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Remnant prairies and high-diversity restorations work together to support wild bees season-long

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Remnant Prairies and High-diversity Restorations Work Together to Support Wild Bees All Season

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Abstract - The presence of diverse bee communities in an ecosystem is vital for maintaining healthy plant communities, promoting habitat resilience, and supporting agriculture. In the US, wild bee declines have led to increased monitoring efforts, but there remain critical data gaps in much of the Midwest. Here, we sought to examine how variation in richness and abundance of flowering forbs influences the richness and abundance of wild bees across "remnant" tallgrass prairies, "high diversity" prairie restorations, and "low diversity" prairie restorations or degraded grasslands in eastern Nebraska. High-diversity plots attracted no bees in the early season due to a lack of forbs but supported the highest average richness and abundance of both bees and native forbs during the mid-season. Remnant plots strongly supported bees in the early season and most consistently throughout all seasons; however, the early season forb community had a very high abundance of nonnative forbs. Our findings indicate remnant prairies and high-diversity restorations each have seasonal forage gaps or limitations, such that maintaining both is necessary to support wild bees throughout the growing season. This research also provides further evidence to the growing body of literature that prairie restoration efforts can promote diverse and abundant wild bee communities similar to, if not better than, remnant prairies.

Introduction

Pollinators play a key role in providing vital ecosystem services; approximately 35% of the global food production relies on animal pollination and ~87% of wild plants rely on insect pollination, most of which is provided by bees (Klein et al. 2012, Ollerton et al. 2011, Potts et al. 2010). Worldwide there are approximately 20,000 known species of bees, ~4,000 of which reside in North America. Although pollinating insects are among the most frequently studied and collected insects, there remain significant data gaps regarding plant-bee interactions of the Midwest. Filling these knowledge gaps would improve our ability to provide supportive foraging habitat for bees, many species of whom are currently in decline.

Habitat loss has been cited as the most significant factor contributing to bee decline, but other factors include exposure to pesticides, transmission of pathogens and parasites, loss of genetic diversity, and climate change (Cameron et al. 2011, Giannini et al. 2012, Goulson et al. 2015, Hatfield et al. 2021, Koh et al. 2016, Mola et al. 2021, Potts et al. 2010, Sánchez-Bayo et al. 2019, Schüepp et al. 2011, Vanbergen et al. 2013, Winfree et al. 2009, Zayed 2009). The decline of bee species richness is reportedly in tandem with the decline of forb richness, specifically in areas where grasslands remain the dominant land cover (Biesmeijer et al. 2006). Such areas, like the North American Great Plains, pose an elevated risk to pollinators because the limited topographic relief and fertile soils have, for decades, encouraged intensive agricultural production resulting in large-scale habitat loss and, thus, the sharp decline of bumble bee species (Hemberger et al. 2021, Niemuth et al. 2017). While habitat availability continues to decrease, efforts to accommodate human population growth and meet food demands are simultaneously increasing the need

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for pollination services (Koh et al. 2016, Lark et al. 2015, Otto et al. 2016, Rashford et al. 2011, Wright and Wimberly 2013). Fortunately, recent research has demonstrated that restoring, managing, and augmenting land with intent to support pollinators can be successful (Denning and Foster 2018, Hanberry et al. 2020, Hopwood 2008, Paterson et al. 2019, Purvis et al. 2020).

A key factor to support pollinators is to maintain or recruit diverse plant communities. Diverse plant communities accommodate a wider breadth of bee niches and offer foraging and nesting resources throughout all growing seasons (Fontaine et al. 2005, Mallinger et al. 2016, Neokosmidis et al. 2018). Additionally, floral diversity provides an array of pollen choices, thereby diversifying a bee's diet, which has been shown to improve bee health, reproduction, and resilience to stress (Vaudo et al. 2015). In landscapes dominated by cropland, it is typically the adjacent natural and semi-natural habitats, such as prairie remnants, woodland edges, or seeded restorations, that maintain diverse plant communities (Delaney et al. 2015, Hines and Hendrix 2005, Kwaiser and Hendrix 2008). Maintaining these natural and semi-natural habitats is necessary to provide diverse foraging and nesting resources, but more broadly, to increase the amount of heterogeneous habitat at the landscape level thereby allowing for the preservation of biodiversity (Delaney et al. 2015, Goulson et al. 2015, Hines and Hendrix 2005, Kwaiser and Hendrix, 2008, Mallinger et al. 2016, Neoskosmidis et al. 2018). These prior studies, and others, emphasize that mitigating habitat loss must be made a priority, and agriculturally intensified landscapes must incorporate more bee-friendly practices (Brown and Paxton 2009, Potts et al. 2010, Sexton et al. 2020).

