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# Diversity of bumble bees and butterflies in Minnesota roadsides depends on floral diversity and abundance but not floral native status

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## Abstract

1. Habitat loss is an important driver in the rapid decline of many insects. The restoration of roadside habitat has been touted as an opportunity to support communities of bumble bees and butterflies, two insect groups of conservation concern. However, it is unclear how current roadside restoration methods translate to pollinator abundance and diversity.
2. Here, we ask how the plant communities of roadsides seeded with native and non-native seed mixes affect bumble bee and butterfly communities 2–20 years after planting.
3. We found that bumble bee and butterfly abundance and diversity were positively correlated with floral abundance and diversity. However, the pollinator community in plots planted with diverse native seed mixes did not differ from that found in plots seeded with species-poor non-native mixes, likely because many forbs in the native seed mixes had poor establishment, and all plots were readily colonised by species that were never planted.
4. While plots with more native flowers did not necessarily support higher pollinator diversity, we did find several native plants that established well in roadsides and supported pollinators, including goldenrods (*Solidago* spp.), milkweeds (*Asclepias* spp.) and wild bergamot (*Monarda fistulosa*).
5. Our data suggest that managing a more diverse and abundant floral community will benefit bumble bees and butterflies. Refining the composition of native seed mixes, adding more floral abundance to non-native mixes and investing in management for native plant communities may increase the habitat value of roadsides for pollinator communities.

KEYWORDS
forbs, Midwest, native vegetation, prairie restoration, rights-of-way, road ecology

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## INTRODUCTION

Many insect species are in decline across the world (Hallmann et al., 2017; Wagner, 2020). These declines have been reported in important pollinator groups, including many species of North American bumble bees (Cameron et al., 2011; Colla et al., 2012; Graves et al., 2020) and butterflies (Schultz et al., 2017; Wepprich et al., 2019). While there are many causes for these declines, habitat loss and fragmentation are key contributors (Hanberry et al., 2021; Hemberger et al., 2021; Potts et al., 2010). One solution to combat pollinator habitat loss is to convert or enhance land currently unsuitable for pollinators, such as agricultural monocultures or degraded land, into more suitable habitat (Thogmartin et al., 2017). In particular, roadsides present a relatively unexploited opportunity for pollinator habitat restoration. With over 10 million acres in the United States alone, roadsides have the potential to combat pollinator habitat loss (Forman et al., 2003; Hopwood, 2008; Kasten et al., 2016). Roadsides are narrow strips of habitat that are exposed to traffic and anthropogenic chemicals (e.g., salts and metals) and are often invaded by non-native plants (Follak et al., 2018; Phillips et al., 2019; Phillips et al., 2021). Despite these differences from traditional restorations and natural areas, pollinators are using roadsides as habitat (Hopwood, 2008; Ries et al., 2001; Saarinen et al., 2005). Specific restoration and management methods can increase the benefit of roadsides to pollinators (Hopwood et al., 2015; Phillips et al., 2020).

Recent policies enacted for declining pollinators have led the U. S. Department of Transportation (USDOT) to encourage managing roadsides for pollinator habitat across the United States (FAST Act, 2015). For example, in the 'Fixing America's Surface Transportation Act', the Federal Highway Administration recommends planting a diversity of native forbs and grasses within roadsides to support pollinators (FAST Act, 2015; Remley & Redmon, 2017). In addition to planting native forbs, other USDOT recommendations for pollinators include protecting remnant habitat, reducing mowing frequency and managing roadsides to maintain plant diversity (Hopwood et al., 2015). However, these recommendations are not always achieved. For example, even if native plants are seeded, they may not establish, they may be outcompeted due to a lack of management plans for invasive species or frequent mowing may cause them to be unusable for pollinators. Given this, it is important to understand how current roadside restoration practices, such as the seeding of native plants, actually affect pollinator communities. Recent studies have shown mixed results for the effects of seeding diverse, native plants on pollinator abundance in roadsides, with one study showing no effect of diverse seed mixes on pollinators (Simanonok et al., 2022) and another showing greater abundance of pollinators in more diversely seeded roadsides (Dietzel et al., 2023).

When considering roadside management for pollinators, restoration efforts must consider the different habitat needs of diverse pollinator species. Our study focuses on bumble bees and butterflies: in Minnesota, the rusty patched bumble bee (*Bombus affinis*) is federally endangered, and the monarch butterfly (*Danaus plexippus plexippus*) is listed as vulnerable by the IUCN, making both groups of particular interest to road managers (FWS, 2017; IUCN, 2023). In terms of habitat, bumble bees require sheltered cavities with insulating material for nesting such as abandoned rodent nests or dried grass thatch, undisturbed ground for overwintering and flowers to provide nectar and pollen as food sources (Curry, 1984; Hopwood et al., 2015). Butterflies require specific host plants on which to lay their eggs as well as flowers to provide nectar for adults (Scott, 1986). While butterfly larvae are often specialists (Kawahara et al., 2023; Scott, 1986), both adult butterflies and bumble bees are foraging generalists, meaning they are not restricted to specific species of flowers on which to feed (Colla & Dumesh, 2010; Stefanescu & Traveset, 2009; Tooker et al., 2002). Thus, even non-native flowers in roadsides may provide foraging resources for butterflies and bumble bees (Goulson et al., 2008; Jain et al., 2016; Seitz et al., 2020). Given these habitat requirements, how do roadside habitat restorations provide vegetative resources used by bumble bees and butterflies?

Supporting pollinators is one of the major proposed benefits of planting native seed mixes in roadsides. Thus, this study focuses on understanding how pollinators are using the roadside plant communities that establish following roadside construction. Here, we provide descriptive data on the bumble bee and butterfly communities occurring in roadside habitats and address several overarching questions. (1) Do more diverse and (2) abundant floral resources support more abundant and diverse bumble bee and butterfly communities? (3) Do plots with more native floral resources, or (4) plots initially seeded with native forbs, support more abundant and diverse bumble bee and butterfly communities? Together, answers to these questions provide insights into how we can improve management of roadsides for pollinators.

