What's the buzz?: a dual-scale assessment of Kansas bumble bee species to inform future conservation efforts

by

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Abstract

The decline of bumble bee (genus *Bombus*) populations across North America, attributed to factors such as habitat loss/ fragmentation, increasing use of pesticides, and climate change, poses significant concerns for both natural ecosystems and agricultural productivity. Two bumble bee species found in the Great Plains are imperiled, which necessitates further research exploring where they are located, how their habitats differ from species that are stable, and what land management techniques can be implemented to benefit the bumble bee community as a whole. In this thesis, I used experimental and modeling methodologies to assess how Kansas bumble bee species are affected by environmental factors on two different scales. On a local scale (Chapter 1), I take an experimental approach by conducting a two-year field study to investigate the direct and indirect effects of bison (*Bison bison*) grazing and fire frequency (common grassland management strategies) on bumble bee abundance, community composition, and plant interactions. I found that the presence of bison indirectly increases total bumble bee abundance by means of increasing floral resource availability; there were interactive effects with fire frequency. Community composition did not differ significantly between grazing treatments; however, there were differences in host-plant interactions among bumble bee species. On a state-wide scale (Chapter 2), I use species distribution models to understand differences in habitat selection and spatial distributions between common and threatened species in Kansas. While most findings were species-specific and not characteristic of "common" or "threatened" groups as a whole, one species of least-concern deviated the most in terms of habitat associations. In general, all species were negatively associated with monoculture crop coverage. Climate factors appeared to be less important drivers of distribution than landscape factors. Model-predicted maps created from each species' most significant set of predictor variables display hotspots

where individuals are most likely to be detected across Kansas. Such maps are crucial for designating priority areas for threatened species protection. Overall, this research provides valuable insights into the ways in which grassland management, land cover, and climate factors affect bumble bee species for the purposes of assisting with targeted conservation efforts across Kansas and the entire Great Plains.

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Introduction

Bumble bees (Hymenoptera: Apidae: *Bombus* Latreille, 1802) are economically and ecologically important insects. Their economic importance comes from the wide range of crops that they pollinate, including tomato, pepper, apple, pumpkin, etc. (De Luca et al. 2013). They are able to increase the quality of such crops due to their ability to buzz-pollinate, a behavior not displayed in commercial honey bees, in which they vibrate their body to release tightly packed pollen grains (Cooley & Vallejo-Marin 2021). They are important to the ecosystem because they help maintain plant diversity and niche behaviors as relative generalists in grassland systems (Brosi & Briggs 2013; Russell et al. 2017).

Unfortunately, some bumble bee species are experiencing patterns of large-scale decline across North America and other parts of the world (Goulson et al. 2008; Cameron et al. 2011). Potential drivers of decline have been attributed to factors such as habitat loss and pesticide exposure due to urbanization and agricultural expansion (Kremen et al. 2007; Lark et al. 2015; Nunes et al. 2024). Climate change can also be damaging in the long term. Extreme temperatures and variable precipitation can affect the bumble bee's ability to acclimate and forage on their preferred host-plants during particular times in the season in certain areas (Pyke et al. 2016; Ojima et al. 2021; Bretzlaff et al. 2023). Finally, land use change including grassland management can shape the entire ecosystem (Raynor et al. 2016; Smith et al. 2016; Rosenberger & Conforti 2022). Bison-grazing and prescribed fire are common strategies used to manage aboveground biomass within tallgrass prairies in the Great Plains region, though it is unknown how they directly, indirectly, and interactively affect Kansas bumble bee communities (Gaskin et al. 2021).

Two out of the six bumble bee species typically found in Kansas are at-risk: the Southern-Plains Bumble Bee (*B. fraternus*), and the American Bumble Bee (*Bombus pensylvanicus*). Due to trends of decline across parts of their ranges, the United States Fish and Wildlife Service has decided that further action is needed to protect both species while they determine whether these species should be listed under the protection of the Endangered Species Act of 1973 (USFWS 2021; USFWS 2024). Proposed actions outlined in their reports include determining primary causes of decline, identifying priority areas, defining critical habitat, and tracking shifts in geographic range to develop protection plans and inform future policy. Though these *Bombus* spp. have been detected across much of the United States, Kansas falls within the western part of most of their ranges. Further research is particularly necessary in Kansas, as it was declared an understudied part of their ranges in a IUCN Red List assessment (Hatfield et al. 2014); therefore, that is the focal area of my current studies.

The overarching questions of my graduate research focused on the first three calls to action within the context of Kansas and the Great Plains region. On two separate scales, I explored: where declining bumble bee species are located and how their habitats (landscape context and climate factors) differ from stable species sharing a range, as well as how land management techniques can be implemented to benefit bumble bee communities as a whole. More specifically, in this thesis I addressed the following two main objectives: (1) On a local scale, assess the effects of grassland management strategies (bison-grazing and prescribed fire frequency) on the abundance, community composition, and host-plant preferences of Kansas bumble bee species using data from an experimental field study, and (2) on a state-wide scale, determine how environmental factors affect bumble bee species distributions in Kansas and compare habitat associations between species of varying conservation concern using a species

distribution modeling approach. Altogether, these results should have implications in the entire Great Plains regions that can be extrapolated to other parts of North America by providing science-based recommendations for midwestern bumble bee protection through the use of appropriate land management strategies, landscape preservation/ restoration characteristics based on each species' habitat associations, and distribution information useful for targeted conservation efforts.

Chapter 1 - Local grassland management strategies affect Great Plains bumble bee (*Bombus* spp.) abundance, community composition, and host-plant preference

Introduction

Bumble bees are in decline worldwide (Cameron et al. 2011; Goulson et al. 2015), which is detrimental because they provide important ecological and economical services through their ability to buzz-pollinate flowering plants (Cooley & Vallejo-Marin 2021). With a decline in those imperiled species, not only may bumble bee community composition shift in areas that are shared by multiple species, but it might also have confounding effects on overall plant fitness (Brosi & Briggs 2013). Bumble bees are considered relative generalists, meaning that they will visit a wide range of flower taxa compared to other pollinating groups, though some do have specific host-plant preferences (Russell et al. 2017). Changes in bumble bee community may arise due to alterations in the flowering plant community where they forage. This can be influenced by the tactics that are used to manage a grassland (Smith et al. 2016; Carvell 2022). Two common types of grassland management strategies used in the Great Plains region to control invasive grasses/ shrubs and open space for native forbs include prescribed fire and grazing (Gaskin et al. 2021). Because grasslands are often a high-quality foraging habitat for bumble bees, it's important to understand how different strategies may affect not only the abundance and species of bumble bees utilizing the area, but also their food resources.

Ungulates alter soil nutrients, bare ground cover, and plant communities due to their varying grazing habits (Kimoto et al. 2012). The effects of typical livestock (e.g., cattle, sheep, yak) grazing effects are studied world-wide and covered extensively in the literature. Effects of

livestock grazing on plant and bumble bee communities typically depends on stocking rates, with higher densities leading to a loss of floral resources as well as bumble bee abundance and diversity (Hatfield & LeBruhn 2007; Xie et al. 2008; Kimoto et al. 2012; Davidson et al. 2020; Carvell 2022). In contrast, effects of grazing by native or re-introduced American bison herds (*Bison bison*) on bumble bee communities in the United States is understudied.

American bison are considered "ecosystem engineers" (Geremia et al. 2019) that play a "keystone role" (Knapp et al. 1999) in North American grasslands based on the way they currently and historically have shaped ecosystem functions. These large ruminants were once widespread across the Great Plains before being hunted nearly to extinction (Potter et al. 2010). They have since increased in numbers across their range, including in areas of Yellowstone National Park, where their grazing intensity has been found to decrease grass height and provide consistently high quality forage (Geremia et al. 2019). Though Kauffman et al. (2023) cautions that vegetation composition can be damaged if bison densities reach past the recommended utilization threshold. In general, bison grazing in tallgrass and shortgrass prairies reduces the dominant grasses and increases plant diversity, including species that are resilient to drought (Towne et al. 2005; Ratajczak et al. 2022; Rebh & Welti 2025). While there is much evidence supporting the significant role bison play in altering aboveground productivity, there are research gaps when it comes to the investigation of effects of bison grazing on native pollinators. Rosenberg & Conforti (2020) discovered a general trend demonstrating lower abundance of bumble bees in agricultural midwestern bison-grazed pastures than ungrazed prairie patches, though results varied heavily by species. In contrast, Butters et al. (2025) documented an increase in overall bee abundance in bison-grazed plots compared to ungrazed plots in Kansas,

accrediting changes in floral resource availability, soil composition, and potential interactions with prescribed fire management tactics.

Prescribed fire is another grassland management technique, often used to control senescent vegetation and woody encroachment (Gaskin et al. 2021). While grazing decreases grass biomass, fire tends to open the prairie by removing old growth and woody vegetation, aiding in the process of nutrient cycling, and plant regeneration (Ojima et al. 1994). Controlled burns in midwestern tallgrass prairies have resulted in higher plant richness and diversity attributed to a decrease in woody vegetation and increased nitrogen fixation (Bowles & Jones 2013). Contrary to the findings of Shafer et al. (2025) that prescribed fire is beneficial for plant species often visited by bumble bees, several studies record a lack of significant direct effect of prescribed fire on bee abundance and community composition (Smith et al. 2016; Tai et al. 2022; Butters et al. 2025).

Fire and grazing can be used independently or as combined management strategies. Prescribed fire may be implemented alone to control woody encroachment and maintain new growth in the prairie (Ojima et al. 1994; Bowles & Jones 2013), or in conjunction with grazing as a means of increasing quality forage for livestock and other herbivores (Raynor et al. 2016). Knowing how fire and grazing affect bumble bees directly, indirectly, and through interactions is important and understudied in the Great Plains region.

The state of Kansas is located within the central portion of the Great Plains, where the aforementioned grassland management strategies are common. Six bumble bee species have ranges that include Kansas: *Bombus impatiens*, *Bombus auricomus*, *Bombus bimaculatus*, *Bombus griseocollis*, *Bombus fraternus*, and *Bombus pensylvanicus* (Williams et al. 2014). These species will henceforth be used interchangeably with their species codes “BIMP”, “BAUR”,

"BBIM", "BGRIS", "BFRAT", and "BPEN", respectively. The latter two species are imperiled and under consideration by the U.S. Fish and Wildlife Service to be protected under the Endangered Species Act of 1973 (USFWS 2021; USFWS 2024). With two imperiled species utilizing managed grasslands in the state, it's important to understand their response to prairie management and disturbance as individual species and a whole community so that property managers are well-informed. If one of those species becomes federally protected, land owners may need to consider changing the way they manage their property for conservation of the species.

I seek to further understand how Great Plains bumble bee abundance, community composition, and visitations to host-plant species, are affected by the individual and interactive effects of prescribed fire and bison-grazing regimes on a local scale. In this study, I describe a field study conducted at an experimental research station in Kansas, USA, aimed at understanding the effects of grassland management strategies on bumble bee and plant communities in tallgrass prairie systems. Through the use of both bee and plant data analyzed using piecewise structural equation models (SEMs) and other approaches, I tease apart the direct and indirect effects of bison grazing and prescribed fire on bumble bee assemblages. Based on the previous research findings outlined above, I make the following general hypotheses: (1) grazing and prescribed fire frequency will have direct and indirect effects on both the floral community and total bumble bee abundance; (2) prescribed fire and grazing will have interactive effects; and (3) bumble bee community composition and host-plant visitations will differ between grazing treatment groups due to species-specific preferences for available forb taxa.

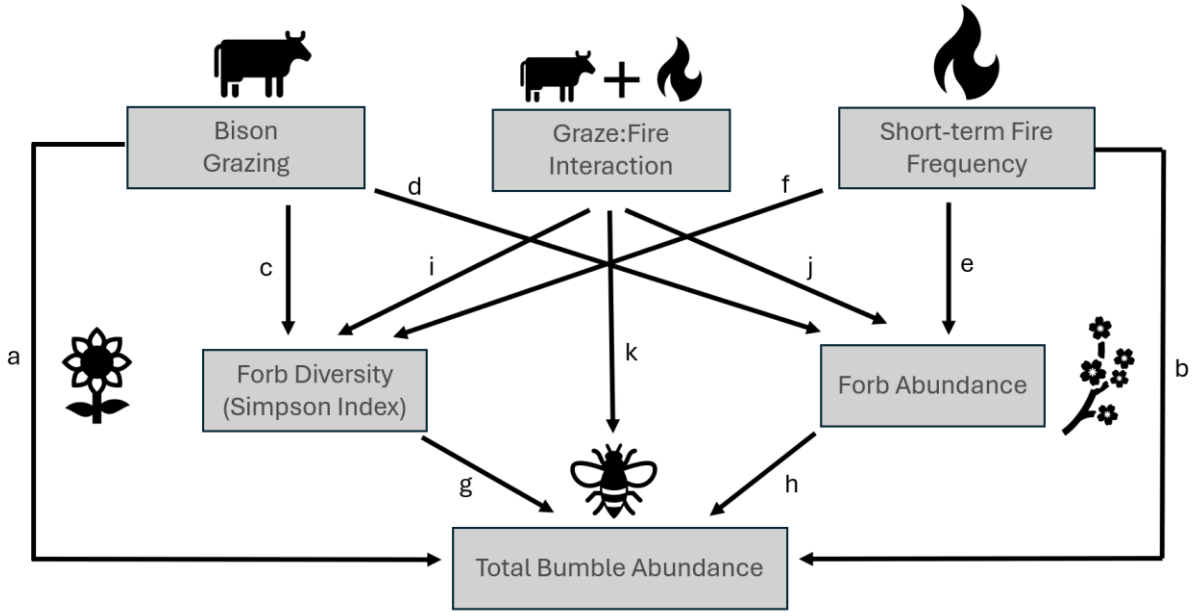

Figure 1.1. Path diagram of the hypothesized links (a-k) between variables included in the initial piecewise structural equation models.

Specifically regarding the possible direct and indirect influences examined using piecewise SEMs, I hypothesize that bison-grazing will positively affect both forb diversity (Figure 1.1d) and forb abundance (Figure 1.1c) based on previous research findings that bison presence is linked to increased plant diversity through preferential feeding on dominant grasses. Additionally, I suspect that greater fire frequency will directly increase both floral community variables (Figure 1.1e and Figure 1.1f , respectively) due to removal of old vegetation growth and promote new, higher quality aboveground biomass in response to prescribed fire. Similarly, I expect the combination of fire and grazing to positively impact forb abundance (Figure 1.1j) and diversity (Figure 1.1i) by effectively removing both dominant grasses *and* wood vegetation. Greater forb diversity and abundance will likely increase total bumble bee abundance (Figure 1.1g and Figure 1.1h, respectively) by providing them with more foraging opportunities near their nesting sites. As such, I expect that both grassland management strategies will have an

indirect, positive effect on total bumble bee abundance by improving floral resource availability. Bison grazing and fire frequency could also have direct effects on total bumble bee abundance (Figure 1.1a and Figure 1.1b, respectively). Trampling by bison may cause direct mortality to belowground nesters; however, rainwater accumulated in wallows created by the large ruminants may have a positive effect by providing the pollinators with a consistent water source for drinking. Prescribed fire in the early spring may directly affect bumble bee abundance by opening up the prairie and making it easier for bumble bee queens to locate abandoned rodent burrows where they can establish their nests for the season. Finally, a direct effect of combining grazing and fire treatments on bumble bee abundance could arise due to the amalgamation of both previously stated consequences when they are used separately (Figure 1.1k). With all of those hypotheses in mind, I hope to uncover bumble bee-friendly land management practices that can be utilized by managers of tallgrass prairies in the Great Plains.

Methods

Study Area

Location

The study took place at the Konza Prairie Biological Station, a long-term ecological research (LTER) station located in the Flint Hills region, which is roughly 18-km south of the Kansas State University campus in Manhattan, KS (Figure 1.2). Covering just under 3,500-ha, this research area established in 1971 includes tallgrass prairie that is separated into watershed treatments that receive varying levels of disturbance by way of prescribed fire and grazing regimes (Knapp et al. 1999).

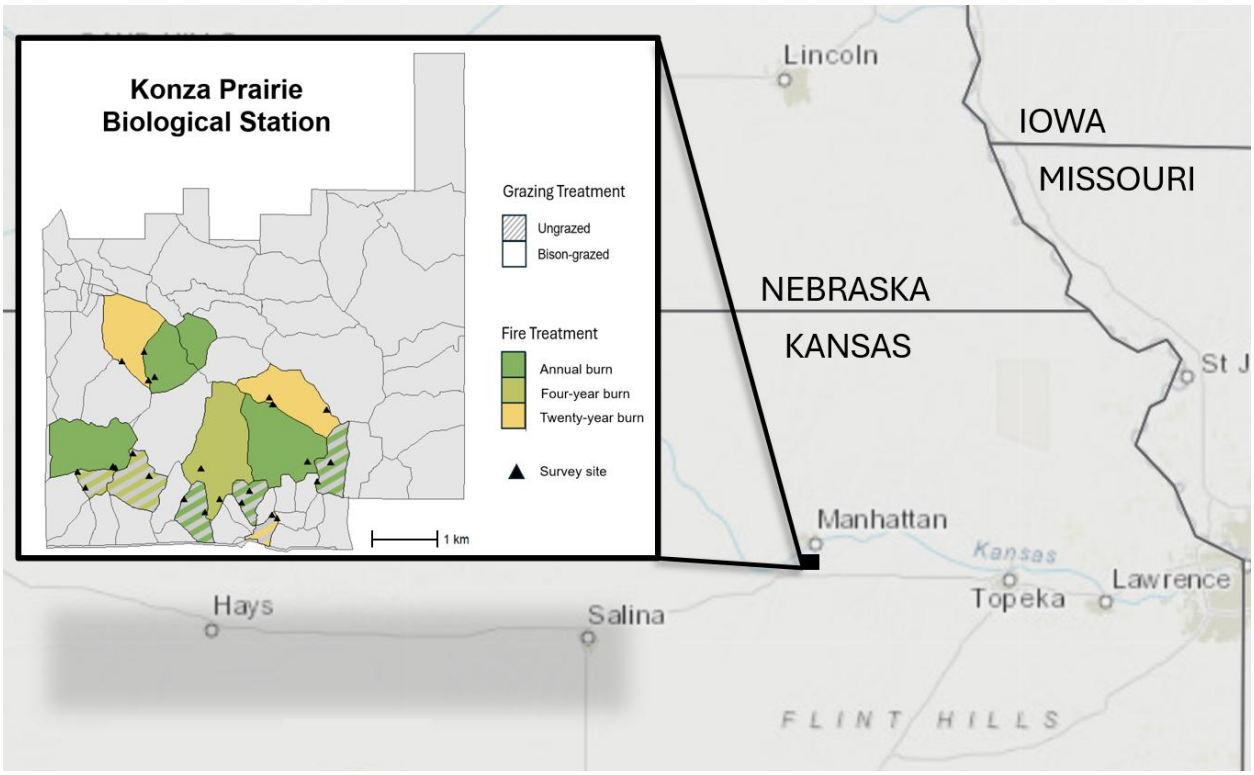

Figure 1.2. Konza Prairie Biological Station LTER watershed experimental design with survey site locations.

Grazers are contained by fences along the border of the watersheds in the same treatment group. Re-introduced bison are present year-round in a roughly 607-ha pasture with minimal human disruption in order to simulate the life of a natural herd in the wild (Konza Environmental Education Program n.d.). Pre-roundup in 2023, there were 212 females and 76 males in the Konza bison herd, while numbers decreased to 171 and 48, respectively, post-cull at the end of the year (Bison Inventory 2023). Herd numbers are monitored to promote a standard grazing rate of roughly ~25% biomass removal per year (Knapp et al. 1999); however, an exact intensity was not guaranteed. Prescribed burns take place in the fall, winter, and spring according to the schedule assigned to each watershed's designated fire treatment; however, most watersheds selected for this study experienced burns only in the spring season.

Site Selection

This study included a total of 24 sites within 12 watersheds experiencing a combination of prescribed fire and grazing treatments. There were two watersheds, each containing two transects, that fell within all possible grazing and fire treatment combinations. Sites were managed by either bison-grazing (n = 12) or the absence of grazing (n=12). Similarly, sites were designated as experiencing prescribed burn rotations every year (n = 8), every 3-4 years (n = 8), or every 20 years (n = 8). Due to inconsistency in the burn schedule in recent years, I converted fire rotation to long-term fire frequency (burns per year over a 20-year period) and short-term fire frequency (burns per year over the past five years). This variable conversion was important because some watersheds that were claimed to experience prescribed burns every twenty years were actually burned nearly every year in the previous five years leading up to the study. I compared model results using both fire frequency variations separately in case recent changes in burn schedule affected bumble bees differently than the long-term disturbance patterns. Each watershed included two 50-m by 30-m rectangular plots with a 50-meter transect through the center. Example images of grazed, ungrazed, burned, and unburned watersheds at Konza can be found in the Appendix (Figures A.1.-A.3.).

Data Collection

All transects were sampled once during the second or third week of each month, between June and September, in 2023 and 2024. With a few exceptions, sampling was conducted over 3-5 consecutive days to minimize effects of changing plant phenology. Surveys included a bee observation period followed by a vegetation assessment. I identified bumble bees to species based on criteria outlined in the Bumble Bees of North American book published by Williams et

al. (2014). I utilized an online Kansas Wildflower & Grasses guide (Haddock 2025) to record plants to species level, if possible. Bees were collected non-lethally using an aerial net.

Sampling Criteria

I only sampled on days when weather conditions were ideal for bumble bee activity to increase detection probability. At each site before a survey, I collected weather data to assess whether or not the survey would proceed. Temperature and wind were measured using a Kestrel 3000 Pocket Weather Meter and the current readings from a weather station closest to the site (Weather Channel 2024). The survey would proceed only if the following criteria were met: (a) temperature greater than or equal to 70 degrees Fahrenheit (20.1 degrees Celsius) and less than 95 degrees Fahrenheit (35 degrees Celsius), (b) average wind speed less than 15 miles per hour (24.1 km per hour), (c) complete absence of precipitation, and (d) ideally cloud clover less than 100%. Sampling was conducted between 7 am and 3 pm, as bee activity tended to decline later in the afternoon.

Bee Survey

I walked along each side of the transect for a total of 20-person-minutes during the observation period. Bumble bees were collected with an aerial net when they were observed visiting a flowering plant. Each individual was identified to species from a 4K-resolution cell phone video recorded of the specimen contained in a clear vial after it was captured. I also recorded the flowering plant that it was observed visiting, identified to genus or species-level. Bees were kept in the vial for up to five minutes and released during the survey in a direction away from the transect to minimize recapture.

Vegetation Survey

During both years of data collection, I measured flowering plant species richness by wandering through the entire rectangular plot and recording each forb species in bloom within the plot at the time of the survey. In 2024, I also conducted a more detailed grid-style vegetation survey that included recording relative abundance within a 2-m belt transect along the center of the plot. Plants were identified to genus or species level, if possible. See the appendix for a diagram showing the plot design (Appendix Figure A.1.).

Data Analysis

Complex Regression Models

I fit linear mixed-effects regression models to understand the effects of grazing treatment (grazed vs ungrazed), fire frequency (short-term and long-term, independently), and the interaction between the two variables on relative bumble bee abundance (i.e., total number of bumble bees captured at each site summed across the entire season). Year was also fixed effect, to identify whether bumble bee abundance differed during the two separate years. Watershed was included as a random effect variable to account for repeated surveys within watersheds and potential spatial autocorrelation with an underlying environmental gradient. I used the 'glmer' function available in the 'lme4' package (Douglas et al. 2015) in the R Programming Environment (R Core Team 2023). I compared the Akaike Information Criterion (AIC) score of models using short-term and long-term fire frequency to determine which fire treatment term resulted in the best relative model performance.

To understand potential direct and indirect effects (mediated by floral resource availability) of fire and grazing on relative bumble bee abundance, I fit piecewise structural equation models (SEMs) using the 'PiecewiseSEM' package in R (Lefcheck 2016). Piecewise

structural equation models allow the incorporation of multiple predictor variables with multiple response variables to understand the direct and indirect effects between links in a dynamic pathway (Lefcheck 2016). As displayed in the piecewise SEM path diagram above (Figure 1.1), my initial model included links between relative bumble bee abundance, floral abundance, floral diversity, grazing treatment (binary categorical), fire frequency (continuous), and the interaction between fire and grazing treatments. All individual models included site and watershed as random effects to account for repeated sampling efforts. Because floral abundance was only recorded in the second sampling year, that single year of data was used in the path analysis – year was thus not included in the models. Variables were removed based on backward variable selection using the 'stepAIC' function available in the 'car' package, until a best-fit model with the lowest AIC score was achieved.