In Nebraska, the City of Lincoln's Parks and Recreation Department took initiative to conserve, connect, and restore tallgrass prairie fragments, of which it is estimated only 1–3% remains in native vegetation throughout the Great Plains (Henwood et al. 2010). The intent of this initiative, known as the Prairie Corridor on Haines Branch (PCHB), is to examine the role that design and management of reconstructed prairie play on plant and pollinator communities and to identify areas and plants within the corridor that support high pollinator diversity.

Through this observational research we examined how vegetation cover at sites within the PCHB influences the richness and abundance of wild bees by utilizing sites that were "remnant" tallgrass prairies, "high diversity" prairie restorations, and "low diversity" prairie restorations or degraded grasslands. We hypothesized remnant sites to have the highest richness and abundance of wild bees, assuming foraging and nesting habitat is more established, followed by high diversity restorations given the expected abundance of flowering forbs.

Methods

Study Area

The study took place in eastern Nebraska within the PCHB, a ~17.7-km nearly contiguous greenway in Lancaster County. The PCHB was initiated in 2012 and was pieced together through 2016 by land acquisition. The acquired parcels ranged in size (1.48–31 ha), vegetation cover (high and low-quality unplowed remnant, high and low-diversity restorations, pasture, hay meadows), age of seeded restoration, and management type and intensity (burn, graze, hay, chemical application, or combination of all four). The restorations were planted in the dormant season in former soybean fields using a high diversity, local eco-type seed mix (150–200 species) (Steinauer 2003). See Supplemental Table 1 (available online at https://eaglehill.us/prnaonline/suppl-files/prna-010g-lamke-s1.pdf) for a detailed list of plots.

Study Design

Throughout the PCHB, twenty 1.2-ha plots were defined in a non-random fashion to align with a parallel vegetation study carried out by the University of Nebraska-Lincoln's School of Natural Resources (UNL-SNR) from 2016 through 2019; see Park et al. (2021) for explanation of vegetation study. Based off of UNL-SNR's study, the plots were sorted into three distinct groups by mean plant species composition per square meter: remnant (13 species/m^2), high-diversity or HD (7.5 species/m^2), and low-diversity or LD (5 species/m^2), which were used here as prescribed treatments. Each plot was visited once every other week between May–October 2017 and April–October 2018, and only when the temperature was 15.5–35˚C, average wind speeds were ≤24 km/hr, and it was not raining. During a single visit to a plot, two transects (2x20 m) were randomly selected to conduct one forb survey followed by one bee survey on each transect. For a forb survey, each blooming species within the transect was (1) identified to the lowest taxonomic rank achievable by the surveyor and (2) quantified by counting the number of stems that emerged from the soil surface and bore open inflorescences. Once identified, the PLANTS Database (USDA 2018) was consulted to standardize scientific names and classify native or nonnative status.

The bee survey began after completion of the forb survey. The surveyor walked the transect at steady, unidirectional, pace over a 5-minute period and collected all wild bees directly from blooming forbs using an aerial net, hand vialing, or visual observation. *Apis mellifera* Linnaeus (European Honey Bees) were not collected or counted in this study. Visual observations were only used when species could be easily identified on the wing, like some *Bombus* Latreille (Bumble Bees) species, or to note the lowest-achievable taxonomic rank of a species that was missed during netting. The 5-minute timer was paused to transfer bees from the net to a kill jar and to record the floral host. Collected specimens were curated, identified (see Supplemental Table 2 [available online at https://eaglehill.us/prnaonline/suppl-files/prna-010g-lamke-s2.pdf]), and housed at the University of Nebraska-Lincoln, with vouchers deposited into the University of Nebraska State Museum.