## MATERIALS AND METHODS

### Study sites

We surveyed 19 roadside revegetation sites in central and southern Minnesota ranging from 2 to 20 years old (Figure 1). Construction and subsequent revegetation plans for roadside sites, including the seeding locations and type of seed mixes used, were obtained from government transportation employees. Sites were included if both a native and a non-native seed mix were used for revegetation in separate areas within the site. Each site contained three plots (native, non-native and typical) for a total of 19 sites and 57 plots. The native plots were planted with a native seed mix containing 16 forb species on average (range, 6–20), and the non-native plots were planted with a non-native seed mix containing two forb species on average (range, 0–4). The native plot and non-native plot within a site were seeded during the same year. A 'typical' plot of unknown seeding history that appeared to be maintained similarly to the seeded plots (i.e., we excluded turfgrass that was frequently mowed) was chosen at least 1 km from each site along the same road as the other two plots. Thus, typical plots were outside the area of known revegetation and were used as a reference to compare the native and non-native seeded

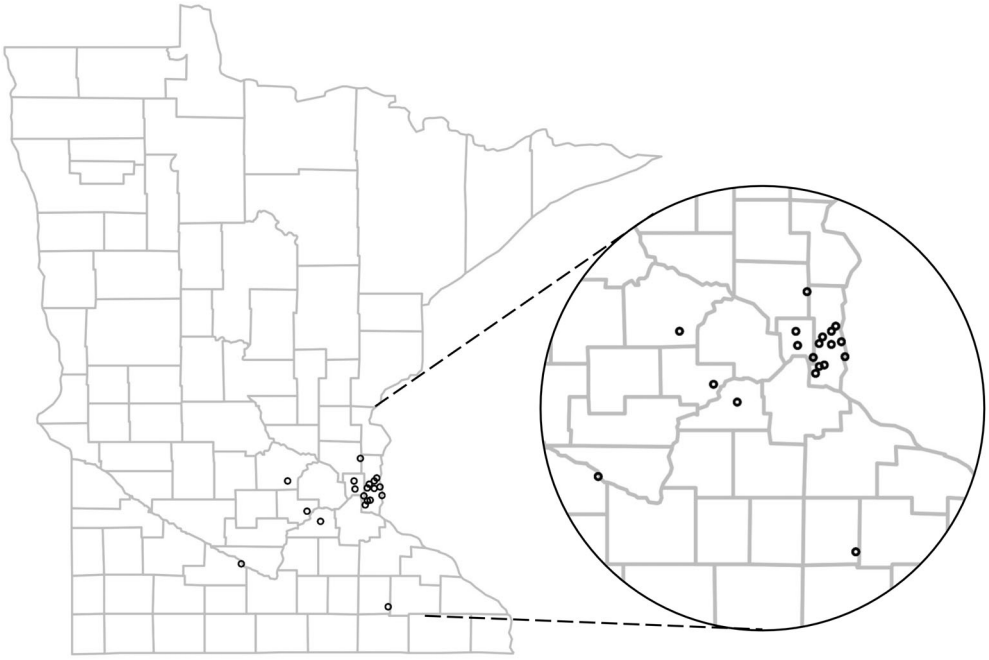


**FIGURE 1** Study site locations in Brown, Carver, Dodge, Ramsey, Scott, Washington, and Wright County, Minnesota. Each site contained a native seeded plot and a non-native seeded plot. A typical plot of unknown seeding history was located at least 1 km from each site and served as a reference for comparison.

plots. Typical plots were of unknown age but were likely older on average than the native and non-native seeded plots in the revegetation sites since the construction plans that we obtained were relatively recent (2–20 years old; median, 8 years old). Typical plots were often grass dominated, a trait that was associated with older native and non-native seeded plots, as reported below. Plot size ranged from 285.2 to 5443.8 $m^2$ (mean = 1380.7 $m^2$, median = 1272.5 $m^2$, SD = 842.8 $m^2$) and varied in shape. The size or shape of the native and non-native seeded plots within the same site was not exactly the same because reseeding locations were dictated by roadside practitioners. The size of a typical plot was comparable with the size of the native and non-native seeded plots within a site. Exact management history, such as mowing frequency, was unknown because records were not kept for past treatments. Roadsides that are not in front of businesses and houses, such as those in this study, are typically mowed at most annually, usually in August (Minnesota Legislature, 2005).

## Surveying methods

Each plot was surveyed for plants six times between 28 May 2021 and 24 August 2021 using 1 × 1 m quadrats placed every 5 m along zigzagging transects at a ~35° angle from the previous transect. Transects were randomly placed and were not fixed (i.e., transects were not in the same location for each of the six surveys per plot). Because plots varied in size, the number of quadrats differed between the plots to ensure consistent sampling effort (i.e., larger plots had more quadrats). Therefore, the number of quadrats per survey ranged from 8 to 70 (mean = 24.6) to account for plot area. We rotated whether we visited each plot during the morning, early afternoon or late afternoon over the six surveys. Only currently flowering forbs, vines, semi-shrubs, shrubs and trees were identified as present in a quadrat. We refer to this group hereafter as 'floral resources', noting that we excluded angiosperms that are not food sources for adult bumble bees and butterflies, such as grasses. Plants not currently flowering were not identified due to the focus on resources for adult bumble bees and butterflies. All floral resources were identified to species using an online field guide to Minnesota flora, except goldenrods that were identified to genus (*Solidago* spp.) (Chayka & Dziuk, 2023). Of the floral resources identified, the vast majority were flowering forbs (99.9%, 8307/8315 quadrats); flowering semi-shrubs and trees were not observed in floral surveys.