Multivariate Community Analysis

I conducted a Permutation Analysis of Variance (PERMANOVA) to test my hypotheses regarding effects of grazing and fire rotation on bumble bee community composition. In the model, the response variable was the site-by-species matrix with Bray-Curtis dissimilarity values calculated from square root-transformed abundance counts for the five bumble bee species detected across both years. Predictor variables included grazing treatment as a factor (e.g., grazed or ungrazed), fire frequency (i.e., number of burns per year), and an interaction term between grazing and fire treatment. Year was also added as another constrained variable since the dataset included resampling across two years. PERMANOVA computes an F-statistic and a probability of significance value (analogous to a p-value) from a large number of permutations that reflects whether each factor in the model is significantly more likely to affect a change in community composition than random chance (Anderson 2001). The term-specific F-statistics

based on sum of squares values, as well as the corresponding probability of significance derived from that statistic, were used to evaluate how grazing and prescribed fire treatment influence the bumble bee community at the sampled sites. A biplot from a constrained distance-based redundancy analysis, using the same model formula as above, created a visual representation of site separation by treatment group and displayed the species driving such patterns. I also assessed the analysis of variance for terms and axes resulting from the ordination, and evaluated the proportion of variation explained by the constrained variables. The 'capscale' function was used for that analysis, which is available in the 'vegan' package (Oksanen et al. 2024).

Interaction Networks

I constructed a bipartite graph to visualize host-plant interactions between bumble bee species using the 'plotweb' function available in the 'bipartite' package in R (Dormann et al. 2008). Data were formatted as a plant-genus by bee-species matrix, showing each individual interaction between detected bees and plant genus they were foraging on at the time of capture. The process was completed for all interactions detected across the two-year study regardless of watershed treatment, as well as two bipartite networks showing differences in interactions between the grazed and ungrazed plots. I calculated species-level specialization values (d') to determine the degree of specialized interactions for each species in the main network. Additionally, I calculated network-level specialization values (H') in both networks derived from the grazed and ungrazed treatment groups to quantify the overall degree of specialized interactions within the communities. Significance was determined by comparing the calculated specialization value to ones derived by 999 randomly generated networks (a null model). This process informs us if the networks/ species interactions observed are truly specialized, or if the patterns arose due to random chance (Bluthgen et al. 2006). Specialization values between

communities in both treatment groups can be directly and statistically compared by calculating derived z-scores, if there is enough repetition. Both measures of specialization in a plant-pollinator context are outlined in the foundational literature by Bluthgen et al. (2006). More recent research provides support that community responses to changing land-use can be explored through the use of interaction network metrics (Weiner et al. 2014).

Results

During the two-year study, I detected 107 bumble bees across all watersheds experiencing different combinations of fire and grazing treatments (Table 1.1). Species included *B. pensylvanicus* (n = 32), *B. fraternus* (n = 20), *B. griseocollis* (n = 18), *B. impatiens* (n = 21), and *B. auricomus* (n= 16). While the two-spotted bumble bee, *B. bimaculatus*, has been found in eastern Kansas, it was not identified during any of the surveys conducted within the study area.

Table 1.1. Summary table displaying total count of each bumble bee species detected in all grazing and fire treatment combinations summed across both years, where fire frequency is represented by the number of burns per year over the past five years (i.e., short-term fire frequency).

Grazing Treatment	Fire Frequency	*Bombus auricomus*	*Bombus fraternus*	*Bombus griseocollis*	*Bombus impatiens*	*Bombus pensylvanicus*
Bison	0.167	4	3	2	5	11
Bison	0.333	2	2	0	2	2
Bison	0.500	5	2	3	4	1
Bison	0.667	0	1	1	0	1
Bison	1.000	4	5	2	8	8
Ungrazed	0.167	0	1	0	1	3
Ungrazed	0.333	0	1	3	1	3
Ungrazed	0.500	0	0	0	0	0
Ungrazed	1.000	1	5	7	0	3

Bumble bee occurrences varied throughout the season. Most *B. griseocollis* and *B. auricomus* were caught in July, *B. fraternus* and *B. pensylvanicus* peaked in both July and September, and *B. impatiens* was almost exclusively found during the September surveys. Overall detection for all species was relatively low in June and August. More details on variation in bumble bee collection by month and year can be found in the Appendix (Figure A.5.). Most bumble bees were detected while foraging on flowers; however, there were a few instances in which they were caught while flying. Those individuals were included in all analyses except the interaction network evaluation.

Grazing and Fire Effects on Bumble Bee Abundance

Both fire frequency variables could not be included in the same regression model due to a high variance inflation factor score (VIF > 10), which is an indicator that the two variables are highly correlated. The VIF score was less than seven for all variables in models that kept the fire frequency periods separate. After comparing AIC scores among models including the two different fire frequency variables, the one incorporating short-term fire frequency calculated over a five-year period had a slightly higher overall AIC score than when long-term fire frequency was calculated over a 20-year period; however, the ΔAIC value was less than 2, indicating that the models should not be interpreted as meaningfully different (Arnold 2010). Because one model was not more competitive than the other, I selected the one using short-term fire frequency based on biological relevance. Given the more dramatic change in recent burn history than over the past two decades, short-term fire frequency may more accurately reflect the current level of disturbance. Additionally, the distribution of records was more even across the short-term fire frequency variable than its long-term counterpart, allowing for less bias towards sites

experiencing one level than another. More details on summary statistics resulting from the alternative model can be found in the Appendix (Table A.1.).

Table 1.2. Summary statistics table from the complex linear mixed effects model incorporating burns per year over a 5-year period (i.e., short-term) as the fire frequency term.

Variable	Estimate	Std. Error	Z value	Pr (>|z|)	
(Intercept)	-305.846	362.494	-0.844	0.3988	
Graze treatment	1.513	0.353	4.287	<0.0001	***
Fire frequency	0.822	0.393	2.091	0.0365	*
Graze:Fire Interaction	-1.250	0.514	-2.433	0.0150	*
Year	0.151	0.179	0.844	0.3988	

From the selected model (Table 1.2), there was no significant difference in bumble bee abundance between the surveys in 2023 and 2024. The interaction of fire and grazing treatment was significant, suggesting that the addition of bison-grazing and a more frequent burning schedule results in fewer total bumble bees than in ungrazed sites that are burned less frequently. The model results identified a positive effect of both bison-grazing and increased fire frequency on overall bumble bee abundance; however, due to the significance of the interaction term, the main effects of both treatments separately may not be valid. The main effect of grazing treatment indicates that the total number of bumble bees detected across a given year was larger in watersheds that were managed with bison-grazing compared to no grazing (Figure 1.3A). The main effect of fire frequency suggests that watersheds that experienced a higher short-term fire frequency (i.e. more burns per year in the past five years) were associated with larger counts of observed bumble bees.

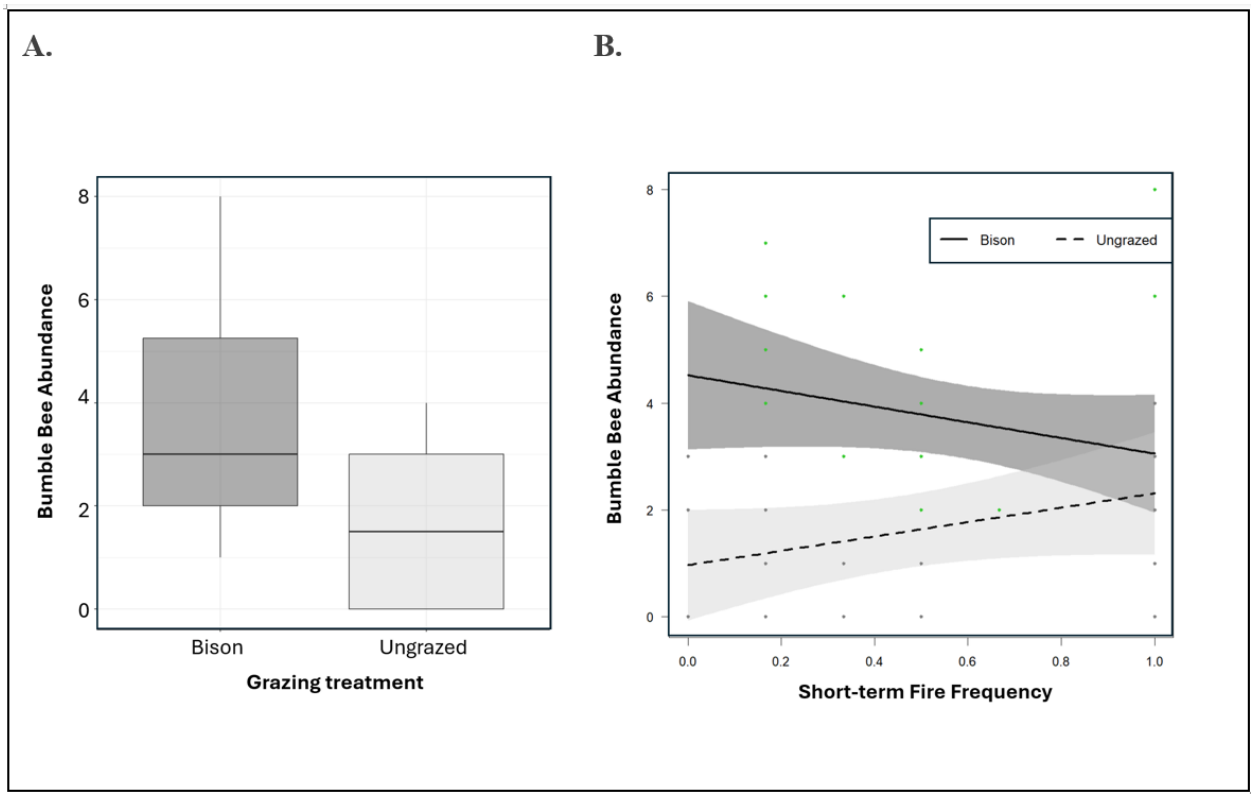

Figure 1.3. Graphs displaying the fixed effect results (after accounting for the random effect) in the best-fit linear mixed effects model. [A] Boxplot of grazing treatment group response on total bumble bee abundance, regardless of fire frequency, [B] Residual plot showing response of bumble bee abundance as short-term fire frequency changes in both grazed and ungrazed watersheds.

In Figure 1.3B, total bumble bee abundance in sites experiencing different fire frequencies was clearly tied to the grazing treatment that the watershed was also experiencing. In grassland patches that experienced nearly no prescribed fire in the past five years, bumble bee abundance was greatest when bison were present and lowest when they were not. The presence of bison drastically increased bumble bee abundance in areas with low fire frequency. With the exception of a few outliers, grazing tended to have a stronger influence on bumble bee abundance when fire frequency was low. While the effects of fire frequency were dependent on the combined grazing tactic, the presence of bison does appear to support consistently high

bumble bee counts, as evidenced by the difference in median values displayed in Figure 1.3A and the bars representing grazed sites located above the other treatment group in Figure 1.3B.

The path diagram in Figure 1.4 is based on the initial piecewise structural equation model that included all potential response and predictor variables that I hypothesized may play a role in moderating bumble bee abundance. This initial model resulted in only two significant links: a strong positive effect of bison-grazing on both forb abundance and forb diversity. The table displaying summary statistics for all variables in the initial model can be found in the Appendix (Table A.2.).

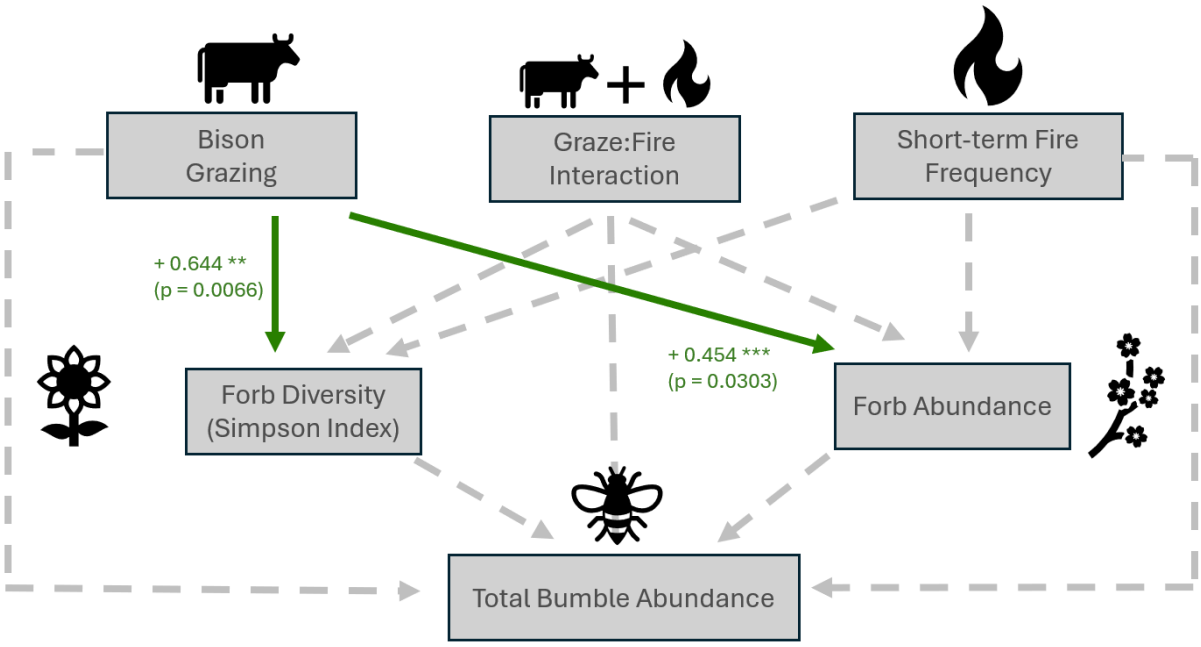

Figure 1.4. Path diagram resulting from the initial piecewise structural equation models where solid green lines represent statistical significance (p-value < 0.05) and non-significant links are shown as dashed grey lines.

In the initial model, the presence of bison grazing did significantly increase forb diversity and abundance. All other links between variables in the model lacked significance. It's possible

that the level of significance between links was dampened by too many variables in the piecewise structural equation models; therefore, I used backwards elimination to select the best-fit model.

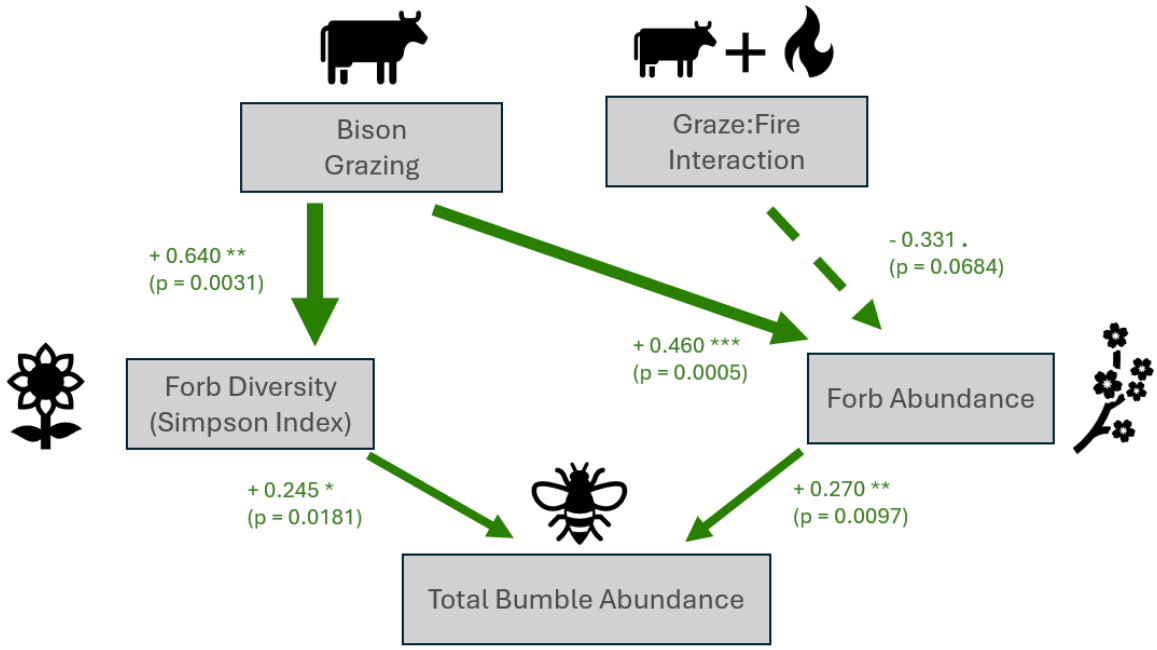

Figure 1.5. Path diagram resulting from the best-fit piecewise structural equation models where solid green lines represent statistical significance (p-value < 0.05), dashed green lines represent moderate significance (p-value = 0.05-0.1), and the thickness of arrows represents relative strength of effect.

The best-fit model (ΔAIC = 2.98) still shows positive relationships between the presence of bison grazing on forb abundance and diversity; however, after removing the insignificant links in the initial model, there is now a statistically-significant positive influence of both floral resource availability metrics on total bumble bee abundance (Table 1.3; Figure 1.5). Bison-grazing strongly increased forb diversity and forb abundance, which in turn increased bumble bee abundance, providing evidence that the presence of bison in the sampled tallgrass prairie

plots indirectly affected the total number of bumble bees found there. There was a significant negative effect of the combined use of increased fire frequency and bison-grazing on forb abundance, which also tied into the indirect effect on bumble bee abundance. Both direct links from the three grassland management variables to bumble bee abundance were not significant and thus removed in the final diagram. Similarly, the effect of fire frequency on the two floral community variables, as well as the interaction term's connection to forb diversity, were removed due to a lack of significance.

Table 1.3. Summary statistics table from the final piecewise structural equation models.

Response	Predictor	Estimate	Std. Error	Df	Crit. Value	Std. Estimate	P-value	
Bumble bee abundance	Forb abundance	0.0058	0.0021	72	7.0599	0.2698	0.0097	**
Bumble bee abundance	Forb diversity	1.1830	0.4700	78	5.8319	0.2445	0.0181	*
Forb abundance	Bison-grazing	47.4792	9.4535	10	25.2243	0.4600	0.0005	***
Forb diversity	Bison-grazing	0.2919	0.0730	9	15.9864	0.6398	0.0031	**
Forb diversity	Interaction	-0.2000	0.0966	9	4.2851	-0.3312	0.0684	.

Community Composition

Most sites included the detection of 1-5 bumble bees across a single year, most of which were from the same species. After removing sites with no bumble bee detection, 38 sites remained that were factored into the analysis. The results of the permutational ANOVA (Table 1.4) show that grazing treatment had a marginally-significant effect on Bray-Curtis dissimilarity in bumble bee community composition. Fire frequency, alone, and its interaction with grazing treatment, were not significantly more likely to affect bumble bee composition than random chance, and thus not found to have a significant effect on the species data. Year had the most significant effect, indicating that community composition changed between the surveys conducted in 2023 and 2024.

Table 1.4. Permutational Analysis of Variance summary statistics from a constrained distance-based redundancy analysis on Bray-Curtis distances for assemblages of bumble bees visiting grassland patches across two consecutive years at the sites experiencing different fire frequency and grazing treatments.

Variable	Df	Sum of Sqs	F	Pr (>F)	
Graze treatment	1	0.667	2.038	0.0870	.
Fire frequency	1	0.614	1.877	0.1090	
Year	1	1.051	3.213	0.0130	*
Graze:Fire Interaction	1	0.369	1.129	0.3300	
Residual	33	10.793			

There is some overlap between the standard error surrounding the mean centroid of grazed and ungrazed sites in ordination space, though visual group separation is apparent (Figure 1.6). Year and grazing treatment were the strongest drivers of bumble bee assemblage, with BIMP, BPEN, and BAUR most associated with those factors. In other words, those bumble bee species were most often found in communities at sites that experienced bison grazing, particularly in the second year of the study. In contrast, BGRIS was most strongly associated with increasing fire frequency and the absence of grazing, while BFRAT occurrence in the community depended on both fire frequency and bison-grazing.

After partitioning square Bray-Curtis distances as a result of the distance-based redundancy analysis, a total of 18.9 % of variation in bumble bee composition among sites was explained by the constrained variables included in the model. The other 81.1% of variation may be explained by environmental, spatial, or temporal variables other than grazing treatment, fire rotation, the interaction between grazing and prescribed fire, and year. Axis 1 and Axis 2 explained 49.0 % and 32.7% of variation, respectively; however, a permutational test assessing

the axes' contributions using 999 permutations failed to show any axes with a significance level less than alpha 0.05.

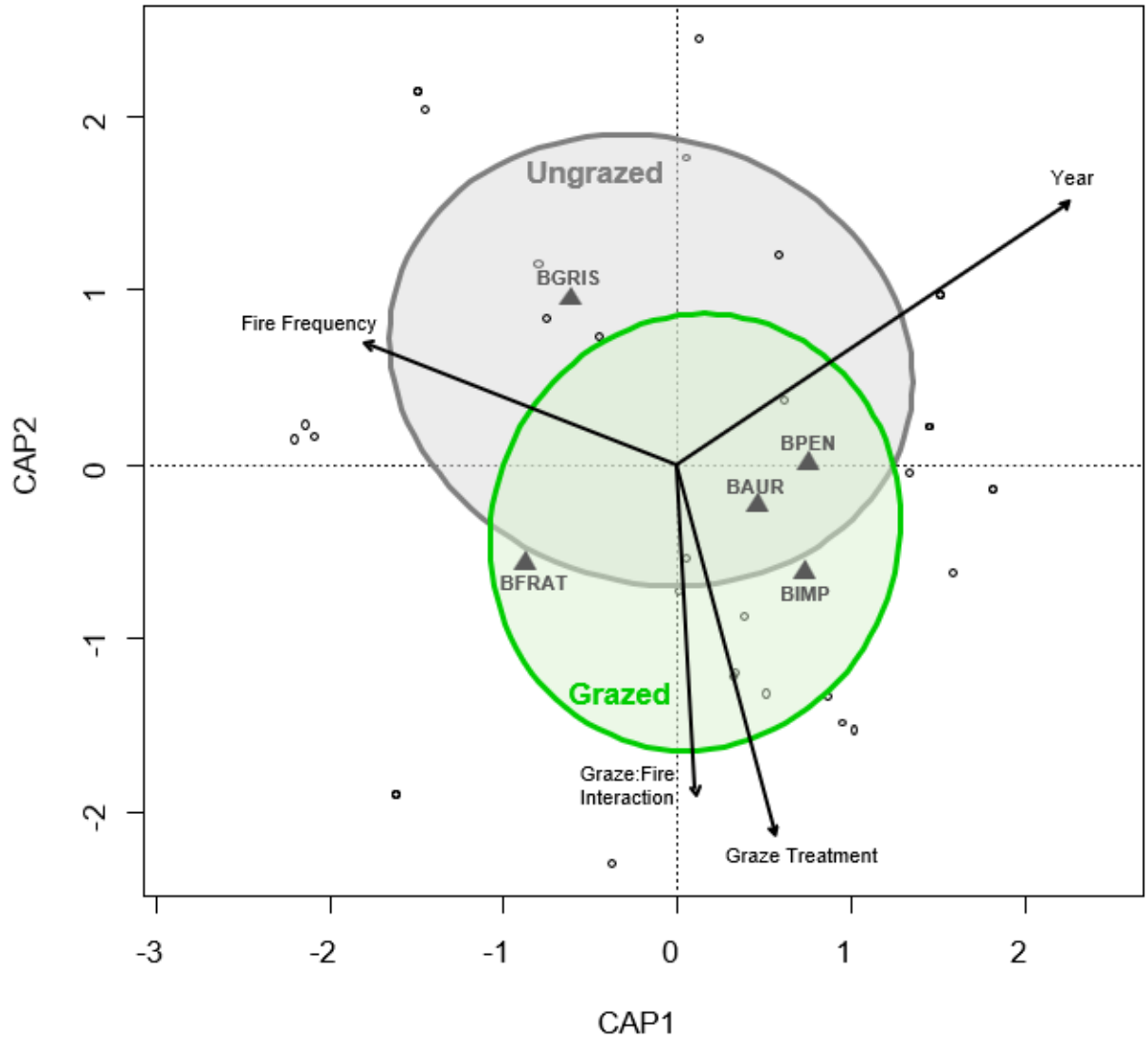

Figure 1.6. Ordination results from a constrained distance-based redundancy analysis where unfilled circles are site scores, grey triangles are species scores, black arrows are vectors displaying the direction and strength of environmental variables in the model, and filled ellipses are grouping patterns of sites falling within the grazed (green) and ungrazed (grey) treatments based on dissimilarity between bumble bee communities. The filled ellipses represent the standard error around mean centroids of each group.