Data Analyses

Five response variables were calculated for each plot: (1) forb richness, (2) forb abundance, (3) bee richness, (4) bee abundance, and (5) bee-visited forb richness, or the flowering forbs bees were observed on within each plot. Surveys conducted in 2017 and 2018 were pooled to increase sampling size because there were no significant differences for any variable between years. Forb richness and abundance variables were normally distributed as determined by Shapiro-Wilk tests, but bee richness, bee abundance, and bee-visited forb richness variables were log-transformed to normalize the data. Each response variable was compared across Treatment, Season, and the interaction of Treatment and Season using two-way Analysis of Variance (ANOVA) statistical models. The natural groupings from UNL-SNR's parallel vegetation study (HD, LD, and Remnant) were prescribed as the Treatment. To account for the uneven distribution of plots per Treatment (HD, $n = 4$; LD, $n = 9$; Remnant, $n = 7$), mean values were calculated for response variables by summing the two transects per survey week per plot per year which yielded 429 data points per variable. Season consists of Early (April 1–June 15), Mid (June 16–August 15) and Late (August 16–October 31). Each ANOVA model was followed by post-hoc Tukey's Honest Significant Difference (HSD) test to determine which means were significantly different (at alpha ≤ 0.05) from each other. Statistical analyses were conducted in R version 3.5.2 using the agricolae package (R Core Team 2018; de Mendiburu 2019).

Results

Significant differences in all five response variables were observed as a function of treatment, season, and the interaction between them. Therefore, only the interaction effects are reported here because the effect of treatment cannot be understood without considering season, nor the effect of season without treatment (forb richness: $F_{4, 420} = 9.18$, $P = 4.09\text{e-}07$; forb abundance: $F_{4, 420} = 4.29$, $P = 0.002$; bee-visited forb richness: $F_{4, 420} = 7.401$, $P = 8.98\text{e-}06$; bee richness: $F_{4, 420} = 7.74$, $P = 5.07\text{e-}06$; bee abundance: $F_{4, 420} = 6.98$, $P = 1.9\text{e-}05$).

Forb Abundance and Richness

A total of 1,118 blooming stems were counted throughout 2017 and 2018 that represented 89 forb species. Richness and abundance of blooming forbs peaked during the mid-season for all treatments. Early season Remnant plots yielded more than 2.7 times the number of forb species than LD plots and 3.4 times more than HD plots (Table 1, Figure 1A). In addition to low forb richness, early season HD plots had a strikingly low average forb abundance of 3.8 ± 7.8 blooming stems per survey, which was 96.4% lower than Remnant plots (Table 1, Figure 1B). However, despite low forb measures in the early season, by mid-season, both the HD and Remnant plots were comparable in terms of forb richness (avg ± SD: 4.8 ± 2.4 species; 4.5 ± 3.7 species, respectively), with an average of 4.2 and 3.9 times more forb species than mid-season LD plots. A similar pattern was observed for mid-season forb abundance: HD and Remnant plots significantly outperformed LD plots (avg ± SD: 87.5 ± 68.2 blooming stems per survey; 122.9 ± 166.1; 54.5 ± 28.5, respectively). From mid to late season, forb abundance within HD plots decreased by 20%; however, they provided an average of blooming stems 2.5 to 2.8 times greater than that of late season LD or Remnant plots (Figure 1B). In the late season, as expected, the average forb richness decreased roughly 37–60% and the average forb abundance decreased ~20–80% compared to the peak in mid-season.