We conducted independent bumble bee and butterfly surveys concurrently with the plant surveys (six times at each plot). All surveys were completed between 0830 and 1600, and were rotated between morning, early afternoon or late afternoon at each plot over the six surveys. Surveys consisted of a modified Pollard walk (Pollard, 1977). We started a timer and began walking at a rate of approximately 0.5 m/s in a zig-zag pattern from one end of the plot to the other to standardise surveying effort in different sized plots. We counted the butterflies and bumble bees within ~1 m to either side of the surveyor's path, recording each individual species and the species of flower they were foraging on, if any. With butterflies, we verified

that their proboscis was extended to the flower before counting it as a foraging butterfly. For bumble bees, we were not able to visually confirm nectar or pollen foraging in the same way, but we still term observations on flowers as foraging. For butterfly surveys, the surveyor paused every 30 s, looked left and right across the entire plot, and counted any large, flying butterflies present that were not previously counted. Large butterflies, such as monarch butterflies, often flushed beyond the ~1 m search radius, and so this modification ensured they were counted in our surveys. We netted and photographed butterflies that could not be reliably identified without capture. For the bumble bee surveys, we netted the first individual we encountered of each species, as well as any other individuals that we could not confidently identify to species in the field. These were transferred into vials in a cooler with ice then photographed and released at the end of the survey. The presence of the endangered rusty patched bumble bee at some sites necessitated that all bumble bee activities were conducted under the authority of Endangered and Threatened Species Permit ES37601C. This ensured non-lethal sampling and handling of all bumble bees in the study. After 15 min of active search time (not including photographing or identification), or after the surveyor reached the end of the plot, the survey ended. We did not restrict our surveys to certain weather conditions with the exception that we did not survey during hard rains.

We identified bumble bees and butterflies to the lowest possible taxonomic unit using local field guides (Brock & Kaufman, 2006; Evans & Portman, 2022), which was usually but not always to the species level. We observed 10 different bumble bee species/species groups and 33 different butterfly species/species groups. Bumble bees and butterflies observed on the wing and unable to be captured for further identification were placed into 'unknown' categories of the lowest identifiable taxonomic group. Expert verification (Dr. Elaine Evans, University of Minnesota) of 247 bumble bee voucher photographs showed we had initially identified 96.0% of photographed bumble bees correctly. All bumble bees observed were native. Two species of butterflies encountered were non-native; the European skipper (*Thymelicus lineola*) and cabbage white butterfly (*Pieris rapae*) are both native to Eurasia and North Africa. Together, these two non-native species comprised 57.2% of our butterfly observations (Table S1). Because we were focused on conservation of native butterflies, we report statistical tests run on the native butterfly community; including non-native butterflies produced qualitatively similar results and are reported in the supplementary tables.

## Statistical methods

Data preparation, analyses, and visualisations were performed in R version 4.2.1 (R Core Team, 2022). We had four research questions, all related to how the plant community or planting variables (seeding treatment) influenced bumble bee and native butterfly diversity (Table 1). To address these, we used abundance (count of individuals) and Shannon diversity from surveys as response variables for bumble bees, native butterflies and all butterflies. We used Shannon diversity to represent diversity in this study because it is equally sensitive to rare and abundant species (Morris et al., 2014). From floral surveys,

**TABLE 1** Models examining the effects of (1) floral diversity, (2) floral abundance, (3) native floral abundance and (4) seeding treatment, on bumble bee and butterfly diversity and abundance.

| Question | Model |
|---|---|
| Q1 | Two-step: 1) glmer(presence/absence ~ floral Shannon diversity + survey time + (1\|round/site), family = 'binomial') |
| | 2) lme(Shannon diversity ~ floral Shannon diversity + survey time, random = ~1\|round/site) |
| | glmmTMB(abundance ~ floral Shannon diversity + survey time + (1\|round/site), family = 'nbinom2') |
| Q2 | Two-step: 1) glmer(presence/absence ~ proportion quadrats with a flower + survey time + (1\|round/site), family = 'binomial') |
| | 2) lme(Shannon diversity ~ proportion quadrats with a flower + survey time, random = ~1\|round/site) |
| | glmmTMB(abundance ~ proportion quadrats with a flower + survey time + (1\|round/site), family = 'nbinom2') |
| Q3 | Two-step: 1) glmer(presence/absence ~ proportion floral quadrats with a native flower + survey time + (1\|round/site), family = 'binomial') |
| | 2) lme(Shannon diversity ~ proportion floral quadrats with a native flower + survey time, random = ~1\|round/site) |
| | glmmTMB(abundance ~ proportion floral quadrats with a native flower + survey time + (1\|round/site), family = 'nbinom2') |
| Q4 | Two-step: 1) glmer(presence/absence ~ seeding treatment + survey time + (1\|round/site), family = 'binomial') |
| | 2) lme(Shannon diversity ~ seeding treatment + survey time, random = ~1\|round/site) |
| | glmmTMB(abundance ~ seeding treatment + survey time + (1\|round/site), family = 'nbinom2') |

*Note*: For Question 3, native floral abundance was determined by calculating the proportion of flower-containing quadrats with native flowers. To model bumble bee and butterfly diversity across all five questions, we used a two-step modelling approach. First, we used a binomial model to predict whether the presence or absence of a bumble bee or butterfly was related to the plant-related predictor variables in questions 1–4. Second, using a restricted dataset in which we removed surveys that did not detect a single bumble bee or butterfly, we performed a linear mixed effects model to explore whether the bumble bee or butterfly Shannon diversity was related to that plant-related predictor variable. To model bumble bee and butterfly abundance across all four questions, we used a zero-inflated negative binomial model. The pollinator survey time (maximum 15 min) was included as a fixed effect to account for observing less bumble bees or butterflies during shorter surveys. The visit number to the roadside site (round) and site number were included as random effects in each model to account for phenology and regional differences.

we calculated the proportion of quadrats containing at least one flower, the proportion of flower-containing quadrats that contained native flowers and floral Shannon diversity. These floral community metrics were used as predictors along with the restoration variable of seeding treatment. None of the predictors were collinear (variance inflation factor <2 for all predictors), using the R package *car* for presence–absence and diversity models and the R package *performance* for species abundance models (Fox & Weisberg, 2019; Lüdecke et al., 2021).