Host-plant Interactions

Between the five bumble bee species detected during the course of the study, 12 different plant genera were visited. Plant genera with the most total visitations included: *Verbena* (mostly hoary vervain), *Salvia* (blue sage species), *Liatris* (rough and spotted blazing star), *Solanum* (nightshades such as buffalobur and Carolina horsenettle), and *Asclepias* (predominantly whorled, green, and butterfly milkweeds).

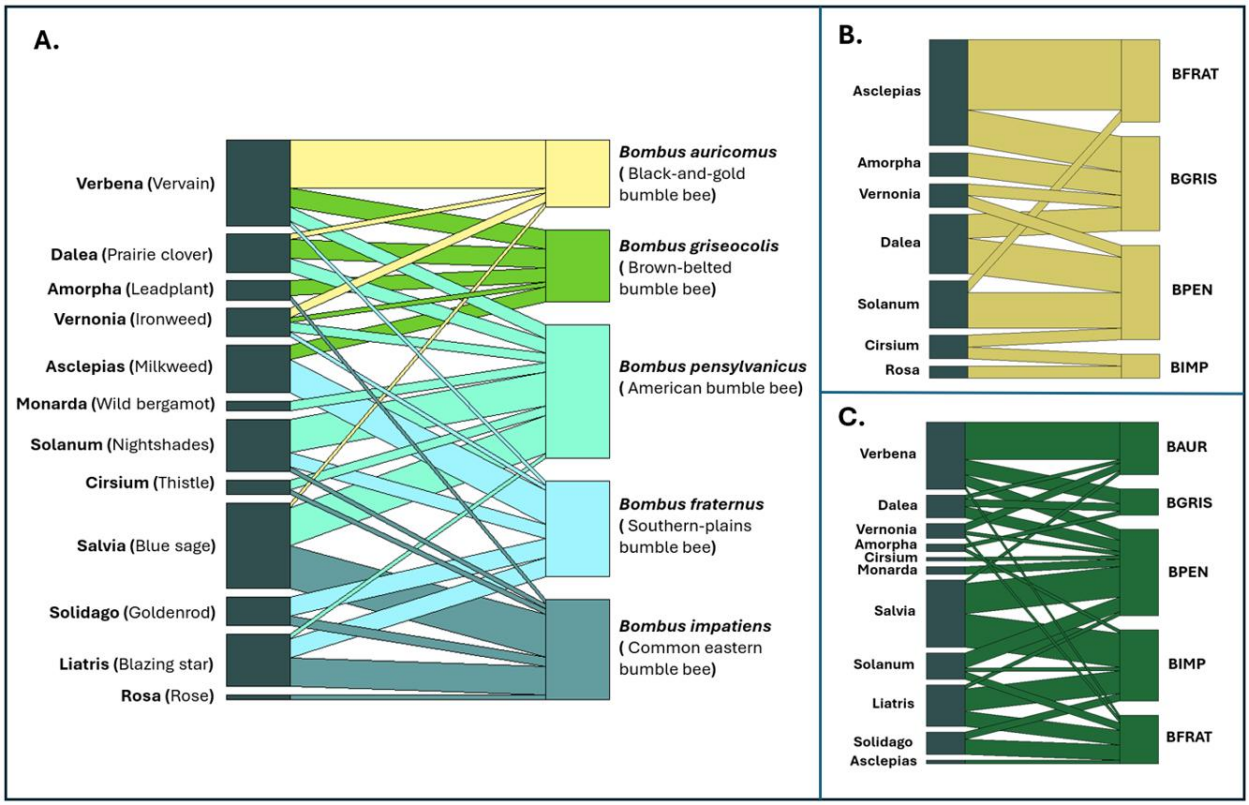

Figure 1.7. Bipartite network plots displaying the frequency of bumble bee species interactions with flowering plant genera [A] regardless of treatment group, [B] in the ungrazed watersheds only, and [C] in the bison-grazed watersheds only.

Bumble bee species interactions with the host-plant genera they were found foraging on at the time of capture are depicted as bipartite network plots (Figure 1.7). Despite significant

overlap in plant-bee species visitations, there is visual separation between plant genera visited by the two bumble bees of least concern, *B. griseocollis* and *B. impatiens* (Figure 1.7A). In contrast, the two bumble bee species of conservation concern that were detected at high frequencies in the grassland-dominated study area, *B. pensylvanicus* and *B. fraternus*, visited the widest range of flowering plant genera, displaying significant overlap with each other and other species. At the species-level, *B. pensylvanicus* was the least specialized (d' = 0.32), while *B. auricomus* had the most specialized interactions (d' = 0.50). The remaining three species are moderately specialized with species-level specialization values between 0.44 and 0.46.

Grazed networks demonstrated more community-level specialization (H' = 0.38, p-value = 0.001) than ungrazed networks (H' = 0.38, p-value = 0.012). Null model analysis suggests that both were more specialized than randomly generated networks. Visually, there are differences between the bipartite plots separated by grazing treatment in Figure 1.7B-C. There are more interactions between bumble bee species and different plant genera in the bison-grazed plots than the ungrazed ones. Due to the relatively low number of total bumble bees detected foraging on a flowering plant during each survey, I did not have enough data to generate z-scores and statistically compare the difference in network-level specialization between grazed and ungrazed watersheds.

Discussion

In general, I found that disturbance is important for Great Plains bumble bee species in tallgrass prairies, though too much combined management may no longer be beneficial. Bison presence had a strong influence on bumble bee abundance in the surveyed patches. The piecewise SEM findings indicate that bison indirectly affects bumble bee abundance through positive changes to their food availability in the form of increased flowering forb abundance and

diversity. This change in plant community by bison-grazing is consistent with the findings by Ratajczack et al. (2022) and Knapp et al. (1999), and the connection to bumble bee abundance provides support for my hypothesis. While Rosenberger & Conforti (2020) also found bison-grazing to be beneficial for some midwestern bumble bee species, to my knowledge, this is the first demonstration that bison-grazing *and* prescribed fire frequency have interactive and indirect effects on those species. In contrast to Butters et al. (2025) which was also conducted at the Konza Prairie Biological Station that found fire frequency did not have a significant effect on overall bee abundance, I did identify a significant effect of fire frequency on bumble bee abundance; however, it was closely tied to grazing treatment. In the absence of intense fire frequency, adding bison greatly improved the total number of bumble bees in a tallgrass prairie. I suspect that the addition of bison in an area not already experiencing consistent fire disturbance can help remove dominant vegetation and open space for forb growth that would not have already been created by a recent prescribed burn. When fire disturbance was already high, there was less of a difference in overall bee abundance when bison were added. My original hypothesis that combining management techniques (i.e. the interaction term) would positively affect forb and plant communities by yielding positive effects of both treatments was not supported by the model results. Instead, I suspect that the combination of both disturbance tactics at high intensities resulted in overgrazing of both the grasses and forbs, as well as not allowing for enough plant regeneration time between prescribed burns. This is more consistent with the intermediate disturbance hypothesis, which states that a lack of disturbance *and* too much of it are not beneficial for biodiversity (Fox 1979).

Despite bison grazing and fire not significantly altering bumble bee community composition, there was still some visual grouping of sites by grazing treatment, with some

species more associated with bison and prescribed fire than other species. Most notably, *B. fraternus* appeared to be particularly influenced by both bison-grazing and increased fire frequency. This suggests that future conservation efforts for that species may consider the implementation of both regimes into grassland management. Brosi & Briggs (2013) propose that a loss of the most abundant bumble bee in a community can have cascading effects on niche partitioning that lowers overall plant fitness. With the two imperiled species also being among the most abundant within my study area, it is crucial to implement grassland management strategies that will allow them to thrive – for the sake of the entire ecosystem.

My analysis of host-plant preferences provides evidence that plant-pollinator interactions are influenced by phenology of both the bumble bee species and plant genus. I suspect that the plant-pollinator visitation mis-match between *B. auricomus* and *B. impatiens* is partially related to the phenological mis-match in both bumble bee prevalence and flowering time of their host-plants. *B. impatiens* was primarily detected towards the end of the summer when late-blooming native forbs, such as *Solidago spp.* and *Liatris spp.*, were in full bloom . In contrast, *B. auricomus* was predominantly detected in the first two survey months, when vervain and prairie clover were prevalent. The other two species, *B. pensylvanicus* and *B. fraternus* were recorded more evenly across the entire summer, which could explain the wider variety of forb genera visited. Regardless, the interaction networks indicate which flowers are important for each bee species. I hope the diagrams of plant genera visited by each bumble bee species displayed in Figure 1.7 can provide support for certain native seed mixes used in areas that aim to attract Kansas bumble bees, particularly the species of conservation concern.

One limitation of the data used in this analysis is that most of the watersheds surveyed were within a 1.5 – 2-km range. That is the maximum flight distance of a bumble bee, though

they will typically forage in nearby patches to minimize energetic tradeoffs (Osborne et al. 2007). Nevertheless, it is possible that there was some overlap in bumble bees recorded in nearby watersheds that experienced different levels of disturbance. This may contribute to the non-significant differences in community composition between treatments. More distinct differences in community composition may be uncovered in future studies that include sites that are more spatially independent across a larger extent (e.g., the entire state of Kansas or Great Plains region). Another complication was the inability to conduct statistical interaction network analyses due to the small number of bumble bees detected per survey. A study on a larger scale may be able to capture more individuals which would allow a deeper exploration into network specialization and host-plant preferences. Research covering a larger extent would also grant the opportunity to study wild bison herds that have evolved grazing patterns across their larger natural migratory range instead of being confined to smaller experimentally managed pastures.

This study has useful implications for tallgrass prairie managers in the Great Plains region who are interested in supporting bumble bee populations. Results suggest that if a prairie is not currently burned or grazed, adding bison or fire, separately, can improve bumble bee abundance; however, if the prairie is already being burned at a high frequency, then adding bison could lead to consequences of too much disturbance, such as overgrazing or slow post-fire recovery. From the other angle, pollinator-conscious land managers with bison already present (e.g. a bison rancher) may consider only low-to-moderate burn schedules, if used in combination with grazing. These results apply to bison ranchers or property managers that are currently, or plan to, manage bison at a similar density as the Konza Prairie Biological Station. Literature cautions that too many grazers per unit area may lead to more overgrazing consequences than with a lower density (Kimoto 2012; Raynor et al. 2016; Davidson et al. 2020). The LTER study

area restricts bison to areas that do and don't experience regular fire within the same grazing range. Bison have been observed spending more time in areas of high fire frequency with greater nutritional forage, potentially resulting in increased grazing intensity in those specific areas. This may bias my results from Konza towards more extreme grazing behaviors and may not be reflected in certain bison ranch operations with a lower density of bison per unit area and equally nutritious forage throughout the provided range.

Overall, this research exposed fascinating new insights into the interactive effects of bison and prescribed fire frequency on bumble bee communities in tallgrass prairies systems. It sheds light on the indirect nature of the effects via floral resource availability, and highlights the species-specific nature of host-plant preferences that vary by grazing treatment for the six bumble bee species found in Kansas. It provides implications for the use of such grassland management strategies to preserve native bumble bee habitat and for the conservation of two imperiled bumble bee species. I hope these findings open doors for future research on the implementation of these regimes in restored grasslands on a larger scale in the Great Plains region.

Chapter 2 - A comparison of the distributions and habitat associations of common and threatened bumble bee species across the state of Kansas

Introduction

Over the past few decades, researchers have identified a large-scale decline of bumble bee occurrences in North America and across the globe (Goulson et al. 2008; Cameron et al. 2011; Cameron et al. 2020). One of the proposed factors affecting their decline is changing land cover (e.g. transition between natural grassland to developed or agricultural land) leading to habitat loss and fragmentation (Kremen et al. 2007). Other possible influences may include a changing climate (Pyke et al. 2016), pathogen transmission and competition from commercial pollinators (Goulson et al. 2015; Alger et al. 2019), and pesticide use (Cameron et al. 2011; Goulson et al. 2015; Janousek et al. 2023). This pattern of decline is concerning because bumble bees provide critical pollination services in both natural and agricultural systems. Bumble bees are generalists that visit a wide variety of native forbs, which helps maintain plant biodiversity within grasslands (Brosi & Briggs 2013; Russell et al. 2017). They are also economically important due to their ability to buzz-pollinate many non-grain crops, such as tomato and pepper, which studies have shown increases crop quality (Cooley and Vallejo-Marin, 2021).

The state of Kansas, located in the Great Plains regions of the United States, is inhabited by six *Bombus* species (Hymenoptera: Apidae). The common eastern bumble bee (*B. impatiens*), brown-belted bumble bee (*B. griseocollis*), two-spotted bumble bee *(B. bimaculatus*), and black-and-gold bumble bee (*B. auricomus*) are currently of least conservation concern, while the Southern-Plains bumble bee (*B. fraternus*) and American bumble bee (*B. pensylvanicus*) are

considered “vulnerable” and “threatened”, respectively, according to the IUCN (Hatfield et al. 2014). Petitions proposing that the latter two imperiled species be listed under the Endangered Species Act were being reviewed by the United States Fish and Wildlife Service (Tyler 2021; Tyler 2022). Following a 90-day review process, the federal agency reported that they consider the evidence of both species’ decline severe enough to warrant further actions (USFWS 2021; USFWS 2024). Important actions outlined in the reports include identifying priority areas, defining critical habitat, and investigating causes of decline.

Two main potential causes of pollinator decline include climate change and habitat loss, which may be expedited by factors such as pesticide usage. In the Great Plains region, mean annual temperature in the year 2050 is projected to increase from the 30-year normal by 2.1-3.3 degrees Celsius, and mean annual precipitation is forecasted to decrease by 7-33 mm (Ojima et al. 2021). Large-scale changes in climate can have direct effects on bumble bees’ ability to thermoregulate (Bretzlaff et al. 2023) and indirect effects on their floral resource availability (Pyke et al. 2016). Studies investigating critical temperatures of North American *Bombus* spp. suggest that an increase in the frequency of extreme weather (hot or cold) may negatively affect the fitness of the organism (Oyen and Dillon 2018). Changes in climatic conditions may also have a role in accelerating other causes of decline, such as habitat loss and fragmentation. In the central Great Plains regions, historical land cover trends show an increase in developed areas and shifts between native grassland and agricultural land (Taylor et al. 2015)**.** The expansion of agricultural land is particularly prominent in the central United States, with grassland being the dominant land cover type displaced (Lark et al. 2015). Because bumble bees forage on native grassland forbs, a decrease in foraging habitat due to changing land cover could have detrimental

effects on their fitness and overall geographic distribution. If they are able to utilize urban green spaces, they may be more resistant to increasing urbanization and agricultural expansion.

In this study, I investigate the geographic distribution and habitat associations of two common (*B. impatiens* and *B. griseocollis*) and two threatened (*B. pensylvanicus* and *B. fraternus*) bumble bee species found in Kansas. I examine features of the landscape around confirmed *Bombus* sightings in order to understand possible habitat preferences that may allow some species to thrive while others decline. Patterns of decline are large-scale for the two imperiled species, but they have been observed more heavily in some regions of their ranges than others (Cameron et al. 2011; Hatfield et al. 2014; Tyler 2021; Tyler 2024). Local landscape factors might explain why the habitat resources they are utilizing within their typical flight range of ~500-m, while surrounding landscape factors are aimed more at larger-scale heterogeneity within generational flight ranges (up to 2-km). Aside from the between-species land cover comparison, I also want to understand where individuals of each species, particularly the ones of conservation concern, may be located across the state. Despite maps of occurrence records being available for both species from the Global Biodiversity Information Facility (GBIF 2020), it is unknown where they may be detected outside of commonly surveyed locations. Incidental sightings show areas of confirmed sightings across space and time; however, there is often an implicit bias in sampling efforts that prevents an accurate depiction of where they have been or currently are found. Just because a location has missing data, doesn't mean the species isn't found there – it just means that nobody has recorded it yet due to lower sampling effort. In Kansas and much of the Great Plains, these 'data graveyards' are often in less developed areas. The IUCN assessment of the two threatened species by Hatfield et al. (2014) highlights a lack of data for *B. fraternus* in Kansas. It also mentions that while *B. pensylvanicus* has seen declines

mainly in the northern portion of the country, it is less studied in other parts of its range. Given that Kansas is within the western part of both imperiled species' ranges where Hatfield et al. 2014 determined more research was needed, I focus my research on Kansas specifically. However, this research has implications for other parts of the Great Plains, as well.

I aimed to locate priority areas in Kansas to focus future data collection and conservation efforts, particularly in areas with missing data. Species distribution modeling considers verified observation records, as well as biotic and abiotic variables, to predict where a species is/ has likely been present across space-and-time. This approach has provided valuable insights for other imperiled bumble bee species, such *B. occidentalis,* in the Pacific Northwest region (Graves et al. 2020; Janousek et al. 2023). Previous studies provide evidence that both climate (e.g., changes to temperature and precipitation) and landscape (e.g., proportion of forest and agricultural cover) factors improve modeling performance and are important drivers of their distributions (Marshall et al. 2018; Janousek et al. 2023). I incorporate similar land cover and climate variables into the species distribution models, and seek to understand which factors are driving the distribution of four Kansas *Bombus* spp. across the state. My main objectives were to (1) generate a detailed map displaying the likelihood of species presence across Kansas in recent years (2018-2023), including areas with poorly-sampled areas, (2) determine which land cover and climate factors significantly influence the occurrence of those bumble bee species in recent years, and (3) compare habitat associations between species, in the immediate area, as well as local and surrounding landscape. This study should yield important insights into critical habitat and priority areas across Kansas for future conservation efforts and targeted surveying efforts.

Materials & Methods

I compiled verified bumble bee observation data from both community science and survey-based sources. I also downloaded monthly climate rasters and yearly cropland data layer rasters (for the years 2018-2023), processing them as outlined below, before extracting the values from each raster that fell within the immediate area (exact land cover pixel), local landscape (a 500-m buffer), and surrounding landscape (a 2-km buffer) of each bumble bee record. I checked for collinearity among variables before completing a between-species habitat analysis from the land cover buffer extract data, as well as a single-species distribution modelling process to generate predictive maps of the likelihood of each species' presence across the state given the most significant climate and land cover variables. A broad overview of this workflow is displayed in Figure 2.1**,** with more details below.

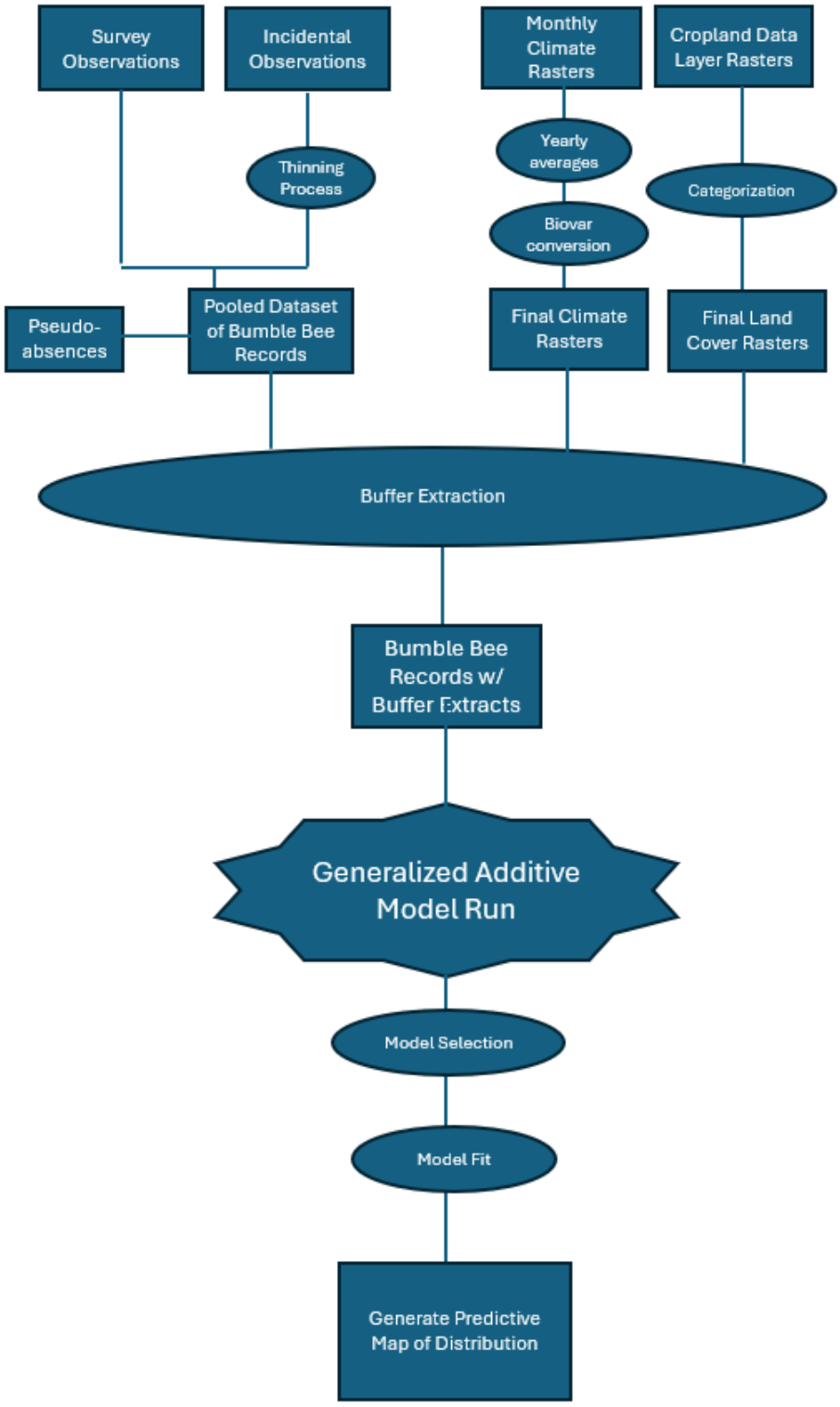

Figure 2.1. Workflow diagram including: (1) data compilation, (2) data processing, (3) buffer extraction from rasters, (4) generalized additive model run, (5) model selection and fit, and (6) final map generation.

Materials

Bumble Bee Data

Incidental observation records for *B. pensylvanicus*, *B. griseocollis*, *B. fraternus*, and *B. impatiens* were downloaded from the Global Biodiversity Information Facility (GBIF) database (GBIF 2025). Search parameters restricted records to those that were collected between the years 2018-2023 (the time period that accurately reflects their current distribution) and within the Kansas state boundary, contained valid latitude and longitude coordinates, and were marked 'verified'. Most sightings were uploaded to GBIF from community science efforts, iNaturalist and Bumble Bee Watch. Records following the same parameters were also downloaded from the Bee Machine database (BeeMachine 2025). BeeMachine is a web and app-focused AI bee identification tool used by community scientists to upload sightings across the globe (Spiesman et al. 2021)**.** Because this source does not yet provide records that have been verified, I only selected sightings that had an identification confidence score greater than 95%. See the Appendix for an exact breakdown of the number of records per source for each species after download (Tables B.1.-B.2.).

To minimize the urban influence from incidental records that are often recorded in densely populated developed areas, I used various statewide survey projects conducted by both non-profit community science-based organizations (Xerces Society 2023) and academic researchers at public and land-grant research universities (Morphew 2019; Brunette 2025) during 2018-2023**.** These surveys included timed bumble bee observations within a given radius at specific locations with potential foraging or nesting habitat. Surveys were often repeated at least twice during each study. All bumble bee sightings, regardless of multiple observations made during the same survey at the same location, were included in the final dataset.