When native status was assessed, Remnant plots were dominated by nonnative forbs in the early season which accounted for 53% of species and 55% of abundance (namely *Melilotus officinalis* [L.] [Yellow Sweetclover]; *Dianthus armeria* L. [Deptford Pink]; *Medicago lupulina* L. [Black Medic]; and *Hypericum perforatum* L. [Common St. John's Wort]). In mid-season Remnant plots, native forbs comprised 62% of total richness and 52% of total abundance, and while the number of forbs decreased in the late season, the proportion of native to nonnative plants increased to 72% richness and 76% abundance. HD plots were dominated by native forbs in the mid season (84% of species, 95% of abundance) and late season (95% of species, 98% of abundance) seasons. In LD plots, the proportion of native to nonnative forbs increased throughout the season in both richness (early: 40%, mid: 61%, late: 69% native) and abundance (early: 19%, mid: 53%, late: 86% native) (Table 2).

Bee Abundance and Richness

A total of 406 bees were used in the analysis, representing at least 44 species. Of the 406 individuals, 104 were not successfully netted, thus only visually identified to genus, and 1 specimen awaits identification (*Lasioglossum (Dialictus)* sp. Curtis). Of interest was a single observation of *Ceratina floridana* Mitchell that may represent a new western record. See Supplemental Table 2 for a list of observed bee species and more information on *C. floridiana*.

HD plots in the mid-season resulted in the highest average bee richness (Avg ± SD: 2.5 ± 2.8 species per survey) and bee abundance (5.6 ± 10.4 individuals per survey), which were 2.5 and 3.4 times higher than Remnant plots and 7.9 and 14.2 times higher than LD plots, respectively. However, no bees were observed in the early season at HD plots, and there was a significant decrease from mid- to late season in both richness (0.9 ± 1.5 species per survey) and abundance (1.1 ± 1.5 individuals per survey). In contrast to this fluctuation, Remnant and LD plots displayed fairly consistent averages throughout the seasons, although Remnant plots had on average 2.9 to 7 more bee species per season and 2.5 to 8 times more bee individuals than LD plots (Table 1, Figure 1D-E).

Bee-visited Forbs

Of the 89 forb species documented, bees were only observed to visit 48 of those species. Across all treatments and seasons there were, on average, 3.2 to 6.4 times more bloom-

Table 1. Descriptive statistics table for all five variables across treatment ("High Diversity" prairie restorations, "Low Diversity" prairie restorations or degraded grasslands, and "Remnant" tallgrass prairies) and season (Early = Apr 1–Jun 15, Mid = June 16–Aug 15, Late = Aug 16–Oct 31) in 2017 and 2018. Total number of species or individuals (n), average values (Avg), and standard deviations (SD) per treatment and season are included for each measure. "Asterisk (*)" indicates the value could be higher because it only includes organisms identified to the species level but there are additional plants or bees identified to the generic level.

		High Diversity			Low Diversity			Remnant		
Measure	Season	n	Avg	SD	n	Avg	SD	n	Avg	SD
Forb Richness	Early	8	0.52	0.77	10	0.23	0.69	27*	2.49	2.55
	Mid	31	4.83	2.37	33	1.14	1.51	37*	4.46	3.66
	Late	25	3.05	3.03	16	0.60	1.08	31	1.77	2.49
Forb Abundance	Early	17	3.800	7.80	21	23.09	161.48	212	104.47	208.02
	Mid	162	87.50	68.20	98	28.15	54.49	350	122.89	166.15
	Late	89	69.67	76.66	49	28.25	74.09	120	24.90	46.84
Bee Richness	Early	0	0.00	0.00	5	0.09	0.41	17*	0.61	1.08
	Mid	21*	2.50	2.84	12*	0.32	0.79	24*	1.018	1.50
	Late	8*	0.91	1.51	12*	0.32	1.33	14*	0.63	1.50
Bee Abundance	Early	0	0	0	5	0.09	0.41	42	0.74	1.42
	Mid	133	5.58	10.42	26	0.40	1.10	91	1.66	3.04
	Late	20	1.10	1.92	32	0.53	2.80	57	1.20	3.99
Bee-visited Forb Richness	Early	0	0	0	4	0.07	0.31	12*	0.44	0.71
	Mid	12	1.292	1.12	12	0.23	0.52	21*	0.69	1.03
	Late	6	0.52	0.873	5	0.12	0.42	9	0.35	0.62