We conducted our analyses separately for bumble bees, native butterflies and all butterflies (Table 1). Overall butterfly analyses were omitted for Question 3 because our question was whether native floral resources affected the abundance or diversity of native pollinators. We focused on native butterflies in this question because the Federal Highway Administration recommends planting native plants in roadsides to support native pollinators (FAST Act, 2015). The response of each group of pollinators was estimated using abundance and Shannon diversity as the response in the following generalised linear mixed effects models. We modelled abundance data using a negative binomial with R package *glmmTMB* (Wenger & Freeman, 2008) and Shannon diversity data using a two-step model (to account for zero inflation in Shannon diversity (Cunningham & Lindenmayer, 2005)). Two-step models of diversity were modelled by first using a binomial model with R package *lme4* to estimate likelihood of presence as a function of the full set of predictors (Bates et al., 2015), then estimating the effect of predictors on Shannon diversity with zeros truncated with R package *nlme* (Pinheiro & Bates, 2000). We included bumble bee or butterfly surveying time (maximum 15 min) as a fixed effect to account for observing less bumble bees or butterflies during shorter surveys at smaller plots. We included a nested random effect for sites within sampling round to account for the temporal pairing of sampling in each round and spatially paired nature of our plot locations within sites (Table 1). Because seeding treatment was a categorical variable in all Question 4 models (i.e., how does seed mix affect pollinator abundance and diversity?), we used type II ANCOVAs to obtain test statistics using the R package *car* (Fox & Weisberg, 2019). If seeding treatment was significant at the $\alpha = 0.05$ level, we conducted post hoc pairwise comparisons with a Tukey adjustment using the R package *emmeans* (Lenth, 2023).

## RESULTS

### Plant community composition

The floral communities in the native and non-native seeded plots converged after planting (Table 2). Non-native seeded plots were colonised by native plants, and native seeded plots were colonised by non-native plants. Native seeded plots had greater floral richness than the non-native seeded plots, but older plots had less floral richness regardless of the initial seed mix. Older plots and typical plots (i.e., plots of unknown seeding history) were grass-dominated (Table 2 and Figure S1).

**TABLE 2** Summary of the plant community in native seeded, non-native seeded and typical plots.

| Seed mix | Age range (years old) | *n* plots | Floral richness in seed mix (mean ± SD) | Cumulative total floral richness (mean ± SD) | Cumulative native floral richness (mean ± SD) | Cumulative non-native floral richness (mean ± SD) | Total floral richness per survey (mean ± SD) | Native floral richness per survey (mean ± SD) | Non-native floral richness per survey (mean ± SD) | Floral abundance (mean ± SD) | Grass cover (mean ± SD) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Native | 0–8 | 10 | 16.3 ± 3.74 | 19.7 ± 7.02 | 8.7 ± 3.09 | 11 ± 4.27 | 6.65 ± 3.49 | 2.68 ± 2.03 | 3.83 ± 2.30 | 0.56 ± 0.29 | 0.44 ± 0.41 |
| Non-native | 0–8 | 10 | 1.6 ± 0.84 | 12.8 ± 6.11 | 3.2 ± 3.29 | 9.6 ± 3.47 | 4.92 ± 2.99 | 0.78 ± 1.30 | 3.95 ± 2.14 | 0.56 ± 0.33 | 0.40 ± 0.40 |
| Native | 9–20 | 9 | 15.78 ± 5.54 | 14.4 ± 5.96 | 6.56 ± 4.64 | 7.89 ± 3.52 | 4.91 ± 2.94 | 1.67 ± 1.61 | 3.11 ± 2.17 | 0.57 ± 0.31 | 0.51 ± 0.40 |
| Non-native | 9–20 | 9 | 2.22 ± 0.67 | 9.22 ± 3.73 | 2.89 ± 1.96 | 6.33 ± 3 | 3.11 ± 1.93 | 0.67 ± 0.95 | 2.39 ± 1.57 | 0.38 ± 0.24 | 0.79 ± 0.26 |
| Typical | | 19 | | 8.21 ± 3.63 | 3 ± 2.33 | 5.21 ± 2.21 | 2.85 ± 1.93 | 0.72 ± 0.96 | 2.03 ± 1.32 | 0.31 ± 0.26 | 0.77 ± 0.28 |

*Note*: Plots are separated into young (0–8) and old (9–20) groupings to show differences in the average plant communities with age since seeding. Floral richness and abundance were surveyed six times per plot throughout the summer. Cumulative floral richness was calculated by summing the total unique species found in each plot over the season (not all species bloom at the same time). Floral richness per survey was calculated by summing the unique species found during each survey at each plot. Grass cover was surveyed once per plot in the early summer. We report the mean and standard deviation (SD) of these plot-level plant community metrics. The seeding histories of typical plots were unknown; therefore, the age and floral richness in seed mix is absent for typical plots.

## Bumble bee and butterfly community composition

We observed a total of 993 bumble bees and 3720 butterflies during roadside surveys (Table S1). We encountered the endangered rusty patched bumble bee six times throughout the summer, but only three times during official surveying. The other three individuals were encountered either before or after the 15-min surveying period and are not included in analyses. Of the three rusty patched bumble bees observed during surveys, two were foraging on alfalfa (*Medicago sativa*) and one was foraging on common St. Johnswort (*Hypericum perforatum*), both of which are non-native to Minnesota.

We observed 89% of bumble bees and 16% of butterflies actively feeding from flowers during Pollard walk surveys. We highlight the most common plant species in our vegetation surveys and which species were most commonly used by foraging bumble bees and butterflies in Table S2. Ten of the fifteen most common floral resources in terms of relative occurrence were species that were not originally planted at the site ('unseeded colonisers'); two of those ten were native. The most common forage species for both bumble bees and butterflies were unseeded, non-native colonisers.

## Influence of the floral community on bumble bee and butterfly communities

(Q1) Roadsides with greater floral diversity had greater bumble bee and butterfly diversity and abundance (Figure 2). Increased floral diversity was associated with an increase in both the likelihood of a plot having bumble bees (Table S3) and the diversity of the bees that were present (Table S4). This same pattern was observed in native butterflies (Tables S3 and S4). Additionally, greater floral diversity was associated with greater bumble bee and native butterfly abundance (Table S5).

(Q2) Roadsides with more flowers (i.e., greater proportion of quadrats containing flowers) had greater bumble bee and butterfly diversity and abundance (Figure 3). Increased floral abundance was associated with an increase in both the likelihood of a plot having bumble bees (Table S3) and the diversity of the bees that were present (Table S4). Similarly, increased floral abundance was associated with an increase in the likelihood of a plot having native butterflies (Table S3), though increased floral abundance was not associated with the diversity of the native butterflies that were present (Table S4). Greater floral abundance was further associated with greater bumble bee and butterfly abundance (Table S5).