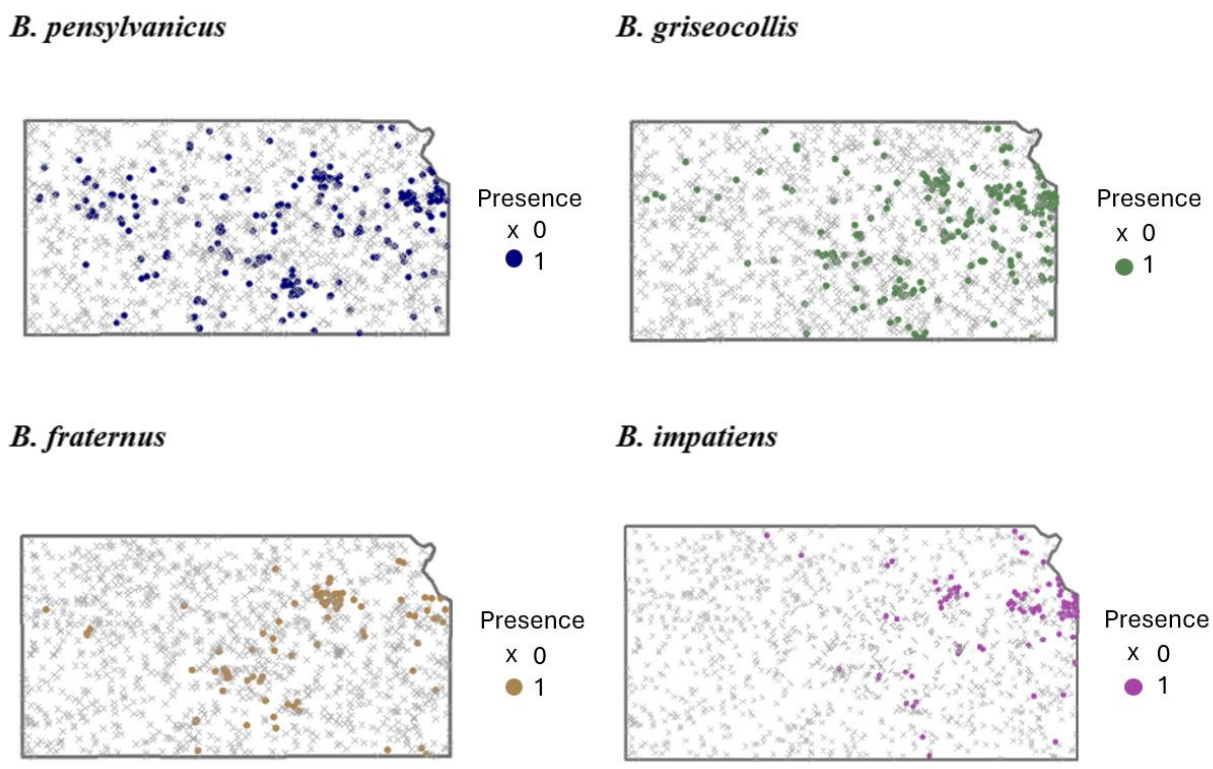

Figure 2.2. Geographic distribution of records for each species after completing the thinning process, where solid circles represent either a verified incidental observation or survey presence, and a grey 'x' symbol denotes either a confirmed survey absence or a randomly selected pseudo-absence point.

Additionally, for the distribution models, I also added 1000 randomly selected pseudo-absence points to each species dataset. Barbett-Massin et al. (2012) recommends the inclusion of 10,000 pseudo-absence points; however, preliminary efforts to model this data with that many background points suggested extensive overfitting. Therefore, my main focus was not on the number of pseudo-absence records, but rather on ensuring they were randomly selected, as it is believed that the most important factor to consider when selecting pseudo-absences for generalized linear or additive models is the method by which they are generated (Barbett-Massin

et al. 2012). The pseudo-absence points were distributed relatively evenly across the entire state (Figure 2.2).

I used a 'simple pooling' approach to combining data by joining both the thinned incidental observations and survey records together into a single dataset with the pseudo-absence points. This is the most common form of data fusion (Fletcher et al. 2019) and it allowed me to maximize the number of confirmed sightings for each species. Most records were collected in 2018, 2022, 2023, and 2024; with that trend being consistent across species (Appendix Figure B.1.). Despite the addition of survey records that are less likely to have an urban sampling bias, there was still some visual clustering around highly populated areas in the eastern portion of the state (Appendix Figure B.2.). Studies facing the same challenge have elected to thin the data even further by setting a predetermined radius around randomly selected points and removing all records that fall within a given radius of that point for a certain number of iterations until the highest number of records are preserved (Rew et al. 2021). I used the 'spThin' package (Aiello-Lammens et al. 2015) in the R Programming Environment to efficiently run the thinning process for all four species datasets. Maps with the distribution of points for each species after thinning with different buffer sizes (500-m, 2-km, and 5-km) for *B. pensylvanicus*, *B. griseocollis*, *B. fraternus*, and *B. impatiens* can be seen in the Appendix (Figures B.3.-B.5., B.6.-B.8., B.9.-B.11., and B.12.-B.14., respectively). Visual clustering was adequately reduced after 100 iterations with a buffer size set to 5-km. By thinning incidental observation records at this buffer size, I assumed that repeated observations of the same individuals were minimized, and sampling effort across all sources was more balanced. Thinned incidental observation records were then added back in the final dataset along with survey records to be used in the following analysis. A detailed

breakdown of the number of records per species in the final dataset post-thinning process is available in the Appendix (Tables B.3.-B.4.).

Land Cover Data

I downloaded cropland data layer rasters from the United States Department of Agriculture CropScape database (USDA 2024). The extent only included Kansas and covered all years during 2018-2023. To minimize the number of variables to analyze in these models, I grouped all land cover types into six overarching categories displayed as individual raster layers (Figure 2.3). Those variables represent different types of potential bumble bee foraging and nesting habitat, and may bring insights into the influence of urbanization or agricultural conversion to monoculture crops. Land cover categories included: Grassland (clover/wildflower, sod/grass seed, grassland/pasture, herbaceous wetland), Developed (open space, medium intensity, high intensity, low intensity), Woodland (deciduous forest, evergreen forest, mixed forest, shrubland, woody wetlands), Grain Crops (winter wheat, sorghum, barley, spring wheat, rye, oats, millet, triticale, corn, popcorn, sweet corn), Bean Crops (soybeans, peas, dry beans), and Bee-pollinated Crops (alfalfa, sunflower, canola, pumpkin, miscellaneous vegetables and fruits).

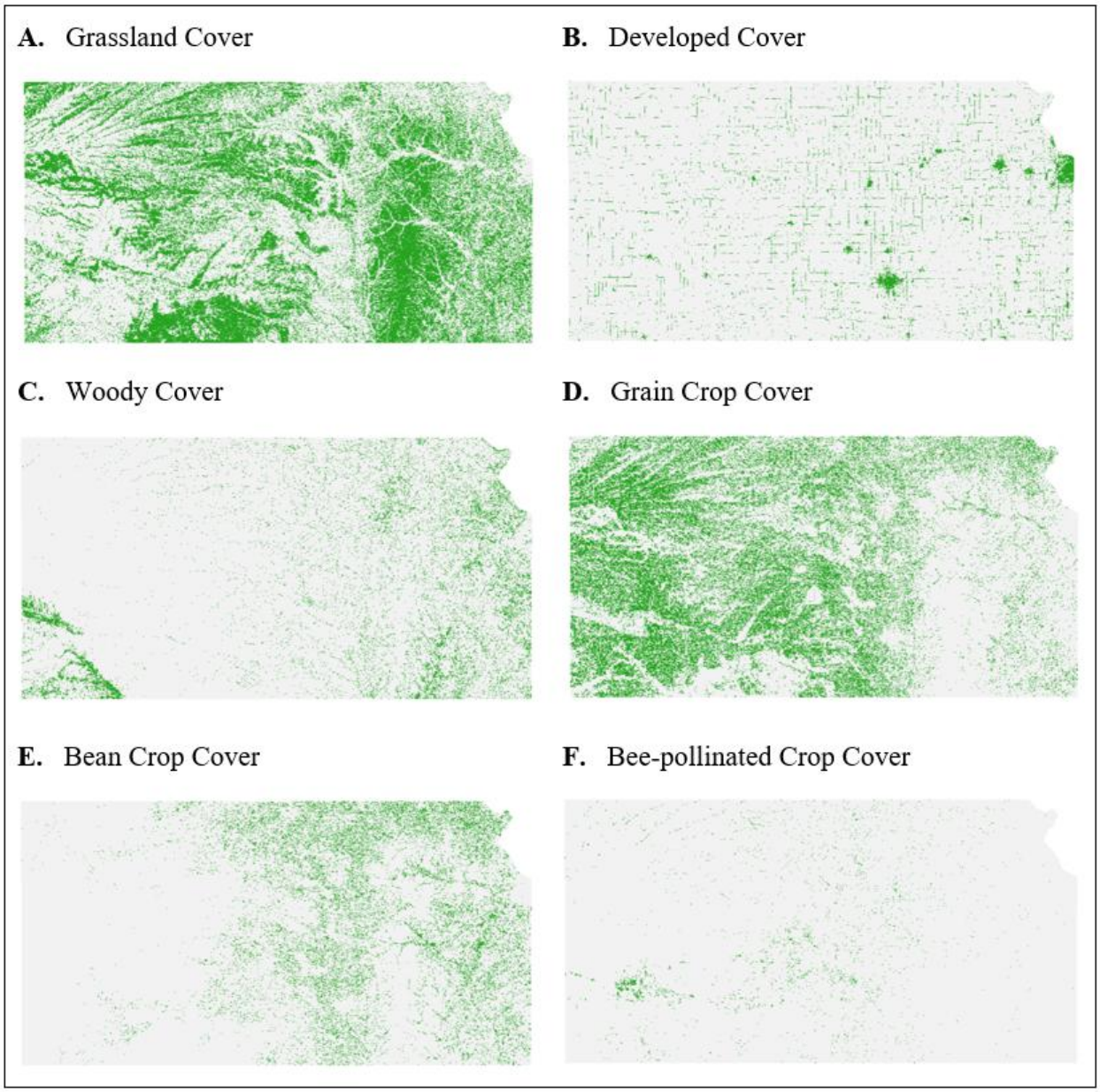

Figure 2.3. Rasters of land cover categories (A-F) derived from USDA CropLand Data Layers in Kansas during 2022. Green pixels represent presence of each land cover type.

To join land cover raster data to the bumble bee records, I performed three separate extractions: the land cover pixel in which each individual was found (immediate area), the percentage of pixels of each land cover type falling within a 500-m buffer (local area), and the percentage of pixels of each land cover type falling within a 2-km buffer (surrounding

landscape). I chose buffer radii based on the general landscape utilization capabilities of bumble bees. Bumble bees can achieve long-distance dispersal over multiple generations plus unusually long forage bouts up to 1.5 - 2-km, thus being affected by the surrounding landscape in that entire area (Hemberger & Williams 2025); however, they may choose to utilize more local resources in a 500 - 1000-m radius depending on availability and energetic tradeoffs (Osborne et al. 2007). The 'extract' function available in the 'raster' package allowed for efficient spatial extractions (Hijmans 2023). See Figure 2.4 for a visual description of the extraction process at each scale. Extracted values were added to the final bumble bee dataset to be used in habitat association analyses and as training data for the spatial point process models.

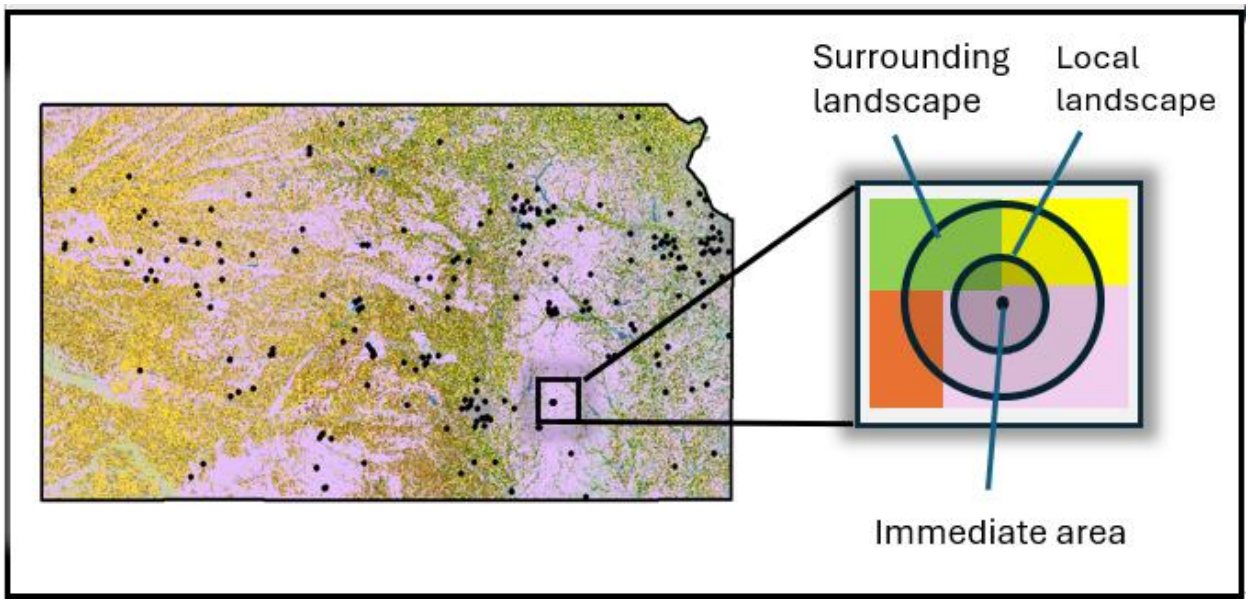

Figure 2.4. Visualization of the land cover and climate raster extraction process from the immediate area, local landscape (500-m buffer), and surrounding landscape (2-km buffer), where the colored pixels represent different raster values.

Climate Data

WorldClim data are widely used in bumble bee species distribution modeling literature (Martins et al. 2015; Rojas-Arias et al. 2022; Singh et al. 2023). Because it is only available up to the year 2000, I manually generated the same 18 biovariables from monthly weather time-series datasets publicly available by the PRISM Climate Group at Oregon State University (PRISM 2023). These data covered the target extent and time period (i.e., within Kansas during 2018-2023). That data were calculated monthly and adjusted to represent the annual measurements of minimum temperature, maximum temperature, and precipitation. From those monthly rasters, I used the 'biovars' function available through the 'dismo' package in R (Hijmans et al. 2023) to create biovariables for each year between 2018-2023. To simplify these data further, I generated a single set of biovariable rasters representing the average values across all six years. The 18 biovariables were highly correlated; therefore, I selected four variables that were not correlated, but meaningful drivers of bumble bee occurrence (Soroye et al. 2020): mean annual temperature (Bio1), temperature seasonality (Bio4), mean annual precipitation (Bio12), and precipitation seasonality (Bio15). The seasonality metrics represent the proportion of extreme weather, as calculated by the standard deviation multiplied by 100. Strong variations in temperature or precipitation, along with general annual increases or decreases due to climate change can affect bumble bee survival and dispersal through floral resource asynchrony and thermoregulation issues.

To more accurately represent long-term climate patterns instead of year-specific weather data, I averaged the biovariables between years to create four individual variables representing climate during the entire six-year period. These data were then standardized using the 'scale' function in R, so values were not in a vastly different range than the land cover data (values

between 0 and 1). The resulting climate variables are displayed as four individual raster layers (Figure 2.5). Similarly to the land cover data, I extracted the mean measurement of each climate variable from the immediate area and two buffer sizes around each bumble bee observation location, which was then added to the final dataset (Figure 2.4).

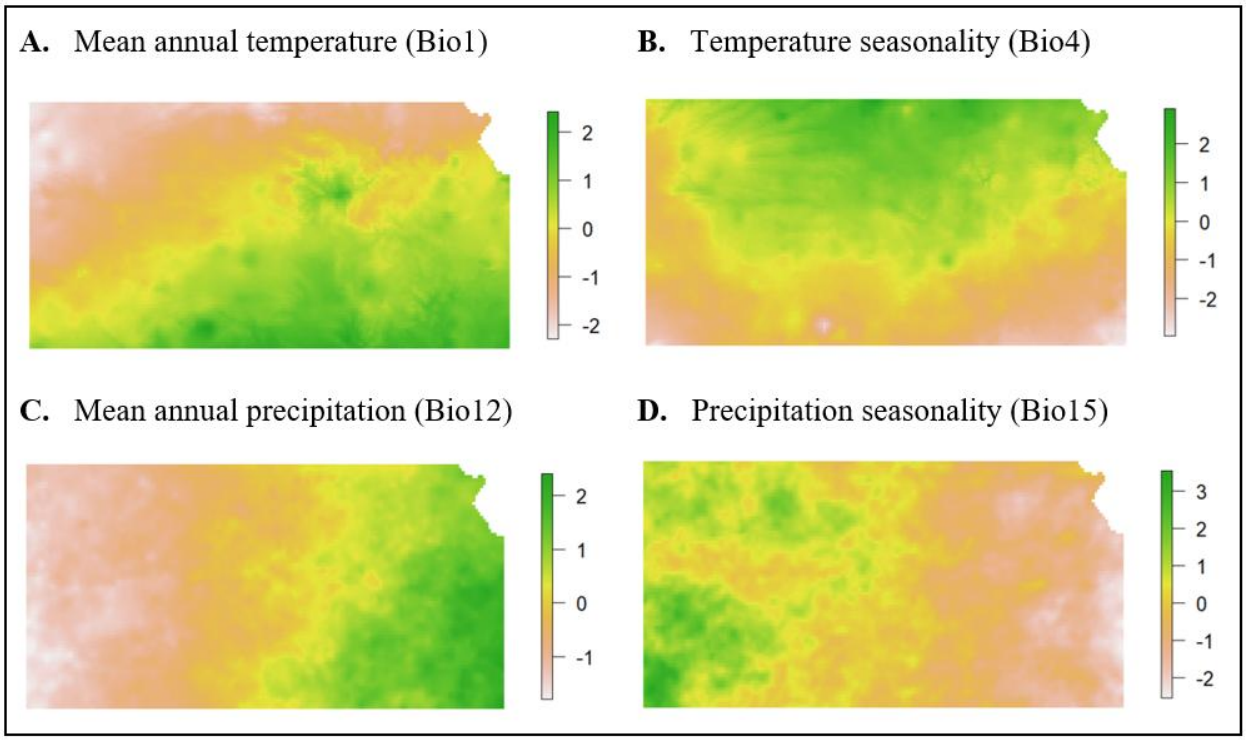

Figure 2.5. Climate variable rasters (A-D) calculated from monthly PRISM rasters that were averaged across 2018-2023, converted into biovariables, and scaled.

Methods

Between-species Habitat Association Analysis

To understand the conditions where each individual was found, I extracted the 30-m by 30-m land cover pixel at the location of detection for all records. On the landscape scale, I used effect size to measure the magnitude of differences between the percentage of each land cover category falling within a 500-m buffer (local landscape) and a 2-km buffer (surrounding

landscape). This metric divides the difference in mean percentage values for each group by the pooled standard deviation (Ialongo 2016), calculated using the 'effsize' package available in R (Torchiano 2020). Because there are a large number of records in each group providing statistical power, typical ANOVA (Analysis of Variance Analysis) and Tukey HSD (Honestly Significant Difference) post-hoc tests could result in significant differences between groups that are not ecologically meaningful (Khalilzadeh & Tasci 2017). Instead of identifying statistical significance based on p-values, I detect "practical-significance" through effect size measures. While Cohen's D has been used to measure effect size in ecological studies that manage large sample sizes (Spiesman et al. 2019), Hedge's G statistic is more appropriate for my data given the unequal sample sizes between groups (Ialongo 2016). The magnitude of effect size is based on the standard deviation between groups where a value between 0-0.2 is small, 0.21-0.5 is medium, 0.51- 1.0 is large, and > 1.0 is very large.

Hierarchical Models for Single-species Distribution Mapping

Presence-only data are easier, faster, and often cheaper to collect than true occupancy data collected by structured surveys in predetermined areas (Hefley and Hooten 2016; Bruninga-Socolar et al. 2023); however, this type of data does not include absences that are necessary for true occupancy modeling (e.g. using the Bernoulli distribution). The nature of these data can be heavily influenced by sampling biases (Hefley et al., 2013), which I correct for by thinning the incidental observations and including survey records in the pooled dataset. When modelling spatial patterns using presence-only data, it is recommended to use pseudo-absence records as background points (Phillips et al. 2006; Wisz & Guisan 2009; Barbett-Massin et al. 2012). I followed Warton and Shepherd (2010) and Dovers et al. (2024) by modelling the Poisson point

process of the intensity of presence as a proxy for true occupancy, using a hierarchical modeling approach.

Hierarchical modeling is a powerful framework for analyzing ecological data. It allows the incorporation of multiple levels of variation in ecological systems, providing flexibility in modelling complex systems. Hierarchical models have two modeling layers: the data model and the process model (Royle and Berliner 1999). The data model is the first layer and it attempts to describe the relationship between the observed data and the parameters of interest in the statistical model. I define the data model in Equation 1 as

$$y_i \sim \mathtt{Bern}(p_i), \tag{1}$$

where y_i is the presence of the ith observation, distributed as a Bernoulli with probability of occurrence p_i for the ith observation. The second layer is the process model, which attempts to describe the underlying process or mechanism that generates the observed data. This step is crucial and what makes hierarchical modeling shine with its flexibility to model the parameter of interest. Given that my parameter of interest was p_i, I modeled it as an inhomogeneous Poisson point process (Warton and Shepherd 2010; Dovers et al. 2024) as it is shown in Equation 2:

$$p_i \sim \mathtt{IPPP}(\lambda_i), \tag{2}$$

where p_i for the ith observation follows an inhomogeneous Poisson point process with an intensity function of λ_i for the ith observation. I then expanded intensity λ_i into a generalized additive model (Wood 2017) in Equation 3:

$$\log(\lambda_i) = \beta_0 + f_1(x_1) + f_2(x_2) + \ldots + f_n(x_n) + \epsilon, \tag{3}$$

where the intensity λ_i is a link logit for Equation 2. This is made by β_0 as the intercept and then a series of functions $f_1(.)$, $f_2(.)$, ..., $f_n(.)$ for covariates x_1, x_2, ..., x_n for n number of variables of interest to model presence of the species. The covariates in these models included the buffer-extracted data from each of the six land cover categories and four climate variables. Generalized additive models are similar to generalized linear models in that they involve a set of covariates/ predictor variables that may explain changes in the response variable; however, it differs in the addition of a set of smoothing functions called "splines" (Mara & Wood 2011; Wood 2015). These splines make it so that data does not need to follow a strict linear relationship (Yee & Mitchell 1991). I added these smoothing terms as location data (latitude and longitude), which is useful in spatial modeling because it results in a smoother prediction in geographic space and can account for non-tested factors that may cause variation in distributional patterns (Garattola et al. 2023). My smoothing terms were selected using restricted maximum likelihood estimation (REML) because it is most compatible with variable selection by backward elimination (Mara & Wood 2011). I used that variable selection method to generate final models using only a set of significant variables. These species-specific models were then fitted to new data that covered the entire extent of Kansas, which was used to generate intensity function predictions across the state for each species. I visually assessed hotspot locations and spatial patterns based on the resulting maps. I also analyzed the effect of all significant variables in the models and compared general trends between species.

Results

Habitat Associations

Immediate Area

For most species, grassland areas, followed by developed and woody spaces, were the most common immediate habitat where individuals were found (Table 2.1). The exception, *Bombus impatiens*, was most often found in developed areas, providing support for my hypothesis that this common species may be thriving due to its tendency to utilize limited resources in overly urbanized areas with a relatively larger percentage of impervious surface. Across the board, crop land of all types did not serve as popular immediate detection spaces. Despite the expectation that bumble bees may be commonly seen visiting bee-pollinated crops in gardens or urban fruit/vegetable farms, that land cover type had the lowest number of observed bumble bees.

Table 2.1. Count of verified sightings for each *Bombus* spp. that was found directly in the 30-m by 30-m pixel cell assigned to all six land cover categories of interest.

Land Cover Category	BPEN	BGRIS	BFRAT	BIMP
Grassland	362	378	167	25
Developed	179	104	60	58
Woodland	36	41	29	18
Grain Crops	3	2	0	3
Bean Crops	2	20	0	2
Bee-pollinated Crops	0	0	0	1
Not Specified	1	8	13	0

There were several instances in which individuals were detected in a land cover category that was not specified, meaning that the original land cover type present was not included in any of my predetermined categories. This may have included areas along open bodies of water (e.g. riparian strips) or patches of bare ground.

Local Landscape

The difference in proportion of grassland in the local landscape was largest between *B. impatiens* and the three other species (Figure 2.6). Only a small effect size corresponded with differences between *B. fraternus* and *B. griseocollis*, while all other comparisons for the grassland land cover type were negligible. The difference in proportion of developed cover at the same scale was large between *B. impatiens* and both *B. griseocollis* and *B. fraternus*. There was a medium effect size between *B. impatiens* and *B. pensylvanicus*. Magnitude was small between *B. pensylvanicus* and both *B. fraternus* and *B. griseocollis*. The last non-crop land cover type, woody cover, did not result in any large effects between species. A medium effect size was identified between *B. impatiens* and both *B. griseocollis* and *B. pensylvanicus*; as well as small differences between *B. fraternus* and both *B. pensylvanicus* and *B. impatiens*.