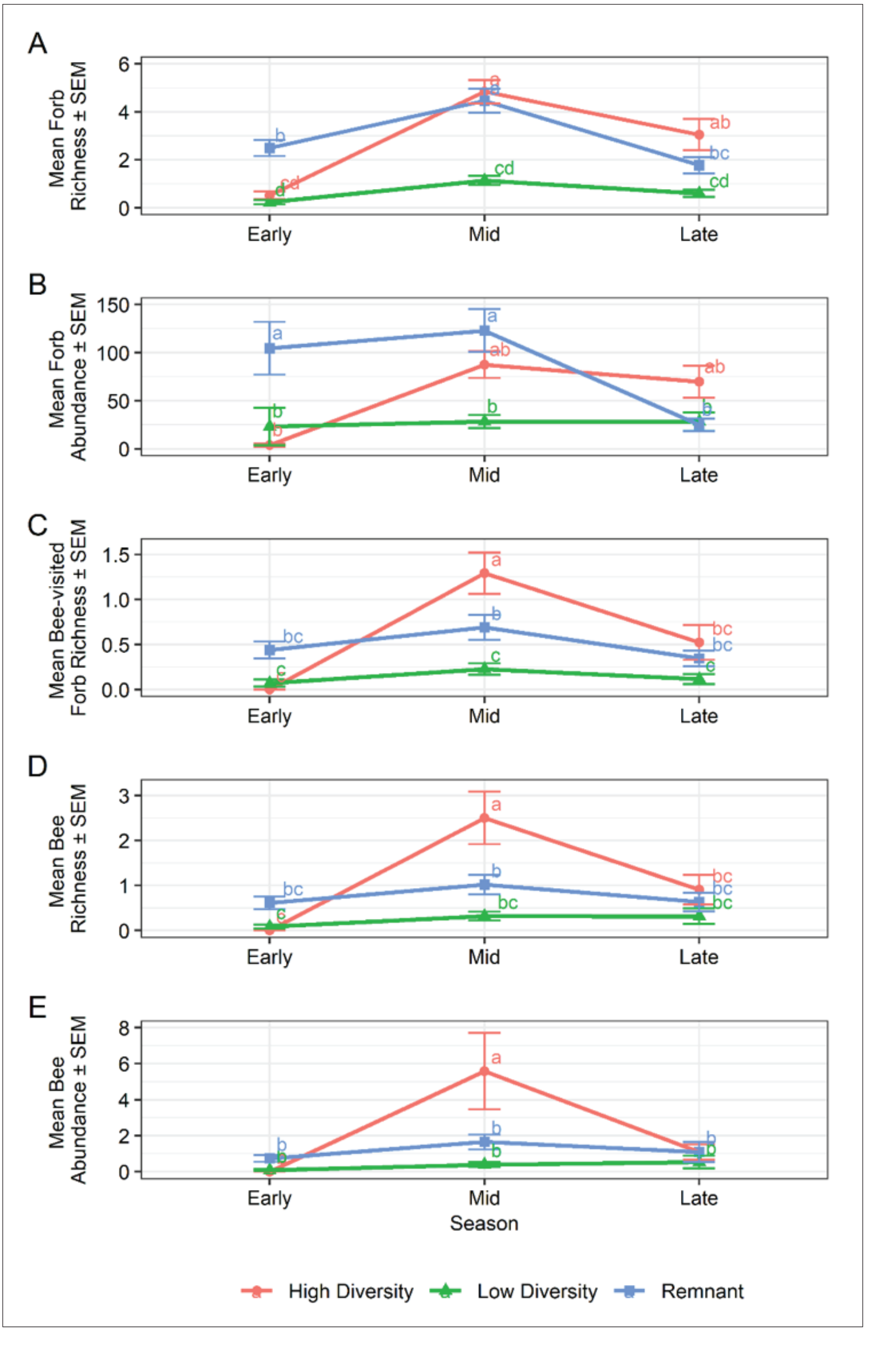

Figure 1. Mean values with standard error from the interaction model (Treatment X Season) are shown for each variable. Treatment includes "High Diversity" prairie restorations, "Low Diversity" prairie restorations or degraded grasslands, and "Remnant" tallgrass prairies of both high and low quality. Season includes "Early," Apr 1–Jun 15; "Mid," June 16–Aug 15; and "Late," Aug 16–Oct 31. Forb richness and abundance variables were normally distributed as determined by Shapiro-Wilk tests; bee-visited forb richness, bee richness, and bee abundance variables were log-transformed to normalize the data. Significant differences within each variable are denoted by letters.