(Q3) Though roadsides with more blooming flowers attracted more bumble bees and butterflies, whether those flowers were native did not affect bumble bee and butterfly diversity nor abundance (Figure 4). Plots with a greater proportion of native blooming flowers did not have an increased likelihood of having bumble bees present (Table S3), nor an effect on the diversity of bumble bee that were present (Table S4). A similar pattern was observed in native butterflies (Tables S3 and S4). Neither bumble bee nor native butterfly abundance was related to the proportion of native blooming flowers (Table S5).

(Q4) Whether the seeding treatment planted in roadsides was native or non-native did not affect the presence, diversity, nor abundance of bumble bees and butterflies (Figure 5 and Tables S3–S5). We were less likely to find a bumble bee in typical plots (i.e., plots of unknown seeding history) than in native or non-native seeded plots, and bumble bee abundance was lower in typical plots than in native or non-native seeded plots (Tables S3 and S5). Bumble bee diversity was not associated with seeding treatment (Table S4). Native butterfly presence and diversity were not associated with seeding treatment (Tables S3 and S4). Native butterfly abundance was lower in typical plots than in native-seeded plots (Table S5).

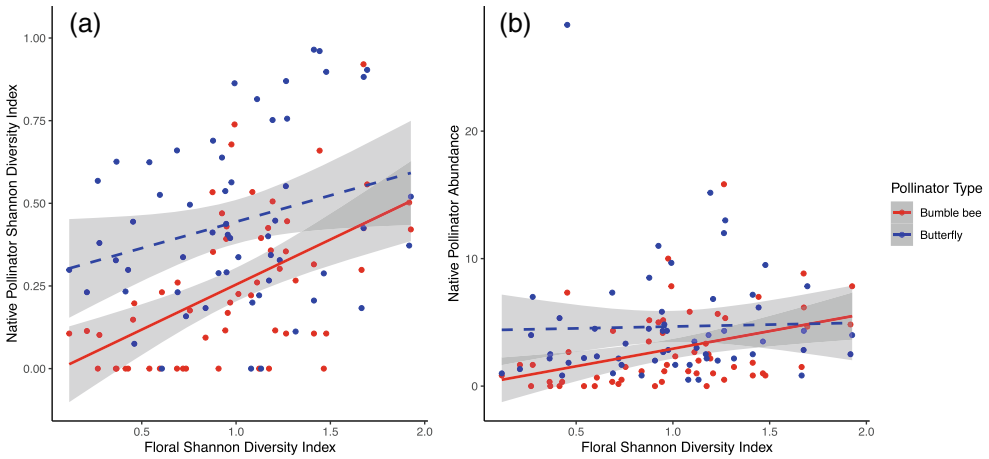



**FIGURE 2** The relationship between bumble bee/native butterfly (a) diversity and (b) abundance with roadside floral diversity. In the full models, the likelihood of a bumble bee (estimate ± SE = 1.17 ± 0.24, $p < 0.01$) or native butterfly (estimate ± SE = 0.65 ± 0.27, $p = 0.02$) being present and the diversity of bumble bees (estimate ± SE = 0.18 ± 0.06, $p < 0.01$) and native butterflies (estimate ± SE = 0.10 ± 0.05, $p = 0.03$) increased with floral diversity. Bumble bee (estimate ± SE = 0.89 ± 0.18, $p < 0.01$) and native butterfly (estimate ± SE = 0.23 ± 0.10, $p = 0.02$) abundance increased with floral diversity. Diversity was measured using Shannon's diversity index. Each point represents the mean pollinator and floral diversity or abundance measured at one plot over all six surveys. Each line is a simple linear trendline and the shaded area is a 95% confidence interval. Butterflies are represented by the blue dashed line while bumble bees are represented by the red solid line.

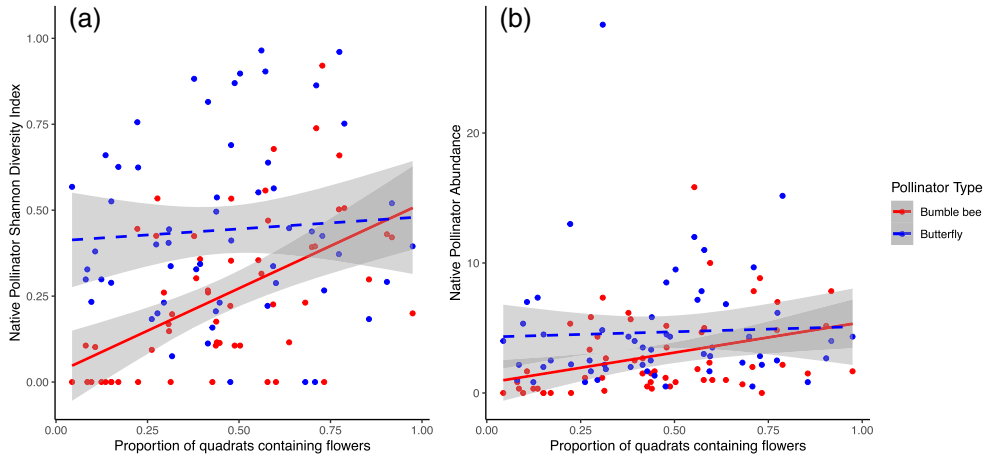



**FIGURE 3** The relationship between bumble bee/native butterfly (a) diversity and (b) abundance with proportion of quadrats containing blooming flowers. In the full models, the likelihood of a bumble bee (estimate ± SE = 3.82 ± 0.57, $p < 0.01$) or native butterfly (estimate ± SE = 2.09 ± 0.64, $p < 0.01$) being present and the diversity of bumble bees (estimate ± SE = 0.51 ± 0.13, $p < 0.01$) increased with floral abundance. Native butterfly diversity was not associated with floral abundance (estimate ± SE = 0.06 ± 0.10, $p = 0.53$). Bumble bee (estimate ± SE = 3.12 ± 0.36, $p < 0.01$) and native butterfly (estimate ± SE = 0.69 ± 0.21, $p < 0.01$) abundance increased with floral abundance. Diversity was measured using Shannon's diversity index. Each point represents the mean pollinator diversity or abundance and mean proportion of quadrats containing blooming flowers measured at one plot over all six surveys. Each line is a simple linear trendline and the shaded area is a 95% confidence interval. Butterflies are represented by the blue dashed line while bumble bees are represented by the red solid line.