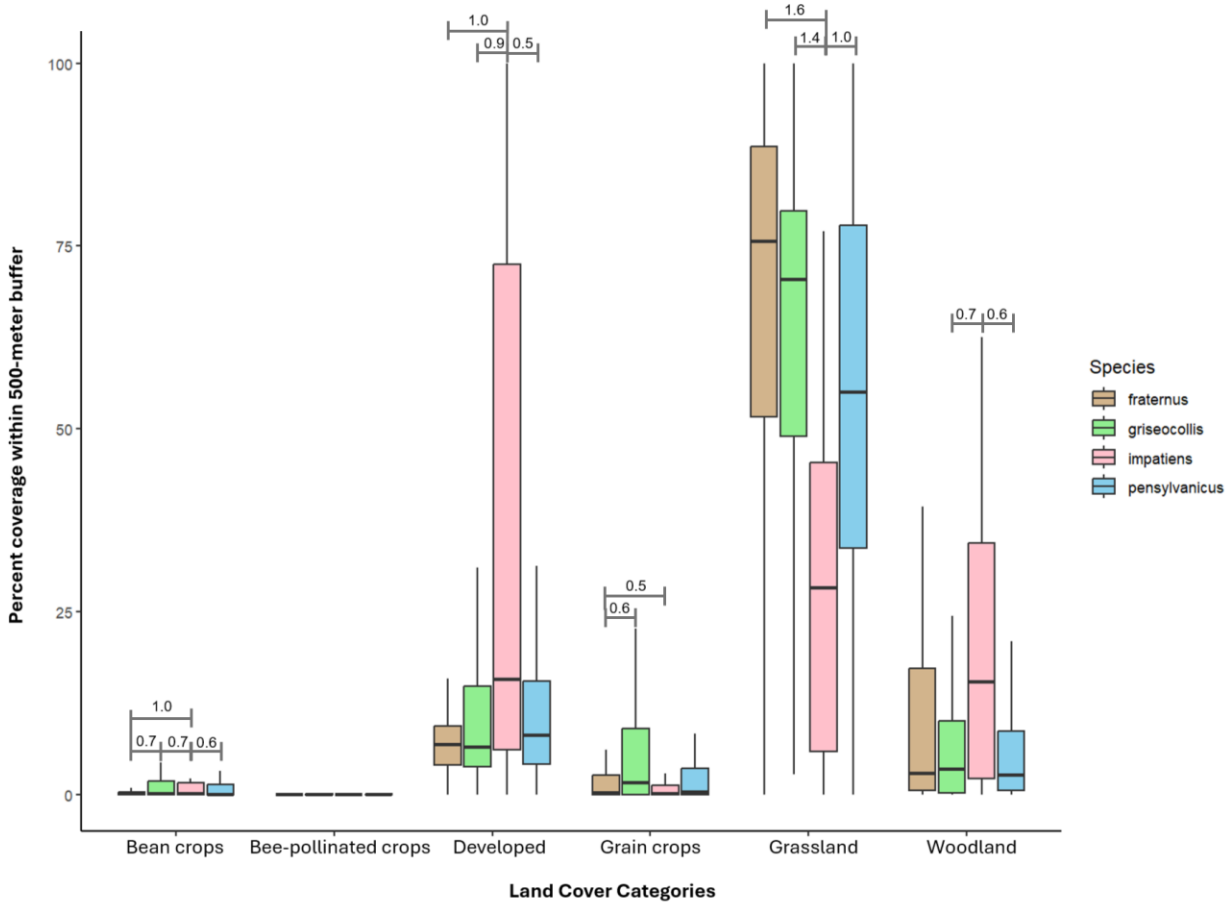

Figure 2.6. Boxplots displaying the percentage of each land cover category falling within a 500-m buffer around verified sightings for the four *Bombus* spp. examined, with Hedge's G estimates (medium – extra large magnitude) displayed between species groups within land cover categories.

As for crop variables, the beans category was the only one to detect a large effect size – between *B. impatiens* and *B. fraternus*. Effect size was medium magnitude between *B. impatiens* and the other two species. *B. griseocollis* also had a medium difference from *B. impatiens* and a small one with *B. pensylvanicus.* Grain crop percentage had fewer practically-significant variables, with the two medium-size comparisons between *B. fraternus* and both *B. griseocollis*

and *B. impatiens*. Small effect sizes were drawn from comparisons between *B. pensylvanicus* and the two species of least conservation concern. No practical-significance was identified between species in relation to percent cover of bee-pollinated crops in the local landscape – all effect sizes were negligible. More information about summary statistics for each species-species land cover variable comparison can be found in the Appendix (Table B.6.).

Surrounding Landscape

Results from land cover extractions at the 2-km scale (Figure 2.7) were similar to those made at the 500-m scale (Figure 2.6), except that more coverage of the three crop types was uncovered. The difference in proportion of grassland in the surrounding landscape was large between *B. impatiens* and all other species. Remaining species combinates had a small magnitude effect size, with the only negligible finding between *B. fraternus* and *B. griseocollis*. Developed land cover falling within the larger buffer resulted in a small effect size between *B. pensylvanicus* and both *B. fraternus* and *B. griseocollis*, with a medium-sized difference from *B. impatiens*. A large effect size was identified between *B. impatiens* and both *B. griseocollis* and *B. fraternus*. No large effects were identified in the between-species comparison of wood coverage within 500-m.

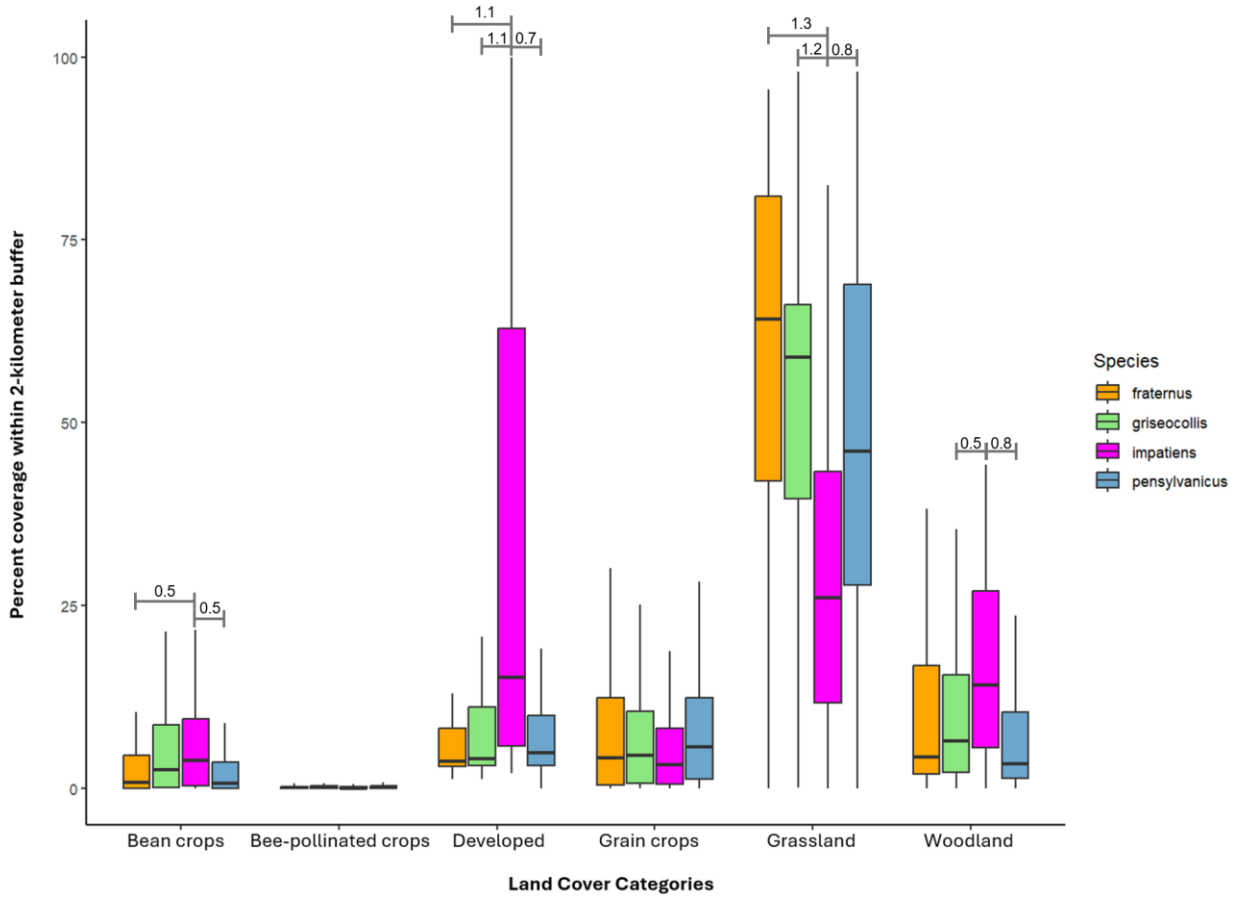

Figure 2.7. Boxplots for percentage of each land cover category falling within a 2-km buffer around verified sightings for the four *Bombus* spp. examined, with Hedge's G estimates (medium – extra large magnitude) displayed between species groups within land cover categories.

Per the Hedge's G values, there was not a difference in percentage of bee-pollinated crops in the landscape surrounding any four species. Only small effects pertained to grain coverage, identified between *B. impatiens* and both *B. griseocollis* and *B. pensylvanicus*, as well as between the two imperiled species. Conversely, bean crop coverage differed between *B. impatiens* and both the imperiled species at a medium size. There was only a small difference when grain coverage was compared between *B. griseocollis* and the two species of concern. All

other comparisons were negligible. More information about summary statistics for each species-species land cover variable comparison can be found in the Appendix (Table B.5.).

Model-predicted Drivers

I used generalized additive models with data from both buffer size extractions and for all species to test the effect of habitat and climate factors on the likelihood of their detection across the state. The initial models were run using all six land cover variables and four climate variables. Tests for multicollinearity revealed no suspected significant correlation amongst the land cover categories of interest (VIF < 10) nor with the four chosen biovariables (VIF < 5). Through the process of backward elimination, I selected only the significant land cover and climate predictor variables that affected intensity function to generate final model predictions. Per the recommendation of Marra & Wood (2011), I used the process of backward selection, in which the variable with the highest and least-significant p-value was systematically removed from the model after each re-run until all remaining terms were at least moderately significant (p-value < 0.8). Additionally, models using environmental data from the two different buffer sizes were compared. I selected the best-performing model for each species based on the lowest AIC (Akaike Information Criterion) score.

Neither the percentage of bee-pollinated crop cover in the landscape nor temperature seasonality (Bio4) were important drivers of the likelihood of any species being present in a given area. Land cover variables were among the most significant terms in the final models, while climate variables had generally weaker estimate values and were only shown to influence select species' intensities across the state.

Table 2.2. Summary statistics of the significant predictor variables for *B. pensylvanicus* using the best-fit generalized additive model.

Variable	Estimate	Std. Error	Z value	Pr (>|z|)	
(Intercept)	-1.296	0.111	-11.624	< 0.0001	***
Developed cover	1.383	0.260	5.317	< 0.0001	***
Woody cover	0.842	0.434	1.942	0.0522	.
Grain crop cover	-2.959	0.406	-7.284	< 0.0001	***
Bean crop cover	-1.823	0.645	-2.826	0.0047	**

The best-fit model for *B. pensylvanicus* was the final model post-variable selection that used data extracted from the 500-m buffer size (Table 2.2). This was compared to the initial model using the same buffer size (ΔAIC = 9.29), and both models using surrounding landscape variables (ΔAIC = 57.17 and 46.53 for initial and final models, respectively). The best-fit model resulted in highly significant smoothing terms (edf = 52.01, chi-sq = 169.5, p-value < 0.0001) and the final variables explained 47.3% of the deviance. This final model suggests developed and woody cover in the local landscape as positive drivers of *B. pensylvanicus* presence across the state, while increased coverage of both crop types typical in monoculture plantings (grains and beans) were strong negative drivers. No climate variables significantly affected the intensity function of this species.

Table 2.3. Summary statistics of the significant predictor variables for *B. griseocollis* using the best-fit generalized additive model.

Variable	Estimate	Std. Error	Z value	Pr (>|z|)	
(Intercept)	-1.423	0.126	-11.279	< 0.0001	***
Developed cover	0.550	0.268	2.050	0.0404	*
Grain crop cover	-1.881	0.365	-5.149	< 0.0001	***
Beans crop cover	-3.812	0.713	-5.347	< 0.0001	***
Mean annual precipitation (Bio12)	0.199	0.051	3.937	< 0.0001	***

The best-fit model for *B. griseocollis* was also the final model that used environmental variables extracted from the smaller buffer size (Table 2.3), when compared to the initial model and pair of models using the 2-km buffer (ΔAIC = 9.14, 45.15, and 134.61, respectively). Similarly, the smoothing terms were highly significant (edf = 43.14, chi-sq = 196.9, p-value < 0.0001), with 49.2% of deviance explained by the final three land cover terms and one climate variable. Percentage of developed cover in the local landscape was associated with a slight positive increase in intensity, while both grain and bean cover were negative drivers of increased bumble bee presence. In contrast to *B. pensylvanicus*, the intensity function of this less imperiled species was positively affected by an increase in mean annual precipitation.

Table 2.4. Summary statistics of the significant predictor variables for *B. fraternus* using the best-fit generalized additive model.

Variable	Estimate	Std. Error	Z value	Pr (>|z|)	
(Intercept)	-2.546	0.261	-9.738	< 0.0001	***
Developed cover	1.018	0.488	2.088	0.0368	*
Grain crop cover	-4.077	0.896	-4.549	< 0.0001	***
Beans crop cover	-4.724	1.710	-2.763	0.0057	**
Mean annual temperature (Bio1)	0.227	0.084	2.713	0.0067	**
Mean annual precipitation (Bio12)	-0.181	0.081	-2.232	0.0256	*

The best-fit model for the second imperiled bumble bee species, *B. fraternus*, was the final model post-variable selection that used terms associated with the 500-m buffer size (Table 2.4). This was compared to the initial model using the same buffer size (ΔAIC = 8.59), and both models using surrounding landscape variables (ΔAIC = 20.92 and 10.92, for initial and final models, respectively). The best-fit model resulted in highly significant smoothing terms (edf = 34.72, chi-sq = 162.1, p-value < 0.0001). The final land cover and climate variables explained 64.8% of deviance in the model, which was relatively high. Similarly to the two species mentioned above, *B. griseocollis* increased likelihood of presence was positively associated with an increase in developed cover in the local landscape, and very strongly affected by bean and grain crop coverage in a negative way. For this species, a larger intensity is predicted in areas with a higher mean annual temperature and a lower mean annual precipitation.

Table 2.5. Summary statistics of the significant predictor variables for *B. impatiens* using the best-fit generalized additive model.

Variable	Estimate	Std. Error	Z value	Pr (>|z|)	
(Intercept)	-2.792	0.900	-3.101	0.0019	**
Grassland cover	-1.923	0.910	-2.114	0.0345	*
Developed cover	1.447	0.814	1.778	0.0754	.
Woody cover	3.455	1.196	2.888	0.0039	**
Grain crop cover	-4.946	1.861	-2.658	0.0079	**
Mean annual precipitation (Bio12)	-0.388	0.192	-2.017	0.0436	*
Precipitation seasonality (Bio15)	-0.428	0.207	-2.068	0.0387	*

Results for *B. impatiens* differed from those of the other species in that the best-fit model was the final model post-variable selection using climate and land cover variable data extracted from the 2-km buffer (Table 2.5). The initial model using data from the surrounding area, as well as both models using a smaller buffer size, resulted in slightly weaker model performance (ΔAIC = 6.82, 11.84, and 6.42, respectively). The climate and land cover variables in the best-fit model explained over half of deviance (52.3%) and the smoothing terms were significant (edf = 5.959, chi-sq = 33.36, p-value = 0.00005). Developed cover and woody cover were positively associated with *B. impatiens* likelihood of presence across the state; vice versa for grassland and grain crop cover, of which the latter predictor variable was very strong. The intensity of this species was also negatively affected by an increase in both mean annual precipitation and precipitation seasonality, meaning that as precipitation increases throughout the year and reaches extremes, this species will have a low likelihood of presence in some areas.

Model-predicted Geographic Distribution

After modeling the intensity function for each group, I fit the best-performing models to new data (50 x 50 grid cells covering the extent of Kansas) to generate heat maps displaying the model-predicted intensity of each species (Figure 2.8). These maps show the likelihood of each species being found per unit area across the state of Kansas during 2018-2023. While the general spatial patterns align with the distribution of confirmed sightings in Figure 2.2, there are increased predictions of presence in areas with missing occurrence data.

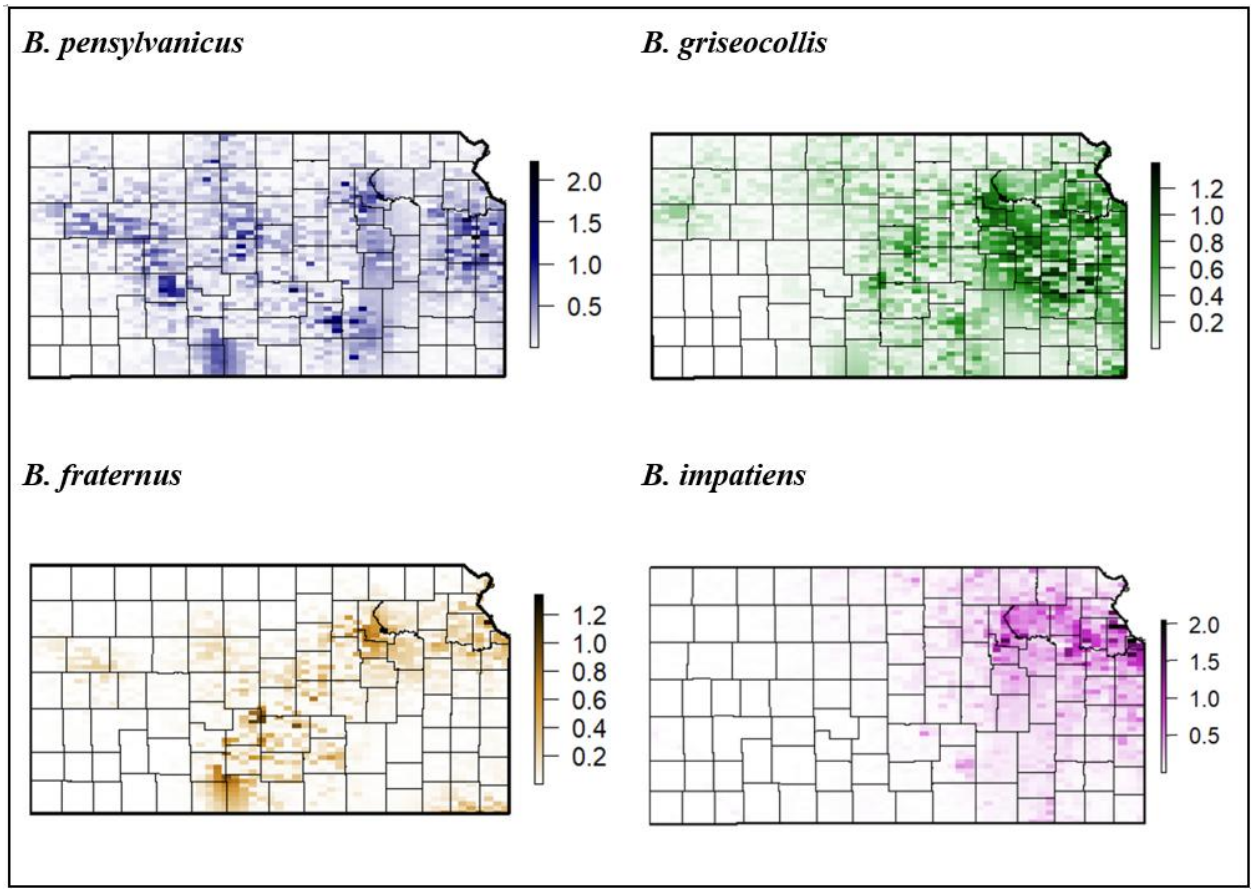

Figure 2.8. Likelihood of presence (intensity function) predictions across Kansas counties for *B. pensylvanicus*, *B. griseocollis*, *B. fraternus*, and *B. impatiens* modeled using the best-fit generalized additive model with an inhomogeneous Poisson point process for each species.

Maps on the left in Figure 2.8 highlight potential critical zones for the two imperiled bumble bee species if they become federally listed. Hotspots for *B. pensylvanicus* are predominately found in areas of grassland cover that are interspersed between crop fields in western and central Kansas, as well as the grassland-dominated Flint Hills region in the eastern portion of the state. Notable locations include Clark & Comanche Counties in the southwest, around the Wichita area in Sedgwick and neighboring counties, the greater Kansas City Metro area south into Anderson and Linn Counties, and up through the Flint Hills region into Riley County. Hodgeman County may be a critical area in the western part of the state, as evidenced by a large cluster of high predicted intensity. There was also a steady intensity across central Kansas with isolated hot spots in Barton and Russell Counties. Hotspots for *B. fraternus* are not as extensive across the state, but are similarly linked to areas with less agricultural fields, more grassland, and some urban cities. The predicted distribution tends to follow a pattern moving westwards from the densely populated areas of Kansas City to Salina, diverting south towards Hutchinson. There is a steady presence in central Kansas, with hotspots near Stafford and Barber Counties. Likelihood of presence in northwest and southeast regions are generally low except for a higher intensity along the southern border in both Labette and Cherokee Counties, where there are higher temperatures and more grassland refuge amongst the surrounding bean crop fields.

While not informative for critical habitat designation, the model-predicted maps for *B. griseocollis* and *B. impatiens* still display interesting spatial trends. *B. griseocollis* has a consistent intensity across most of the state, with limited predicted presence in the southwestern region. Conversely, *B. impatiens* appears to be mainly constrained to eastern Kansas, with intensity gradually dropping off moving westward. There was a steady presence in the Flint

Hills; however, extremely high intensities are clustered around the densely-populated row of cities along Interstate 70 – Manhattan, Topeka, Lawrence, and Kansas City.

Discussion

In general, I found that significant predictor variables affect the likelihood of presence for all species in slightly different ways. Differences in habitat associations on the landscape scale were more-so species-specific than characteristic of "common" and "imperiled" groups. The two threatened species did not have uniquely shared habitat associations that differed from the two common species. This trend is corroborated by Liczner & Colla (2020), who found that even two at-risk species sharing a similar range in California had slightly different habitat associations. Trends in spatial patterns across the state were highly dependent upon the species of interest; however, several drivers of such distributions were shared.

Overall, crop cover is neither important for immediate detection of bumble bees, nor as a beneficial land cover type in the surrounding landscape. Monoculture crops, like beans and grains, were negatively associated with the likelihood of presence for all species in Kansas, indicating that continued agricultural expansion from native grasslands to those crop fields as historically reported by Lark et al. (2015) could cause detrimental effects to bumble bee communities as a whole. One possible solution to minimize downsides of crop production in the state could include increasing heterogeneity in the landscape. Hemberger & Williams (2025) recently found that western bumble bee species benefit from landscapes that have multiple cover types present, which is consistent with my findings that large areas of one crop type is disadvantageous for the Kansas species investigated. Planting or conserving prairie strips around or within those crop fields would decrease the percentage of non-beneficial crop cover, increase the percentage of grasslands with the potential for higher quality forage, and allow the area to

support more pollinators through this addition of positively associated habitat. In addition to landscape simplification, an increase in agricultural cover is often accompanied by an increase in pesticide concentration, which has negative effects on North American bumble bee health and distributions (Cameron et al. 2011; Gradish et al. 2018; Janousek et al. 2023). Lobbying to reduce the use of neonicotinoid pesticides on crop fields in the United States, as successfully achieved by the European Union in 2013 (Wood & Goulson 2017), could limit harmful pesticide exposure for midwestern bumble bees living in areas with intense agricultural expansion.

Additionally, the likelihood of presence for all species was positively associated with developed areas in the landscape. It is possible this result arose due to the nature of the occurrence data, despite my efforts to account for urban sampling biases; however, it could also be a natural association for species across the board. Urbanization may not be critically damaging, as long as there are still foraging opportunities around. Local floral resource availability is important for bumble bee abundance in both developed and agriculturally dominant extents (Nunes et al. 2024). Areas of low intensity development, such as urban parks, roadside plantings, and residential gardens, may provide a particular refuge for bumble bees, including *B. pensylvanicus* and *B. fraternus* (Novotny et al. 2021). My findings do not suggest that threatened species in general are underutilizing developed areas more than common species; however, *B. impatiens* appears to have a particular affinity for urban areas, both in terms of immediate detection and landscape-level influences on its spatial distribution. Given the preference of *B. impatiens* towards developed areas, I expect that it will become more prominent in cities such as Hutchinson, Dodge City, and Wichita as it continues to move westward past its native range due to commercial use for crop pollination (Velthuis & van Doorn 2006).

