG bees in areas with high compact soils may release AG bees from foraging competition thus allowing for them to increase (Wignall et al. 2020; Wojcik et al. 2018). Next, it is possible that compact soils may have more abandoned small mammal burrows which in turn may allow cavity nesting bee species (e.g., *Bombus* spp.) to utilize these burrows as their own nests (Lanterman et al. 2019; Potts et al. 2005). Finally, while the distances between our sampling transects showed no spatial autocorrelation, bees may have moved between transects and outside the study area, and therefore may not nest in the area captured. However, foraging distances are associated with body size and sociality (Kendall et al. 2022) and the only bees that could move greater distances are AG bees which were a small portion of the bees sampled (honey bees 0.09%, bumble bees 4.6%, and carpenter bees 1.8%). Regardless, further research on how disturbances affect nesting preferences of AG bees are needed, especially for bees with long foraging distances.

Variability in pollinator responses to disturbances

Overall, we found that fire and grazing have significant indirect effects on the pollinator community through their impacts on nesting resources. In particular, bee abundance and richness were affected by changes in soil properties such as bare ground cover and soil compaction, despite disturbance-mediated changes in floral resources. These findings indicate that more studies need to examine the impact of fire and grazing on soil properties, and not just floral resources. Furthermore, the impact of fire and grazing affected AG and BG nesting bee groups differently suggesting that the effectiveness of land management strategies can vary with bee functional groups. While our study is focused on tallgrass prairies, other managed systems such as sagebrush rangelands, and pine savannas have also found increased bee diversity following fire and with grazing (Goosey et al. 2024; Mason et al. 2021; Ulyshen et al. 2023). Greater bare ground cover and reduced litter cover are often associated with areas following disturbances, which can have varying effects on AG and BG bees: greater bare ground cover can increase access to nests for BG bees while reduced litter layer can decrease nesting material for AG bees. Because access to both food and nesting resources are important for central place foragers such as bees, more studies that examine the causal mechanisms of land management strategies on AG and BG bees are needed to better inform land managers and mitigate global bee decline.

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Data availability Data will be available for private download through the Dryad reviewer URL upon acceptance of the manuscript.

Declarations

Conflict of interest We declare no conflict of interest.

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