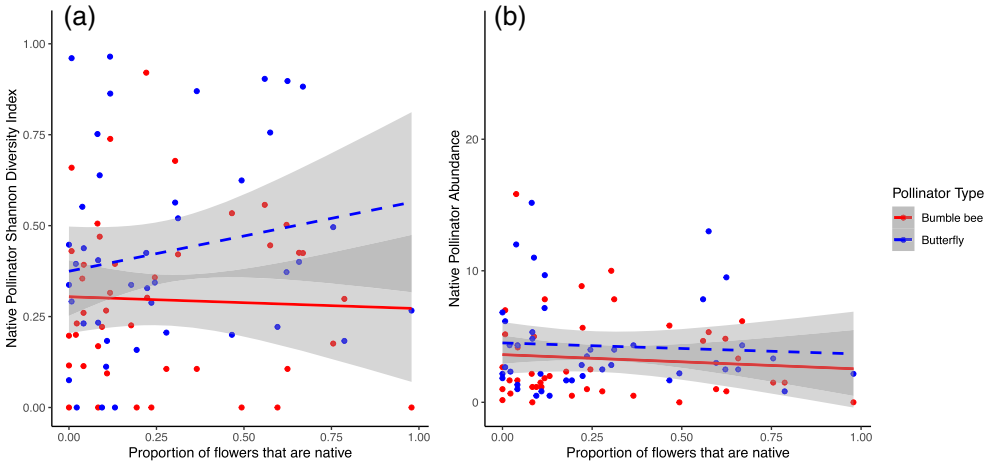



**FIGURE 4** Relationship of bumble bee/native butterfly (a) diversity and (b) abundance with the proportion of flowers that are native. In the full models, the likelihood of a bumble bee (estimate ± SE = −0.09 ± 0.38, $p = 0.81$) or native butterfly (estimate ± SE = −0.32 ± 0.53, $p = 0.54$) being present and the diversity of bumble bees (estimate ± SE = 0.07 ± 0.11, $p = 0.53$) and native butterflies (estimate ± SE = 0.12 ± 0.09, $p = 0.19$) were not associated with native floral abundance. Bumble bee (estimate ± SE = −0.19 ± 0.34, $p = 0.57$) and native butterfly (estimate ± SE = −0.05 ± 0.19, $p = 0.78$) abundance was not associated with native floral abundance. Diversity was measured using Shannon's diversity index. Each point represents the mean pollinator diversity or abundance and mean proportion of quadrats with blooming flowers that contain natives measured at one plot over all six surveys. Each line is a simple linear trendline and the shaded area is a 95% confidence interval. Butterflies are represented by the blue dashed line while bumble bees are represented by the red solid line.

## DISCUSSION

Roadsides with more abundant and diverse flowers supported more abundant and diverse bumble bee and butterfly communities. This finding is supported by other studies that show the importance of floral resources (Kelleher & Choi, 2020; Lane et al., 2020; Paterson et al., 2019). We also found that plots seeded with diverse native mixes did not support larger nor more diverse bumble bee and butterfly communities than plots seeded with relatively low diversity non-native mixes despite native seed mixes containing on average eight times as many species of forbs, including species that have varied phenology such that some species should be flowering at any given

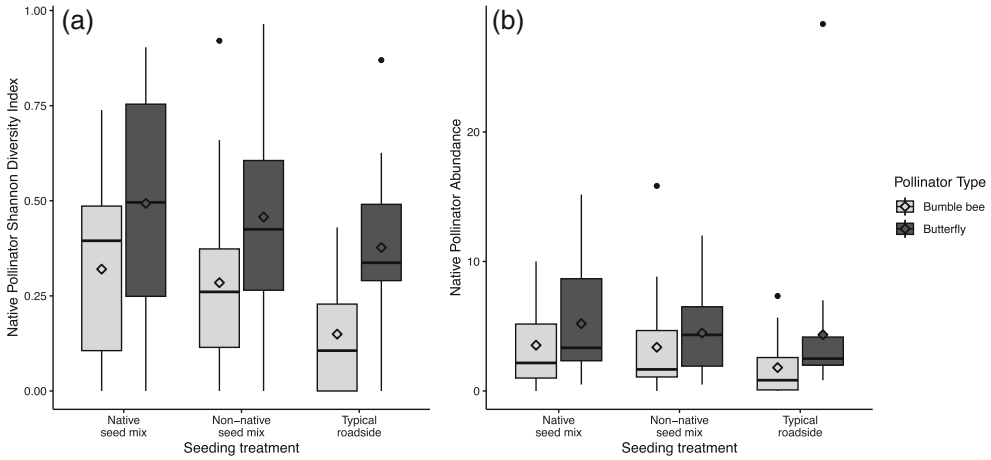



**FIGURE 5** (a) Diversity and (b) abundance of bumble bees and butterflies in roadside plots planted with native seed mixes, non-native seed mixes, and typical roadsides. In the full models, the likelihood of a bumble bee being present was greater in native (estimate ± SE = 1.51 ± 0.33, $p < 0.01$) and non-native (estimate ± SE = 1.37 ± 0.33, $p < 0.01$) seeded plots than in typical plots. Native butterfly presence was not associated with seeding treatment ($p = 0.26$). Bumble bee ($p = 0.81$) and native butterfly ($p = 0.39$) diversity was not associated with seeding treatment. Bumble bee abundance was greater in native (estimate ± SE = 0.82 ± 0.24, $p < 0.01$) and non-native (estimate ± SE = 0.85 ± 0.24, $p < 0.01$) seeded plots than in typical plots. Butterfly abundance was greater in native seeded plots than typical plots (estimate ± SE = 0.42 ± 0.13, $p < 0.01$). Each data point used to create the boxplots is the mean pollinator diversity or abundance measured at one plot over all six surveys. Open diamonds represent the mean, the solid bars represent the median, and the boxes represent the upper and lower quartile. Typical roadsides have unknown seeding histories and were at least 1 km from the native and non-native seeded plots.

time during the season (MnDOT, 2014). However, the seeded plant community is not effectively establishing or persisting—native and non-native seeded plots converge on similar plant communities shortly after planting (Table 2; Figure S1; Mitchell et al., 2022). At the same time, the introduced species that readily colonised both native and non-native seeded roadsides still provided floral resources for the generalist bumble bees and butterflies in this study. We found that bumble bee and butterfly diversity and abundance in roadsides are dependent on the diversity and abundance of floral resources regardless of whether these flowers are native.