While grassland was not a significant variable in the SDMs for *B. griseocollis*, *B. fraternus*, or *B. pensylvanicus*, their respective model-predicted distribution maps do show strong predicted presence in those areas, possibly due to the opposing effect of grain cover. I suspect that the negative effect of crop coverage was more significant than the positive effect of grassland. Those three species were also most commonly found with grassland in the immediate and surrounding area, indicating that it is still an important cover type for bumble bee habitat. Even though I expected bee-pollinated crops to attract bumble bees due to their requirement of buzz-pollination which bumble bees excel at (De Luca et al. 2013), this land cover type lacked strength in the results. This is likely attributed to relatively fewer pixels across the state, leading to underrepresentation in the surrounding landscape. Bumble bees may be visiting backyard gardens; however, if they are smaller than the raster's resolution, the land cover pixel would be classified as a different, nearby category. More data in urban farm and garden systems may uncover stronger associations on the local scale.

Overall, most practically-significant differences in habitat associations on both the local and surrounding scale were driven by *B. impatiens*. It was associated with more developed cover, less grassland, and more bean crop cover in the landscape than the other species. All other slight variations in habitat associations were species-specific and didn't supply clear trends. From the generalized additive model results, *B. impatiens* was also the only species that was negatively associated with an increase in grassland. I speculate that this species may be of least conservation concern because it is able to extensively utilize nesting and foraging habitat in highly developed areas, while not having to rely on surrounding native grasslands where the other species are most commonly detected.

The results suggest that, of the two imperiled species, *B. pensylvanicus* is associated with a presence of woody cover in the local landscape, possibly due to its tendency to use ground litter to protect their above-surface nests (Williams et al. 2014). Critical habitat for this species may include areas with some degree of grassland, forest, and developed land cover types. Neither precipitation nor temperature were important drivers of this imperiled species' distribution in Kansas. This species also had the highest number of observations relative to the other three *Bombus* spp. investigated, indicating that it is still doing relatively well in this part of its range despite patterns of large-scale decline observed elsewhere. *B. fraternus* tended to be found in areas with higher temperatures and lower precipitation. These findings suggest that this species may do well in Kansas during upcoming years, as the state is expected to become even warmer and drier over the next 30 years due to climate change (Ojima et al. 2021). All other critical habitat recommendations are similar to those that affected all species, as discussed above.

My findings provide valuable information that can be used to inform future conservation efforts for *B. pensylvanicus* and *B. fraternus* in Kansas. I highlight the climate and land cover types that are most strongly associated with the presence of those species, which should be considered when attempting to restore/ generate habitat for them in areas of currently low abundance. Additionally, the intensity maps for *B. pensylvanicus* and *B. fraternus* display potential priority areas where the species are likely to have been found in recent years across Kansas. I suggest increasing survey efforts in counties with a high predicted intensity that are currently lacking data on the maps in Figure 2.2.

In the future, I hope to explore these data in an integrative species distribution modeling framework (Koshkina et al. 2017). Data integration by combining occurrence records from both surveys and incidental observations using a Bayesian hierarchical modelling approach is

uncommon in the literature, but has many benefits (Fletcher et al. 2019). I attempted to correct for the implicit urban bias from presence-only data by thinning incidental observations; however, future research might consider accounting for observer bias within the model. Warton et al. (2013) proposes the inclusion of two separate sets of variables in the hierarchical model: (1) one that may explain observer bias, such as proximity to roads or highly populated cities; and (2) one that addresses true changes in species occurrence, such as habitat characteristics. These methods have been demonstrated in other wildlife systems (Koshkina et al. 2017; Garattola et al. 2023), but lack extensive application in the current study of at-risk bumble bees. With the continued threat of bumble bee decline looming, it is important to continue making advancements in conservation research using different modeling techniques.

Despite this chapter focusing mainly on bumble bee associations in a single state that required more research (Hatfield et al. 2014), it has implications for further research across the entire country, which is crucial given that listing a species under the Endangered Species Act is a federal concern. This study took place in an area where the species appear to be doing well, relative to more heavily researched parts of their ranges; therefore, conclusions about critical habitat characteristics drawn from this research may assist in conservation efforts (e.g., habitat restoration and land management) across other areas of North America where they have seen historic declines. This information is also useful for species distribution models constructed to predict where their geographic ranges may shift in the future according to different projected land cover and climate change scenarios.

Using a simple data-pooling approach, this research exposed fascinating insights into the habitat associations and geographic distributions of four *Bombus* spp. in Kansas. My findings shed light on species variation in the utilization of different land cover types within local and

surrounding landscapes, and highlights the distinct preference of *B. impatiens* towards developed areas, more so than the other species. This study provides implications for the effects of urbanization, agricultural expansion, and climate change on distributions of Kansas bumble bee species across the state and emphasizes the importance of species-specific considerations when making habitat restoration or classification plans for particular taxa. The model-predicted distribution maps should help inform the development of priority areas for the two imperiled species along the western portion of their range, and hopefully the habitat association findings will be beneficial in defining critical habitat in the event that *B. pensylvanicus* and/or *B. fraternus* become endangered on the federal level.

Conclusion

Through the application of both an experimental study on the local scale, and a model-focused examination on the state-wide scale, I was able to uncover valuable information that can be used to support Kansas bumble bee species. The first chapter provided guidance for pollinator-conscious land managers in the Great Plains who are interested in utilizing bumble bee-friendly practices. It revealed that bison-grazing and prescribed fire, two disturbance methods commonly used in the Great Plains, have potential to benefit *Bombus* spp. and the forb communities that they rely on, if applied responsibly. It also highlighted forb taxa commonly visited by each species to inform targeted tallgrass prairie seed mixes for midwestern bumble bee that are more or less specialized foragers. The second chapter sheds light on land cover and climate factors associated with imperiled and common bumble bee species found in the Great Plains. It uncovered the negative impact of agricultural expansion and potential benefits of urban greenspaces as refuge in developed areas for all species, regardless of conservation status. The model-predicted distribution maps in Kansas will be very useful for future *Bombus* protection and targeted surveying efforts in understudied parts of the state. In general, this research provided evidence that the two imperiled species may be doing well in Kansas, despite patterns of decline in other parts of their ranges that are more heavily studied. Both *B. pensylvanicus* and *B. fraternus* were among the most abundant species observed at my sites in Eastern Kansas (Chapter 1), and did not have the lowest relative number of state-wide occurrences reported from incidental or survey-based data sources that were used to construct my SDMs (Chapter 2). That may not always be the case, though, which is why this current study and continued research are so valuable. I hope that this additional research along the western part of their ranges will help land managers and policymakers make informed decisions when it comes to future conservation

efforts for Kansas bumble bee species; whether they are within the state, the larger Great Plains region, or another portion of their range to which these results can be extrapolated. With the help of dedicated community scientists, pollinator-conscious land managers, well-informed policymakers, and further research investigating other understudied parts of their ranges, I have faith that we can all come together to protect these important pollinators.

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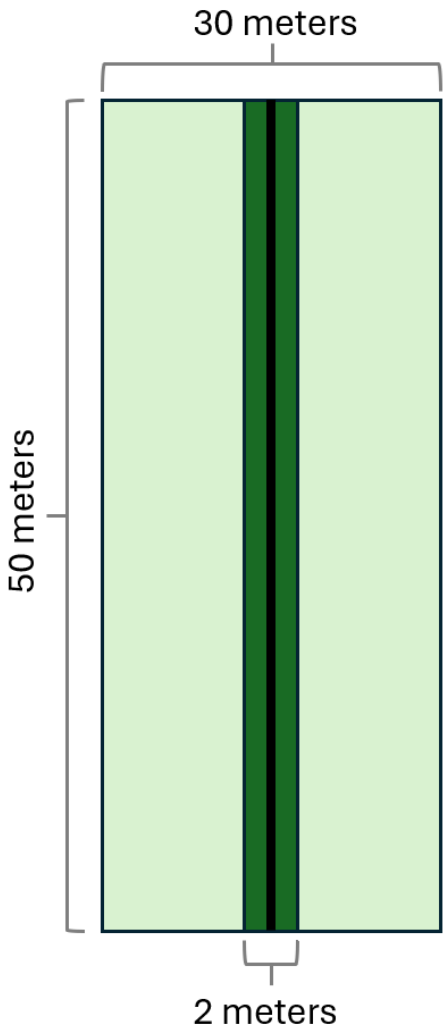
Appendix A - Supporting figures and tables from chapter 1

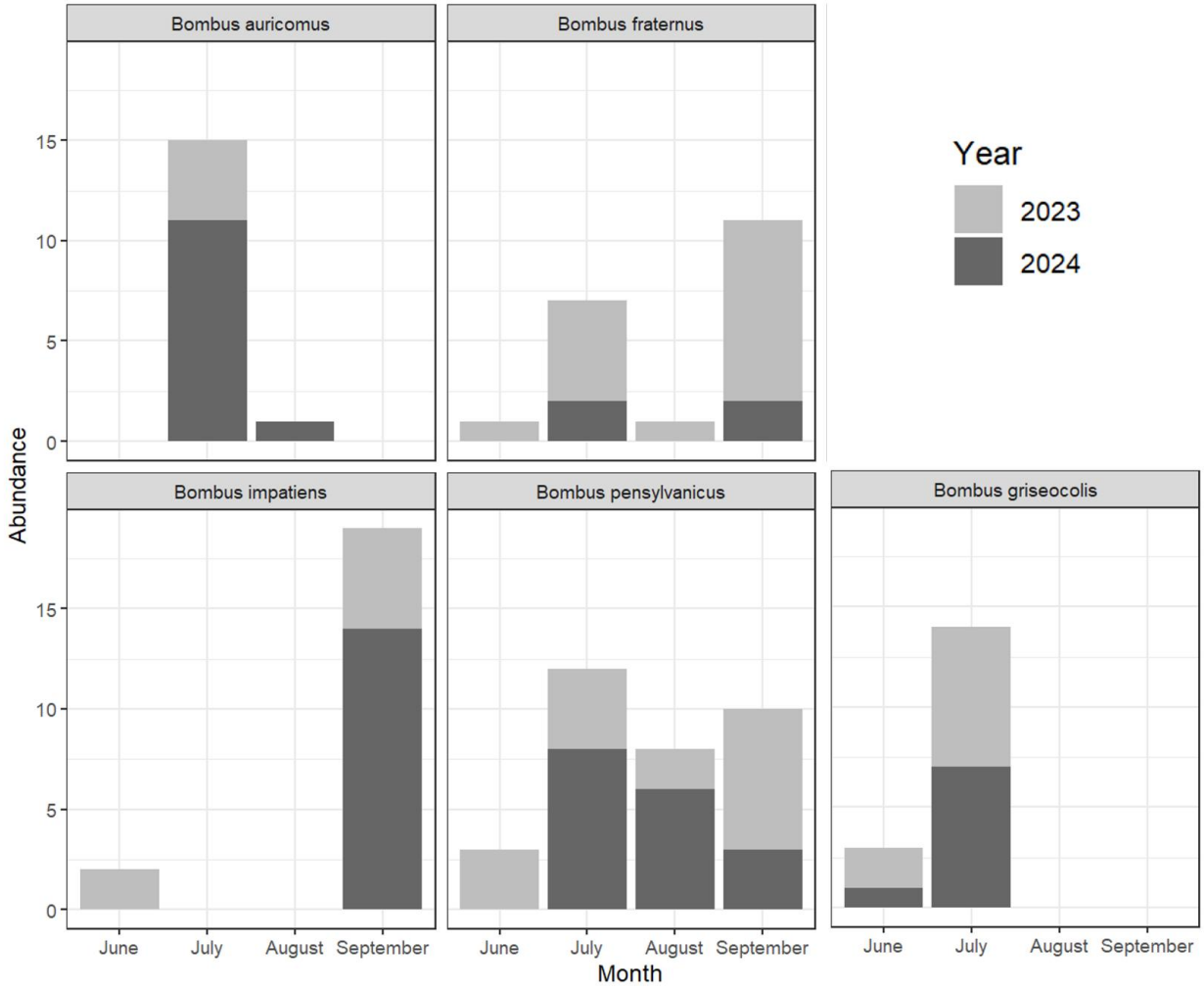


Appendix Figure A.1. Diagram of the plot design established at each site with the Konza Prairie Biological Station, in which bumble bee surveys were conducted within the light green portion and vegetations surveys along the dark green rectangle surrounding the 50-m transect.

Appendix Figure A.2. Example image of a watershed at the Konza Prairie Biological Station that experienced bison grazing.

Appendix Figure A.3. Example image of a watershed at the Konza Prairie Biological Station that experienced no grazing.

Appendix Figure A.4. Example image of a newly-burned (left) and unburned (right) watershed at the Konza Prairie Biological Station by the end of the season (November).



Appendix Figure A.5. Bumble bee species abundance by month for both years of data collection.

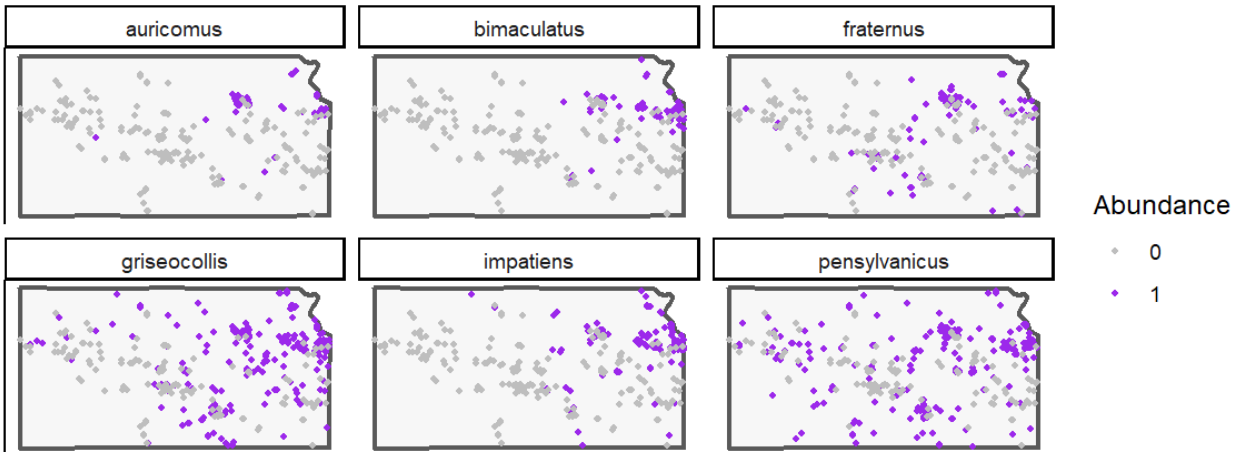
Appendix Table A.1. Summary statistics table from the complex linear mixed effects model incorporating burns per year over a 20-year period (long-term) as the fire frequency term.

Variable	Estimate	Std. Error	Z value	Pr (>|z|)	
(Intercept)	-262.177	361.337	-0.726	0.4681	
Graze treatment	1.327	0.337	3.941	<0.0001	***
Fire frequency	0.864	0.396	2.182	0.0291	*
Graze:Fire Interaction	-0.932	0.494	-1.889	0.0589	.
Year	0.130	0.179	0.726	0.4681	

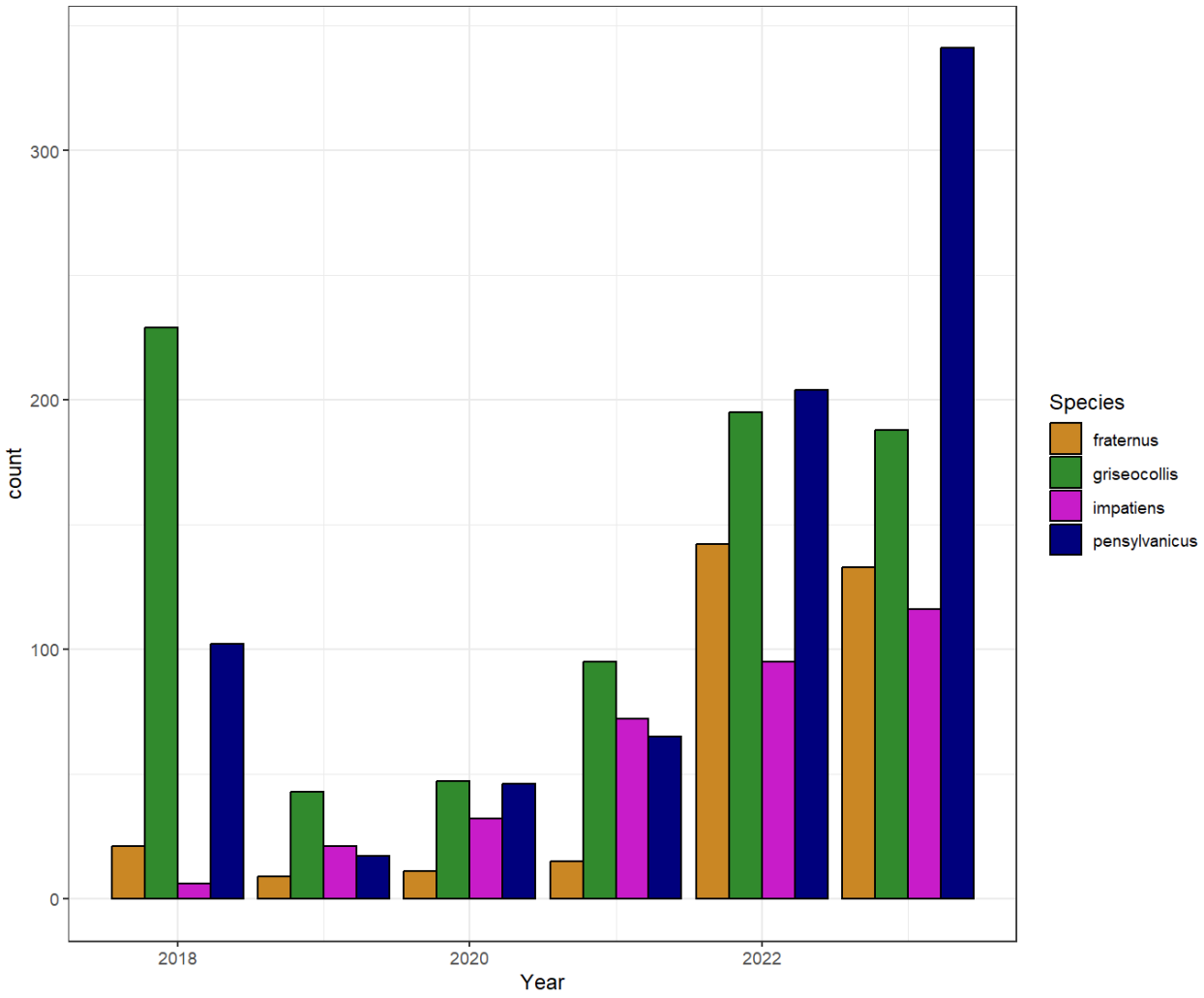
Appendix Table A.2. Summary statistics table from the initial piecewise structural equation model before backward elimination variable selection.

Response	Predictor	Estimate	Std. Error	Df	Crit. Value	Std. Estimate	P-value	
Bumble bee abundance	Bison-grazing	0.5245	0.4568	13	1.2990	0.2376	0.2755	
Bumble bee abundance	Fire frequency	0.5054	0.3746	8	1.82	0.1702	0.2150	
Bumble bee abundance	Forb abundance	0.0045	0.0024	86	3.2263	0.2107	0.0760	
Bumble bee abundance	Forb diversity	0.9206	0.5394	86	2.7523	0.1903	0.1008	
Bumble bee abundance	Interaction	-0.5109	0.6193	8	0.6794	-0.1749	0.4329	
Forb abundance	Bison-grazing	46.8558	17.8364	8	6.9010	0.4539	0.0303	*
Forb abundance	Fire frequency	-7.8962	16.6817	8	0.2241	-0.0569	0.6486	
Forb abundance	Interaction	3.1736	27.1879	8	0.0136	0.0232	0.9100	
Forb diversity	Bison-grazing	0.2940	0.0807	8	13.2673	0.6443	0.0066	**
Forb diversity	Fire frequency	0.0046	0.0755	8	0.0038	0.0075	0.9527	
Forb diversity	Interaction	-0.2046	0.1230	8	2.7669	-0.3389	0.1348	

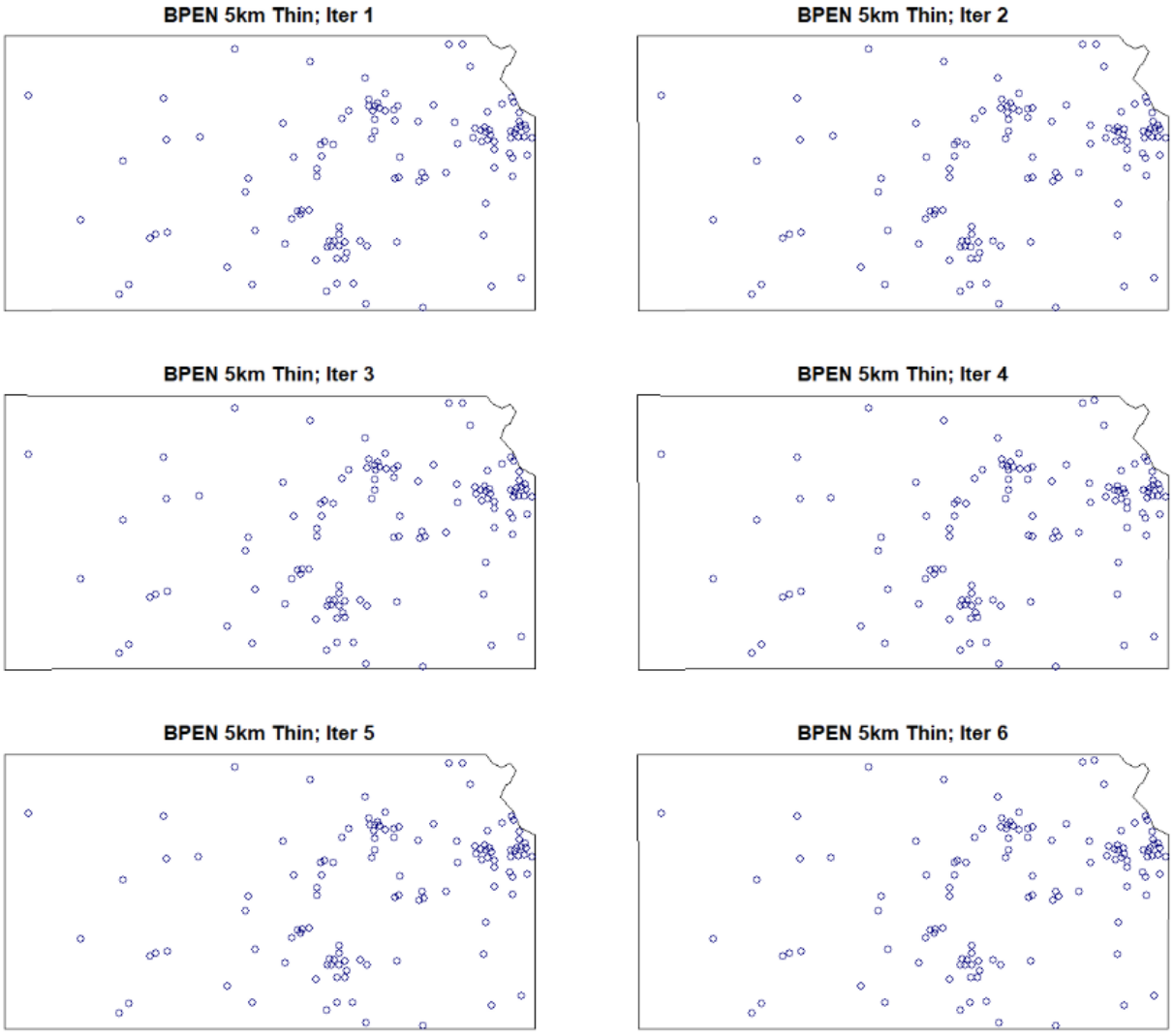
Appendix B - Supporting figures and tables from chapter 2



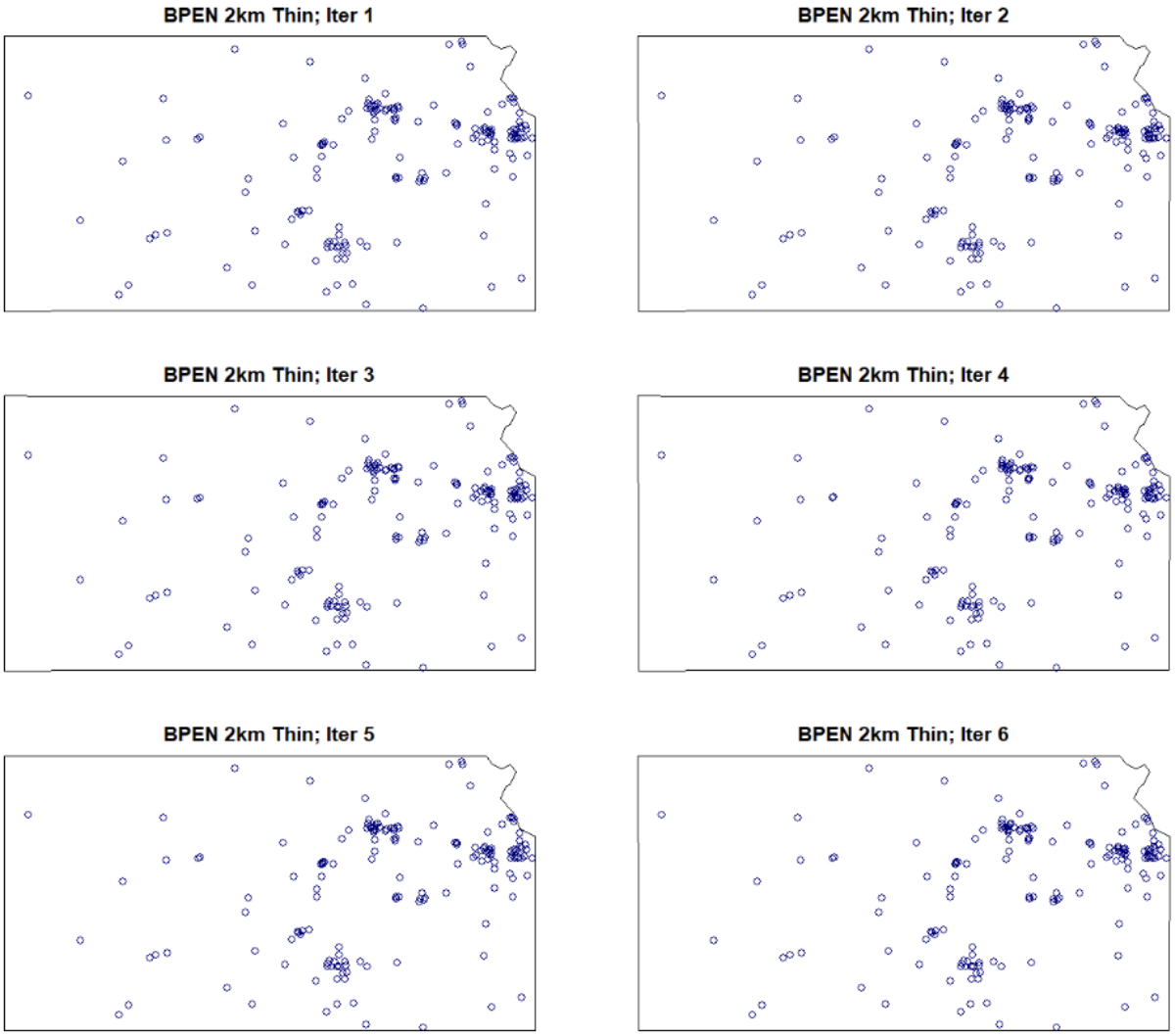
Appendix Figure B.1. Known presence and absence locations of each Kansas bumble bee species from the pre-thinned data collected between 2018 – 2023.