In our study, bumble bee communities were more strongly predicted by floral diversity and abundance than were butterfly communities. We predict bumble bees are predominantly using roadsides for foraging, whereas butterflies may be using them for other purposes, such as oviposition and shelter. The dependence of butterflies on host plants suggests butterfly diversity to be dependent not only on the proportion and diversity of blooming flowers, but on the diversity of non-blooming host plants as well (Hopwood et al., 2015; Yamamoto et al., 2007). Since we only surveyed floral resources, our dataset is not suitable to answer questions about host plants. Bumble bees may also use roadsides for nesting in addition to foraging; this too was outside the scope of our study. Regardless of other factors that may affect bumble bee and butterfly diversity in roadsides, roadsides with more blooming flowers and a greater diversity of flowers support a greater diversity and abundance of both bumble bees and butterflies.

While the native status of flowers in roadsides did not predict pollinator abundance, diversity or foraging (see also Seitz et al., 2020), we still detected several high-value native plants in roadsides. For example, wild bergamot (*Monarda fistulosa*) accounted for many foraging observations by bumble bees and native butterflies despite low occurrence (Table S2). Wild bergamot was also over six times more likely to be found at sites where it was seeded, further making it a good candidate for pollinator seed mixes (Mitchell et al., 2022). For the most part, however, bumble bees and butterflies in this study foraged on plant species in proportion to the abundance of those plants in roadsides. Previous studies have shown that while generalist pollinator species (such as those in our study) use non-native floral resources, many specialist pollinators, which were not studied here, are associated with native floral resources (Lopezaraiza–Mikel et al., 2007; Seitz et al., 2020; Williams et al., 2011).

There are some features of our study we wish to highlight to reduce misinterpretations and clarify the limitations of our dataset. We did not limit bumble bee and butterfly surveys to ideal weather conditions, nor time of day. Flower detection is usually not weather nor time-of-day dependent, although some species, such as those in Nyctaginaceae and Cichorieae, flower only at certain times of the day (Cruden, 1973; Schwarz et al., 2021). Wild four o'clock (*Mirabilis nyctaginea*), which blooms in the afternoon, was found at one plot. While our detection of flowers that bloom at specific times of day was likely less than those that are not time-of-day dependent, we rotated whether we visited each plot during the morning, early afternoon, or late afternoon over all six surveys to mitigate temporal effects. Due to differences in detecting pollinators compared to flowers, we may not have observed any bumble bees nor butterflies in a plot with abundant floral resources due to weather conditions. Because of this, we could not analyse the data on a fine scale in which we looked at a particular plot on a particular date. Instead, we constructed our analyses across all six surveys conducted across all sites.

Certain species of bumble bees and butterflies may also have been less likely to be detected due to life history, seasonality, behaviour, or habitat preferences (Graves et al., 2020; Nowicki et al., 2008). Additionally, we only surveyed bumble bee and butterfly species which are foraging generalists as adults.

Our findings should not be extended to apply to all pollinators as we only examined adult bumble bees and butterflies. We did not collect data on other bee species including species that require specific forage species and are therefore likely more dependent on native floral resources (Fowler, 2016; Rotchés-Ribalta et al., 2018; Thorp & Leong, 1998). We also only surveyed plants with blooming flowers; therefore, we are unable to determine how larval host plants affect butterfly diversity, since while butterflies are foraging generalists, they often require specific host plants on which to lay their eggs (Cariveau et al., 2019). Monarch butterfly larvae specialise on milkweed species (*Asclepias* spp.), which are common in roadsides (Kasten et al., 2016), but other butterfly species' host plants may be less prevalent, such as violets (*Viola* spp.)—the host plants of Greater Fritillaries (*Speyeria* spp.). Despite our finding that native plants did not affect the presence of bumble bees or butterflies in roadsides, native seed mixes are still an important tool for roadside pollinator management due to their support of specialist pollinators.

Our data suggest that to support pollinators in roadsides, we need to manage for increased floral diversity and floral abundance. However, simply planting more diverse native seed mixes is not sufficient to substantially increase floral diversity (Table 2; Mitchell et al., 2022). In plots planted with diverse, native seed mixes, relatively few species establish and persist, and much of the diversity at a plot is from unseeded colonisers (Tables 2 and S2). Three of the four most common floral resources were unseeded, non-native colonisers—bird's-foot trefoil (*Lotus corniculatus*), white sweet clover (*Melilotus alba*), and creeping thistle (*Cirsium arvense*) (Table S2). This same trend has been shown in other disturbed, low-maintenance restorations (Lybbert et al., 2022). We see the result of this ineffective plant establishment in the pollinator community—bumble bee and butterfly communities are as equally diverse in the native-seeded plots as in the non-native seeded plots despite native seed mixes having an average of eight times as many forbs included in the mix. We see two options for management strategies to increase floral diversity and abundance. First, managers pair the substantial investment in diverse native seed mixes with a commitment and additional investment to carry out best management practices, which may include more thorough site preparation and post-seeding management as is done in many prairie restorations, such as burning, grazing, removing non-native plants or supplemental seeding (Griffin et al., 2017; Hopwood et al., 2015; Tölgyesi et al., 2022). This option would be costlier but may be worth the investment for high-priority sites. If the plant communities in our native plots more closely reflected the composition of the native seed mixes being used, we are confident these plant communities would provide excellent pollinator habitat. Second, managers implement a 'more flowers everywhere' approach to roadside management. We suggest that the forb species that do not readily establish be removed from native seed mixes, which will reduce seed mix costs. These streamlined, less-expensive seed mixes could be used more broadly (i.e., at more and larger sites), increasing the number of flowers on the landscape. Furthermore, existing non-native mixes could be bolstered with native forbs that readily establish and that pollinators use, such as goldenrods (*Solidago* spp.) (over two times more likely when seeded), milkweeds (two to nine times more likely when seeded), and wild bergamot (over six times more likely when seeded) (Table S2; Mitchell et al., 2022). For roadside managers, these options need not be mutually exclusive, and managers could greatly increase the quality of roadside habitats by using both strategies, depending on the project budgets and goals. The composition of the pollinator community (e.g., specialists versus generalists) in roadsides is undoubtably affected by the plant species which establish. Managers should think critically about which pollinator species they wish to support when choosing species to include in seed mixes.