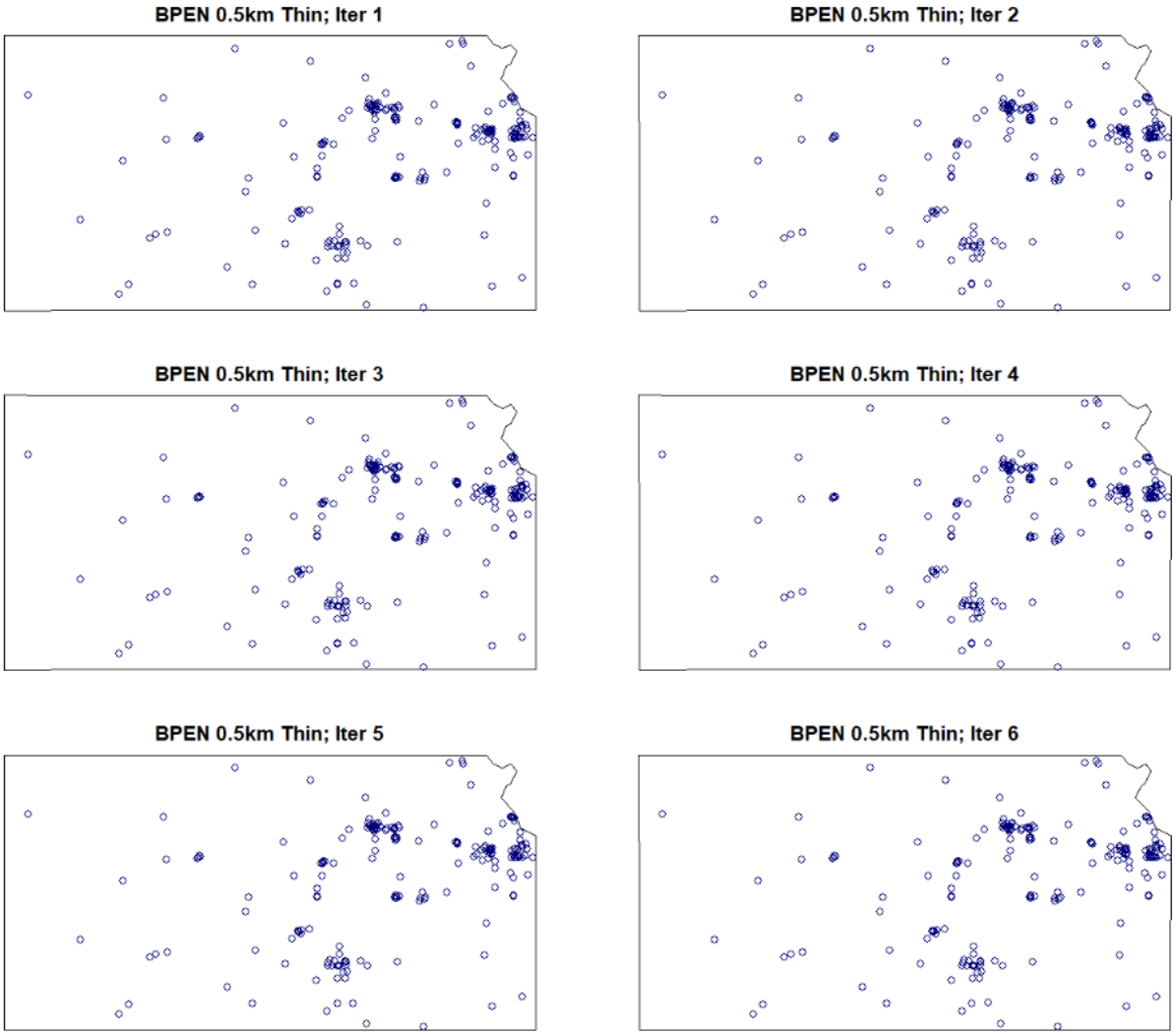
Appendix Figure B.2. Count of records collected per year between 2018 – 2023 for each bumble bee species.



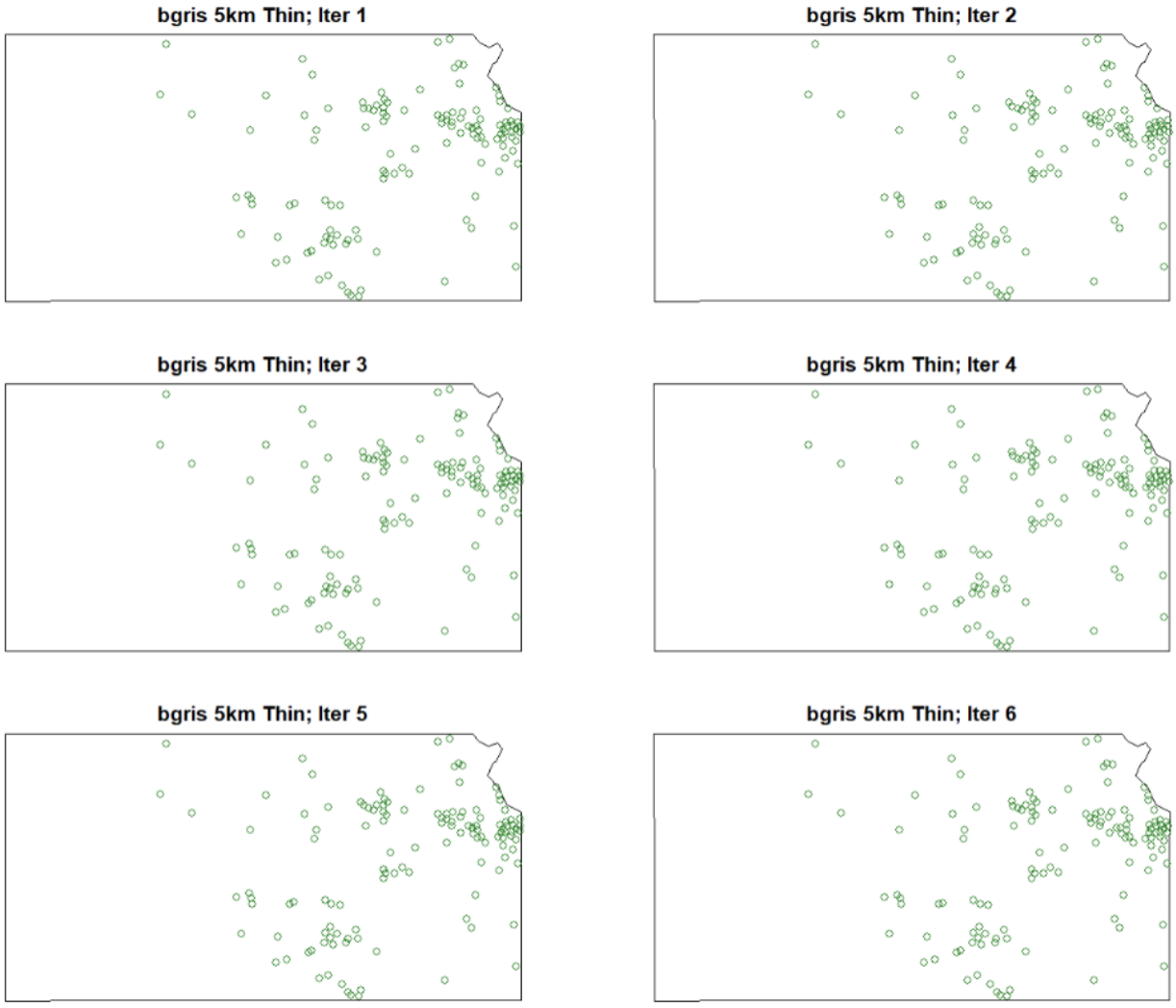
Appendix Figure B.3. Distribution of *B. pensylvanicus* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 5 km (final number of records = 119; completed iterations = 100).



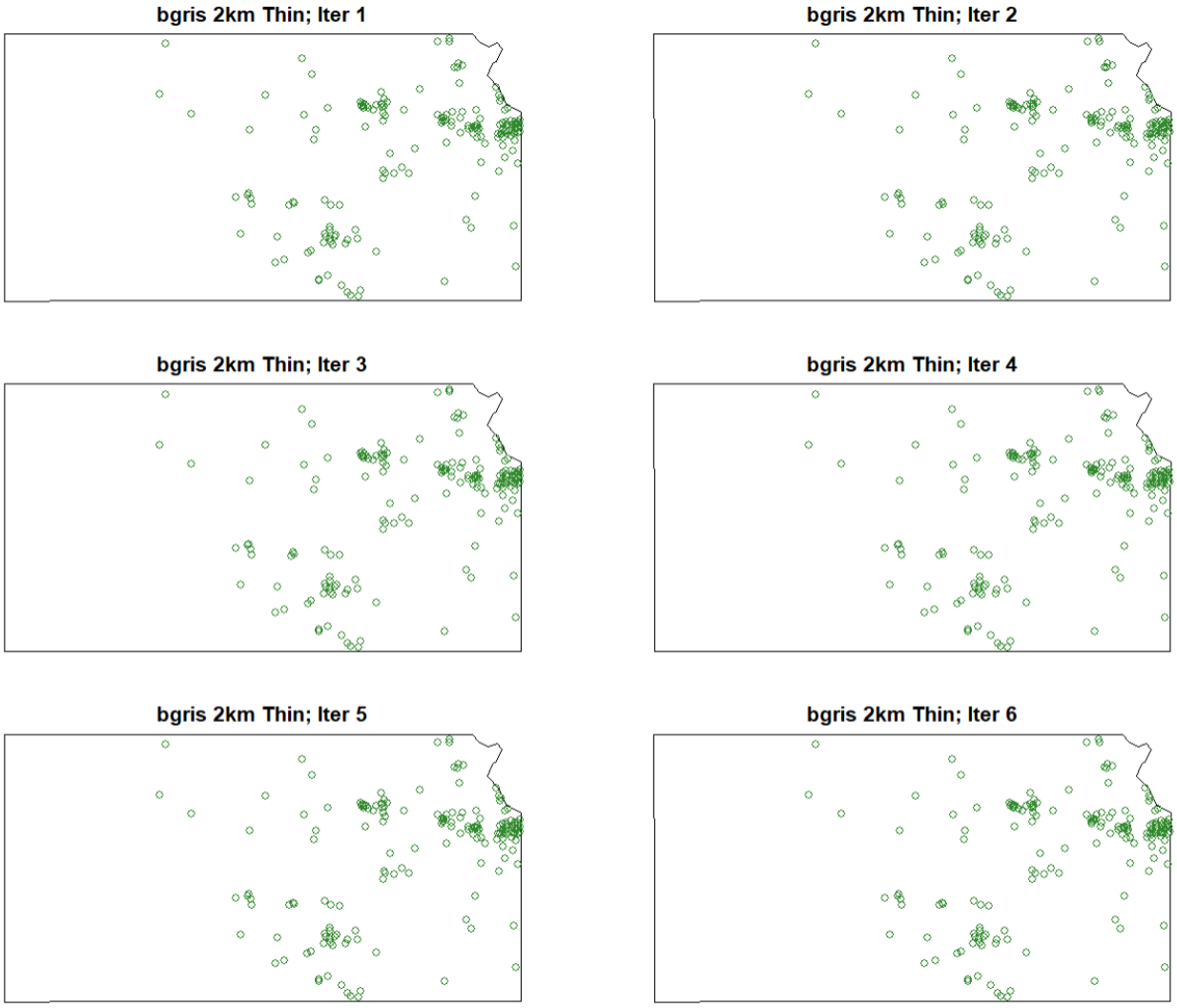
Appendix Figure B.4. Distribution of *B. pensylvanicus* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 2 km (final number of records = 161; completed iterations = 86).



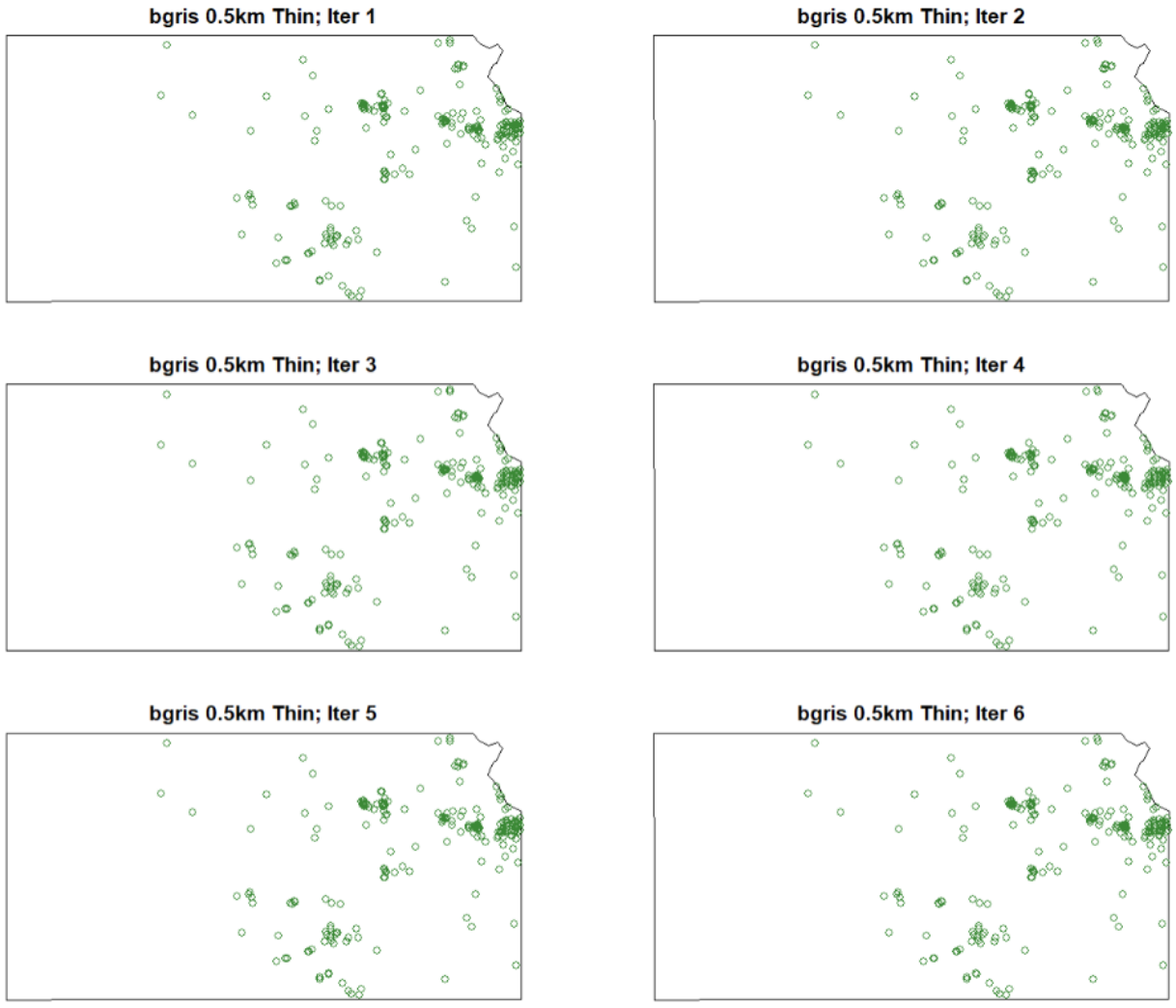
Appendix Figure B.5. Distribution of *B. pensylvanicus* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 500 m (final number of records = 202; completed iterations = 100).



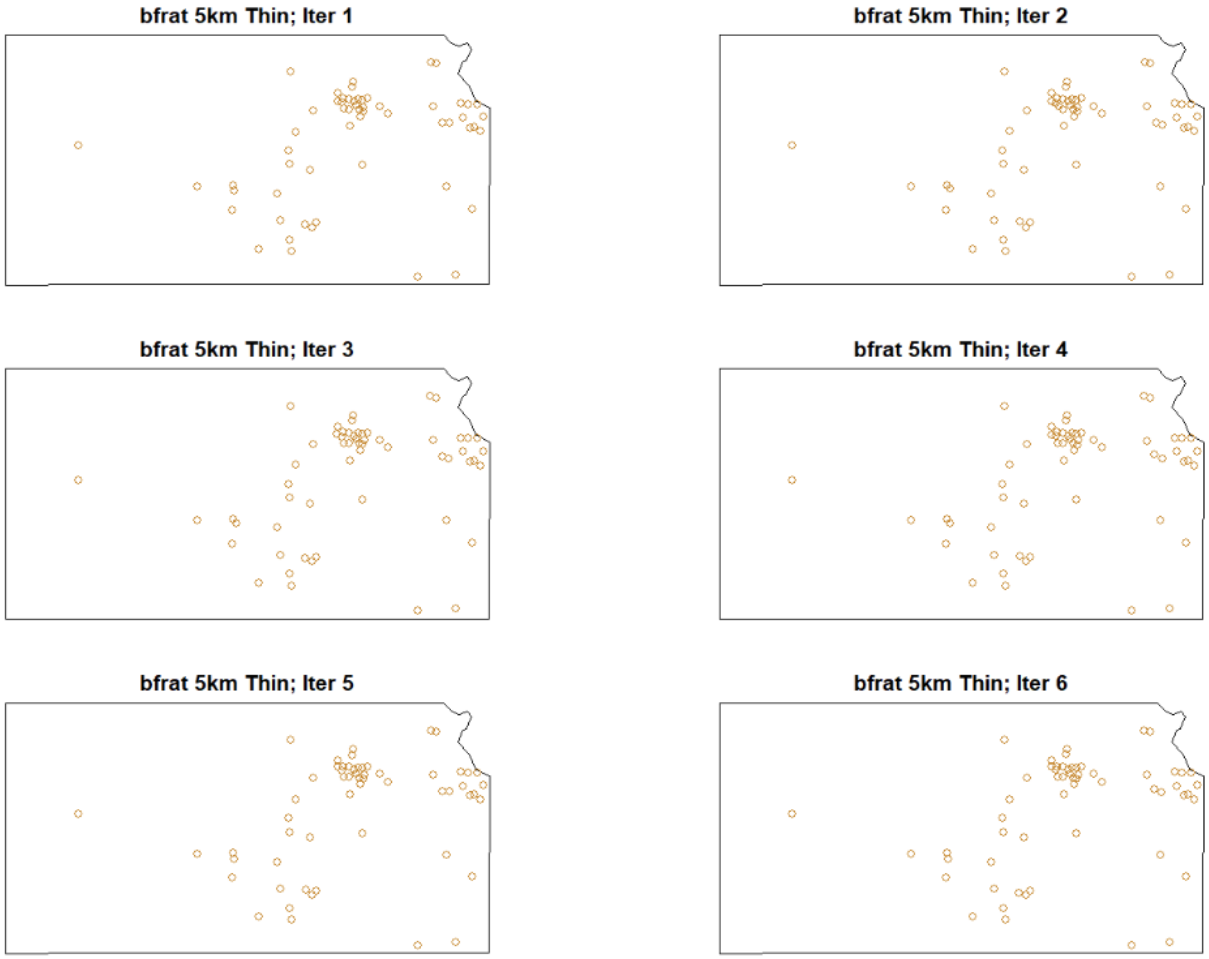
Appendix Figure B.6. Distribution of *B. griseocollis* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 5 km (final number of records = 121; completed iterations = 40).