In summary, cultivating the appropriate vegetation community along roadsides to help reach diverse goals is a complex challenge. Our work and others have demonstrated the potential for roadsides to support declining insects (Hopwood, 2008; Phillips et al., 2020), and we think roadside managers have a tremendous opportunity to create and maintain crucial habitat for declining pollinators. We have highlighted what is and what is not working with current practices and offered recommendations on how these practices could be modified to cost-effectively benefit bumble bees and butterflies.

## AUTHOR CONTRIBUTIONS

**Ashley L. Darst:** Conceptualization; writing – original draft; writing – review and editing; formal analysis; investigation; visualization; methodology. **Timothy S. Mitchell:** Conceptualization; investigation; methodology; writing – review and editing; formal analysis; supervision; funding acquisition; project administration. **Michael R. Verhoeven:** Writing – review and editing; methodology; formal analysis; conceptualization. **Elaine Evans:** Validation; writing – review and editing; funding acquisition. **Luke Tonsfeldt:** Investigation; writing – review and editing. **Savannah Kjaer:** Investigation; writing – review and editing. **Emilie C. Snell-Rood:** Conceptualization; funding acquisition; writing – review and editing; project administration; supervision.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data, code, and bumble bee photo vouchers that support the findings of this study are openly available in the Data Repository for University of Minnesota at https://doi.org/10.13020/021p-qh16.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Data S1.** Supporting Information.

**Table S1.** Bumble bees and butterflies recorded during roadside surveys from May 28, 2021 to August 24, 2021. The total abundance is the total number of each species or species group we observed during all surveys regardless of plot seeding. The relative abundance is the proportion of each species or species group relative to the total abundance of its respective group (bumble bees or butterflies). Abundance is shown separately for the number of species and species groups we observed in plots planted with native seed mixes and those planted with non-native seed mixes. Non-native pollinators are denoted by (*) and pollinators of conservation concern are bolded. All photo vouchers identified as *Bombus auricomus/pensylvanicus* were verified as *B. auricomus*.

**Table S2.** Foraging observations for bumble bees and butterflies during roadside floral surveys from May 28, 2021 to August 24, 2021. The floral abundance is the total number of quadrats containing each species across all plot types. Relative occurrence is the proportion of the abundance of each species relative to the abundance of all species. Number of sightings is the number of times either a bumble bee or a butterfly was observed foraging on that species. Relative sightings are the proportion of foraging observations on each species relative to the total number of foraging observations for either bumble bees or butterflies.

**Table S3.** Statistical outputs for binomial models examining the effects of 1) floral diversity, 2) floral abundance, 3) native floral abundance, and 4) seeding treatment on bumble bee and butterfly presence/absence (presence = 1, absence = 0). For Question 3, we asked whether native butterfly species were preferentially attracted to native floral resources; therefore, the probability of detecting any butterfly species (including both native and non-native species) was not analyzed. Significant parameters ($P < 0.05$) are bolded, except for intercept and survey time.

**Table S4.** Statistical outputs for linear mixed effects models examining the effects of 1) floral diversity, 2) floral abundance, 3) native floral abundance, and 4) seeding treatment on bumble bee and butterfly Shannon diversity (*H*). For Question 3, we asked whether native butterfly species were preferentially attracted to native floral resources; therefore, butterfly Shannon diversity including both native and non-native species was not analyzed. Significant parameters ($P < 0.05$) are bolded, except for intercept and survey time.

**Table S5.** Statistical outputs for generalized linear mixed effects models examining the effects of 1) floral diversity, 2) floral abundance, 3) native floral abundance, and 4) seeding treatment on bumble bee and butterfly abundance. For Question 3, we asked whether native butterfly species were preferentially attracted to native floral resources; therefore, butterfly abundance including both native and non-native species was not analyzed. Significant parameters ($P < 0.05$) are bolded, except for intercept and survey time.

**Figure S1.** Early season forb, grass, and ground cover with A) increasing plot age and B) in native, non-native, and typical plots. Cover was estimated in the field using cover classes (0-1%, 1-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-99%, 99-100%) and was assigned as the average value of each class (due to averaging cover classes, total cover in a quadrat sometimes exceeded 100%). Proportion cover represents this average cover for forb, grass, or ground in a quadrat divided by the total cover in a quadrat. Each point used to create the figures represents one quadrat surveyed once in early summer. Open diamonds represent the mean, the solid bars represent the median, and the boxes represent the upper and lower quartile. Typical roadsides have unknown seeding histories and were at least 1km from the native and non-native seeded plots.

**Figure S2.** Abundance of other arthropods sampled by sweep netting in roadside habitats. These samples are combined from native and non-native plots. To collect data on a range of insect groups that may include pollinators, we complemented surveys of bumble bees and butterflies with sweep net surveys. During the middle three rounds of sampling (18 June–29 July 2021) we performed sweep netting for other arthropods at native and non-native seeded plots. Using a sweep net, we took 15 sweeps, with one sweep every meter, through the base up to the top of vegetation and transferred the contents into zip lock bags which were frozen. We processed samples by removing the arthropods from vegetation in the bag and then identifying insects and spiders to order.

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