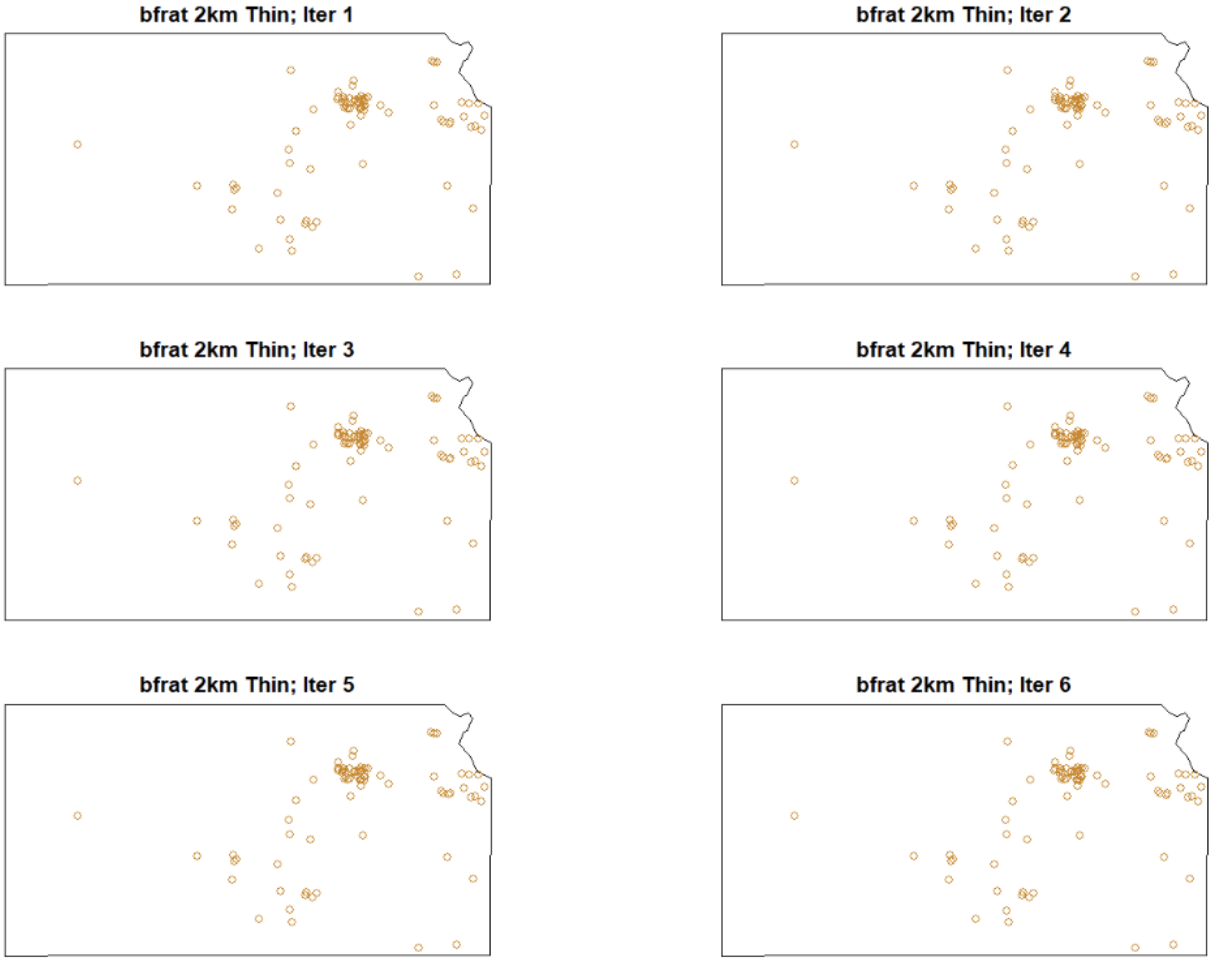
Appendix Figure B.7. Distribution of *B. griseocollis* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 2 km (final number of records = 171; completed iterations = 100).



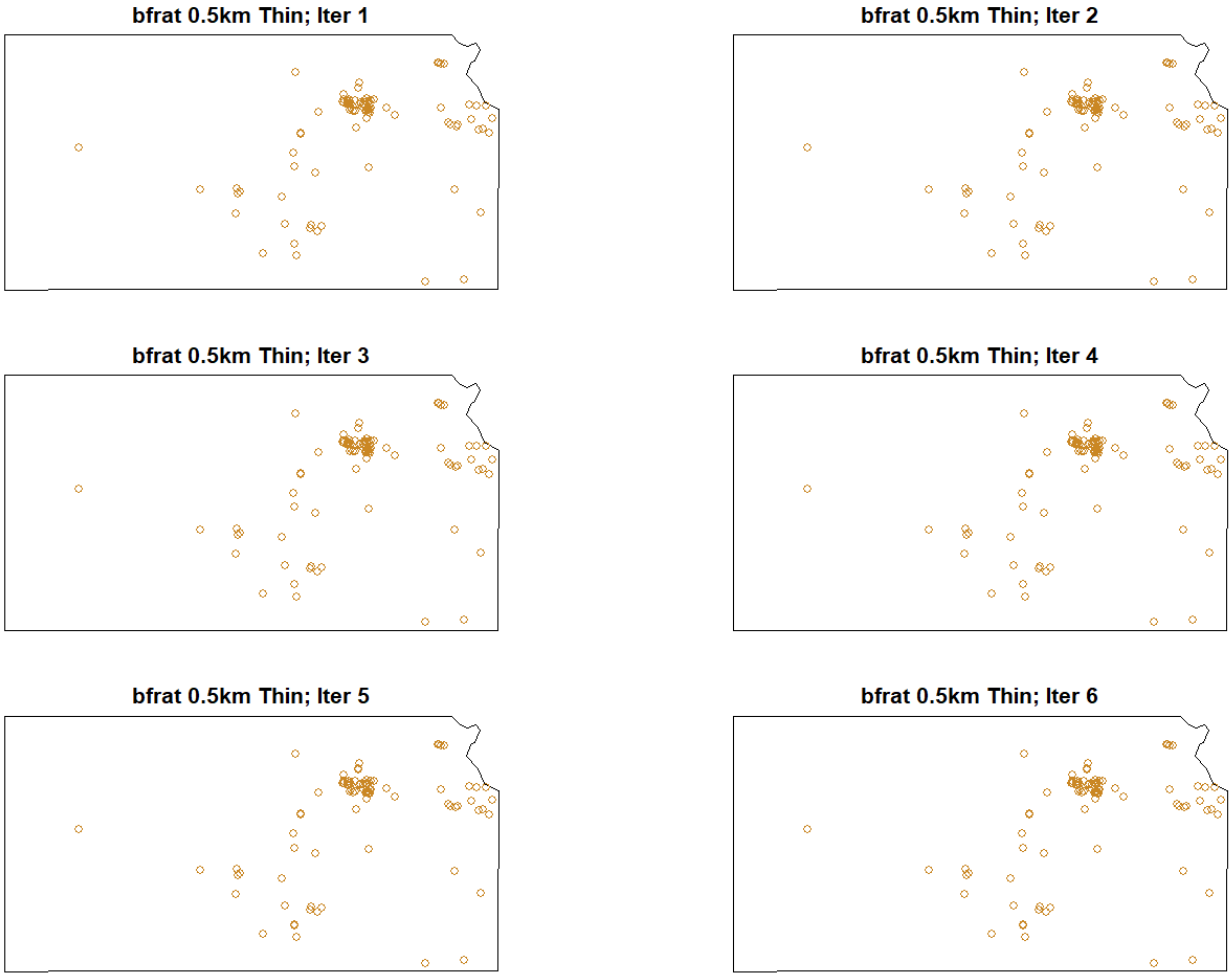
Appendix Figure B.8. Distribution of *B. griseocollis* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 500 m (final number of records = 212; completed iterations = 100).



Appendix Figure B.9. Distribution of *B. fraternus* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 5 km (final number of records = 58; completed iterations = 100).

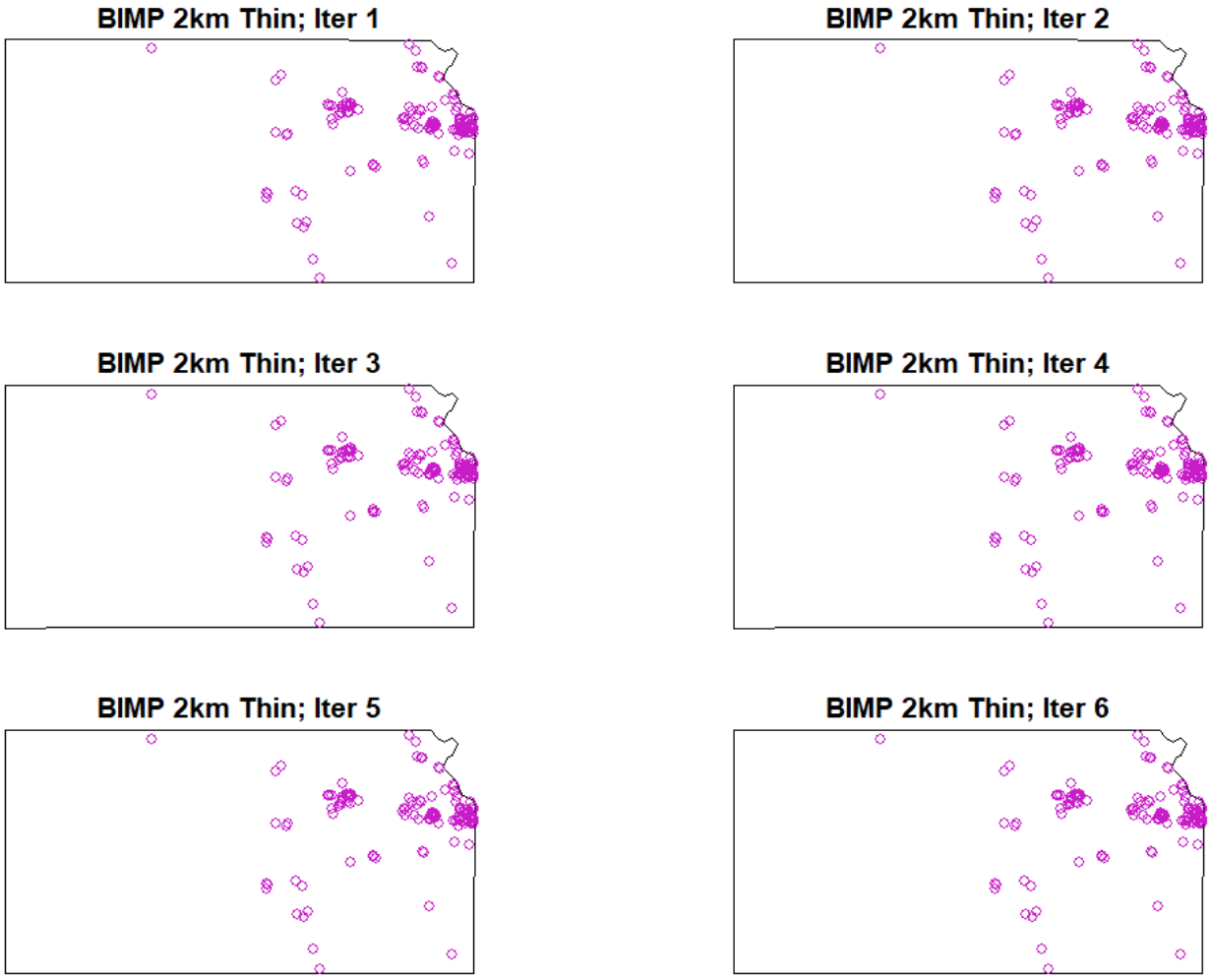


Appendix Figure B.10. Distribution of *B. fraternus* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 2 km (final number of records = 77; completed iterations = 100).

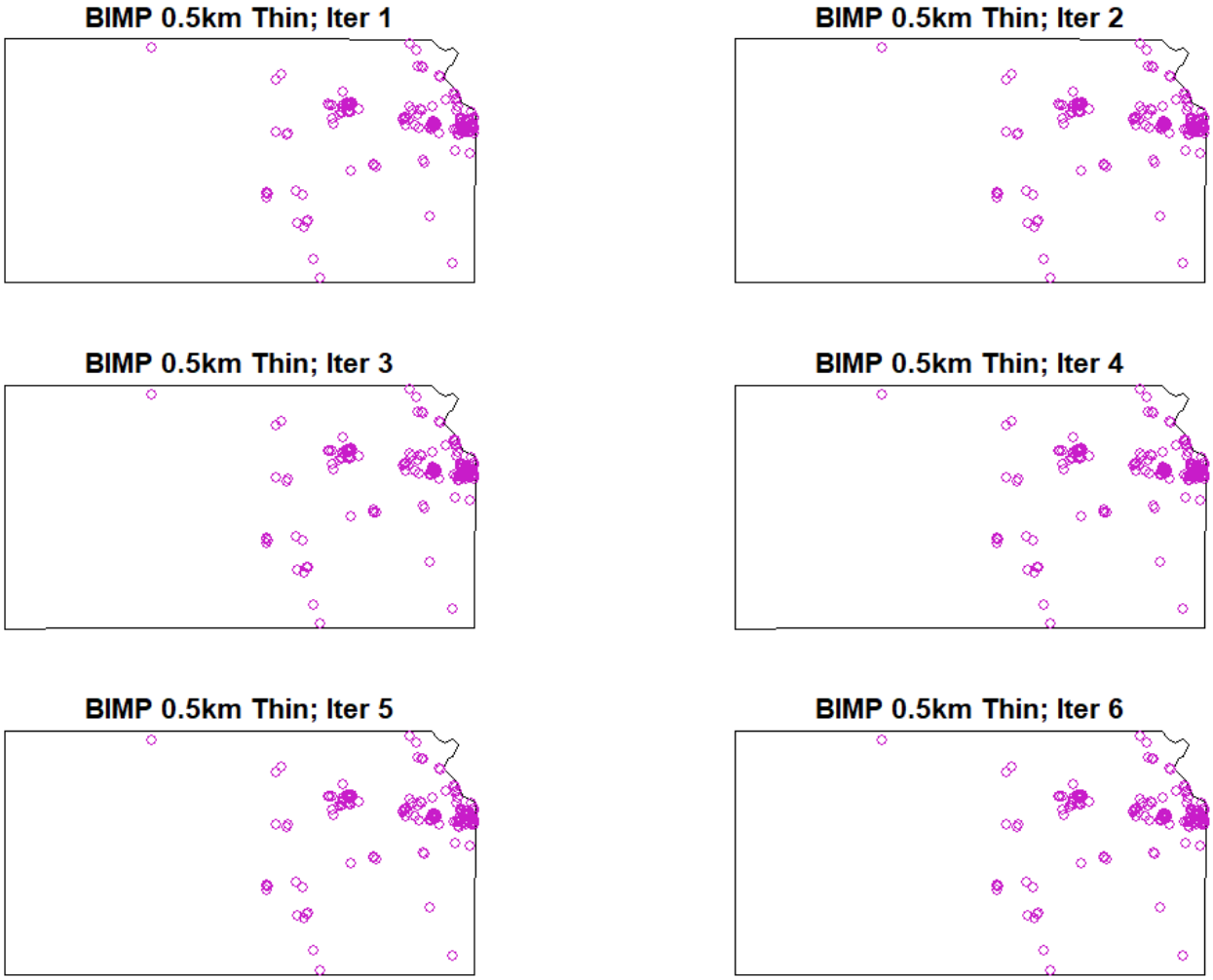


Appendix Figure B.11. Distribution of *B. fraternus* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 500 m (final number of records = 92; completed iterations = 100).

Appendix Figure B.12. Distribution of *B. impatiens* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 5 km (final number of records = 79; completed iterations = 9).



Appendix Figure B.13. Distribution of *B. impatiens* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 2 km (final number of records = 118; completed iterations = 94).



Appendix Figure B.14. Distribution of *B. impatiens* incidental observation records from six randomly selected iterations of the thinning process with buffer size set to 500 m (final number of records = 170; completed iterations = 100).

Appendix Table B.1. Total number of presence records from survey and incidental observation data sources per species (pre-thinning process), where the source codes are as follows: "PA.gb" = survey records from Brunette 2025, "PA.bba" = survey records from the Great Plains Bumble Bee Atlas, "PA.crp" = survey records from Morphew 2019, "PO.gbif" = incidental observation records from the Global Biodiversity Information Facility, and "PO.bm" = incidental observation records from BeeMachine.

Source	Data Type	BAUR	BBIM	BFRAT	BGRIS	BIMP	BPEN	Totals
PA.gb	Survey	10	1	10	27	3	72	**123**
PA.bba	Survey	128	25	184	192	27	322	**878**
PA.crp	Survey	4	1	17	206	1	81	**310**
PO.gbif	Incidental	50	133	90	342	219	257	**1091**
PO.bm	Incidental	7	7	30	30	92	43	**209**
Totals	**----**	**199**	**167**	**331**	**797**	**342**	**775**	**2611**

Appendix Table B.2. Total number of absence records from survey data sources per species (pre-thinning process), where source codes are as follows: "Abs.gb" = known absence records from Brunette 2025, "Abs.bba" = known absence records from the Great Plains Bumble Bee Atlas, and "Abs.crp" = known absence records from Morphew 2019.

Source	Data Type	BAUR	BBIM	BFRAT	BGRIS	BIMP	BPEN	Totals
Abs.gb	Known absence	14	19	16	9	18	11	**87**
Abs.bba	Known absence	100	103	85	74	100	44	**506**
Abs.crp	Known absence	141	144	135	77	144	97	**738**
Totals	**----**	**255**	**266**	**236**	**160**	**262**	**152**	**1331**

Appendix Table B.3. Total number of presence records from survey and incidental observation data sources (post-thinning process), where the source codes are as follows: "PA.gb" = survey records from Burnette 2025, "PA.bba" = survey records from the Great Plains Bumble Bee Atlas, "PA.crp" = survey records from Morphew 2019, and "Thinned" = survey records that remained after thinning with a 5-km buffer size.

Source	Data Type	BIMP	BGRIS	BPEN	BFRAT	Totals
PA.gb	Survey	3	27	72	10	**112**
PA.bba	Survey	27	192	322	184	**725**
PA.crp	Survey	1	206	81	17	**305**
Thinned	Incidental	76	128	119	58	**381**
Totals	**----**	**107**	**553**	**594**	**269**	**1394**

Appendix Table B.4. Total number of absence records from survey and random-generation data sources per species (post-thinning process), where the source codes are as follows: "Abs.gb = known absence records from Brunette 2025, "Abs.bba" = known absence records from the Great Plains Bumble Bee Atlas, "Abs.crp" = known absence records from Morphew 2019, and "Quad" = randomly generated pseudo-absence/ quadrature points across Kansas.

Source	Data Type	BIMP	BGRIS	BPEN	BFRAT	Totals
Abs.gb	Known abs	18	9	11	16	**54**
Abs.bba	Known abs	100	74	44	85	**303**
Abs.crp	Known abs	144	77	97	135	**453**
Quad	Pseudo-abs	1000	1000	1000	1000	**4000**
Totals	**----**	**1262**	**1160**	**1152**	**1236**	**4810**

Appendix Table B.5. Summary statistics for effect size (Hedge's G) analysis comparing percentage of each land cover type falling within a 2-km buffer around individuals of each species.

Group1	Group2	Land Cover	Buffer	Estimate	Magnitude	Confidence_Interval
BPEN	BGRIS	grassland	2-km	-0.242728	small	[-0.359, -0.126]
BPEN	BGRIS	grassland	2-km	-0.242728	small	[-0.359, -0.126]
BPEN	BIMP	grassland	2-km	0.818586	large	[0.608, 1.029]
BFRAT	BGRIS	grassland	2-km	0.168096	negligible	[0.022, 0.314]
BFRAT	BIMP	grassland	2-km	1.336089	large	[1.092, 1.58]
BGRIS	BIMP	grassland	2-km	1.182361	large	[0.966, 1.399]
BPEN	BFRAT	developed	2-km	0.305512	small	[0.161, 0.45]
BPEN	BGRIS	developed	2-km	0.233722	small	[0.117, 0.35]
BPEN	BIMP	developed	2-km	-0.709317	medium	[-0.919, -0.5]
BFRAT	BGRIS	developed	2-km	-0.09261	negligible	[-0.238, 0.053]
BFRAT	BIMP	developed	2-km	-1.127391	large	[-1.366, -0.889]
BGRIS	BIMP	developed	2-km	-1.081118	large	[-1.296, -0.866]
BPEN	BFRAT	woodland	2-km	-0.242587	small	[-0.387, -0.098]
BPEN	BGRIS	woodland	2-km	-0.225149	small	[-0.341, -0.109]
BPEN	BIMP	woodland	2-km	-0.774463	medium	[-0.984, -0.565]
BFRAT	BGRIS	woodland	2-km	0.028591	negligible	[-0.117, 0.174]
BFRAT	BIMP	woodland	2-km	-0.439926	small	[-0.666, -0.213]
BGRIS	BIMP	woodland	2-km	-0.532327	medium	[-0.741, -0.323]
BPEN	BFRAT	grains	2-km	0.294341	small	[0.15, 0.439]
BPEN	BGRIS	grains	2-km	0.152296	negligible	[0.036, 0.268]
BPEN	BIMP	grains	2-km	0.369075	small	[0.162, 0.576]
BFRAT	BGRIS	grains	2-km	-0.141848	negligible	[-0.288, 0.004]
BFRAT	BIMP	grains	2-km	0.136433	negligible	[-0.088, 0.361]
BGRIS	BIMP	grains	2-km	0.232395	small	[0.025, 0.44]
BPEN	BFRAT	beans	2-km	0.017913	negligible	[-0.126, 0.162]
BPEN	BGRIS	beans	2-km	-0.314228	small	[-0.431, -0.198]
BPEN	BIMP	beans	2-km	-0.510461	medium	[-0.718, -0.303]
BFRAT	BGRIS	beans	2-km	-0.327842	small	[-0.474, -0.181]
BFRAT	BIMP	beans	2-km	-0.519183	medium	[-0.747, -0.292]
BGRIS	BIMP	beans	2-km	-0.173642	negligible	[-0.381, 0.034]
BPEN	FRAT	bee-pollinated	2-km	-0.067588	negligible	[-0.212, 0.077]
BPEN	BGRIS	bee-pollinated	2-km	-0.005559	negligible	[-0.121, 0.11]
BPEN	BIMP	bee-pollinated	2-km	0.078407	negligible	[-0.128, 0.284]
BFRAT	BGRIS	bee-pollinated	2-km	0.058719	negligible	[-0.087, 0.205]
BFRAT	BIMPO	bee-pollinated	2-km	0.137093	negligible	[-0.087, 0.362]
BGRIS	BIMP	bee-pollinated	2-km	0.07848	negligible	[-0.129, 0.286]

Appendix Table B.6. Summary statistics for effect size (Hedge's G) analysis comparing percentage of each land cover type falling within a 500-m buffer around individuals of each species.

Group1	Group2	Land Cover	Buffer	Estimate	Magnitude	Confidence_Interval
BPEN	BFRAT	grassland	500-m	-0.15497	negligible	[-0.299, -0.011]
BPEN	BGRIS	grassland	500-m	-0.00646	negligible	[-0.122, 0.109]
BPEN	BIMP	grassland	500-m	1.004769	large	[0.792, 1.217]
BFRAT	BGRIS	grassland	500-m	0.494225	small	[0.347, 0.642]
BFRAT	BIMP	grassland	500-m	1.569512	large	[1.319, 1.82]
BGRIS	BIMP	grassland	500-m	1.401992	large	[1.181, 1.623]
BPEN	BFRAT	developed	500-m	0.420489	small	[0.275, 0.566]
BPEN	BGRIS	developed	500-m	0.363311	small	[0.246, 0.48]
BPEN	BIMP	developed	500-m	-0.53471	medium	[-0.743, -0.327]
BFRAT	BGRIS	developed	500-m	-0.0099	negligible	[-0.156, 0.136]
BFRAT	BIMP	developed	500-m	-1.05418	large	[-1.291, -0.818]
BGRIS	BIMP	developed	500-m	-0.88676	large	[-1.099, -0.674]
BPEN	BFRAT	woodland	500-m	-0.20936	small	[-0.354, -0.065]
BPEN	BGRIS	woodland	500-m	-0.19781	negligible	[-0.314, -0.082]
BPEN	BIMP	woodland	500-m	-0.6471	medium	[-0.856, -0.438]
BFRAT	BGRIS	woodland	500-m	0.123733	negligible	[-0.022, 0.27]
BFRAT	BIMP	woodland	500-m	-0.26787	small	[-0.493, -0.043]
BGRIS	BIMP	woodland	500-m	-0.72056	medium	[-0.931, -0.51]
BPEN	BFRAT	grains	500-m	-0.25916	small	[-0.404, -0.115]
BPEN	BGRIS	grains	500-m	-0.36248	small	[-0.479, -0.246]
BPEN	BIMP	grains	500-m	-0.13369	negligible	[-0.34, 0.072]
BFRAT	BGRIS	grains	500-m	-0.56432	medium	[-0.713, -0.416]
BFRAT	BIMP	grains	500-m	-0.50221	medium	[-0.729, -0.275]
BGRIS	BIMP	grains	500-m	0.050518	negligible	[-0.157, 0.258]
BPEN	BFRAT	beans	500-m	-0.11408	negligible	[-0.258, 0.03]
BPEN	BGRIS	beans	500-m	-0.42813	small	[-0.545, -0.311]
BPEN	BIMP	beans	500-m	-0.6133	medium	[-0.822, -0.405]
BFRAT	BGRIS	beans	500-m	-0.72259	medium	[-0.873, -0.573]
BFRAT	BIMP	beans	500-m	-1.02952	large	[-1.266, -0.793]
BGRIS	BIMP	beans	500-m	-0.70739	medium	[-0.918, -0.497]
BPEN	BFRAT	bee-pollinated	500-m	-0.08158	negligible	[-0.226, 0.063]
BPEN	BGRIS	bee-pollinated	500-m	-0.03354	negligible	[-0.149, 0.082]
BPEN	BIMP	bee-pollinated	500-m	0.031787	negligible	[-0.174, 0.238]
BFRAT	BGRIS	bee-pollinated	500-m	-0.16437	negligible	[-0.31, -0.018]
BFRAT	BIMP	bee-pollinated	500-m	-0.08781	negligible	[-0.312, 0.137]
BGRIS	BIMP	bee-pollinated	500-m	0.064841	negligible	[-0.142, 0.272]