ing forb species accounted for in surveys than were utilized by bees. The highest average number of bee-visited forb species was at HD plots (Ave ± SD: 1.3 ± 1.1) during the mid-season, which was 1.9 times higher than Remnant and 5.7 times higher than LD plots (Table 1, Figure 1C). When native status was assessed for the 48 bee-visited forb species, 32 were native, 13 were nonnative, and 3 were naturalized (such as *Taraxacum officinale*) or are only identified to a genus containing both native and nonnative plants. In terms of abundance, 83% of all bee visits were to native plants. Aside from the early season when no bees were collected, all bee-visited forb species within HD plots were native. Additionally, in the early season Remnant and LD plots more species of native forbs were visited by bees despite the higher abundance of nonnative forbs available (Table 2).

Discussion

By comparing seasonal averages across all treatments for richness and abundance of flowering forbs and wild bees, we show that high-diversity restorations planted with native, local ecotype seeds contribute valuable habitat for wild bee communities. As expected, forb richness and abundance peaked in the mid-season for Remnant and HD plots which aligns with flowering phenology of the Midwest (Kirt et al. 1995). However, despite the similarity

Table 2. Raw values for forb richness, forb abundance, and bee-visited forb richness to illustrate the distribution and availability of native and nonnative forbs across treatments and seasons. "Native" and "NonNative" categories were classified using the PLANTS Database (USDA 2018). "Asterisk (*)" indicates a column that contains a naturalized forb species, or a forb only identified to a genus that contains both native and nonnative species.

	High Diversity			Low Diversity			Remnant		
	Early	Mid	Late	Early*	Mid	Late	Early*	Mid*	Late
Available forb richness: Native	6	26	23	4	20	11	15	23	23
Bee-visited forb richness: Native	0	12	6	2	8	5	6	13	7
Available forb richness: NonNative	2	5	2	6	13	5	12	14	8
Bee-visited forb richness: NonNative	0	0	0	1	4	1	5	9	1
Total richness	**8**	**31**	**25**	**10**	**33**	**16**	**27**	**37**	**31**
Available forb abundance: Native	7	154	87	4	52	42	101	183	91
Available forb abundance: NonNative	10	8	2	17	46	7	111	167	29
Total abundance	**17**	**162**	**89**	**21**	**98**	**49**	**212**	**350**	**120**

of forb availability here, HD restoration plots supported significantly higher averages of bee richness and abundance than Remnant prairie plots. This finding aligns with recent research demonstrating the value of high-diversity restorations to bees and their ability to support pollinators comparable to, if not better than, remnant vegetation (Breland et al. 2018, Denning and Foster 2018, Griffin et al. 2017, Lane et al. 2020).

A specific attribute of high-diversity restorations is the higher abundance of native plants compared to Remnant and LD plots. Throughout mid and late seasons, HD plots were dominated by native plants, in both richness and abundance, and all bee visits in HD plots were to native plants. This is interesting because Remnant and HD plots showed on average a near equal richness of forbs. Remnant plots had double the abundance of forbs, and yet HD plots had more than double the richness and abundance of bees than Remnant plots. This suggests that wild bees prefer native plants, even when there is a higher abundance of nonnative plants available like what was observed in early season surveys at Remnant and LD plots. Recent research also identified that wild bees visit native forbs more often; however, upon calculating a ratio for forb selection or avoidance by wild bees, Simanonok et al. (2021) found that a bee's forb use and forb selection were not correlated, thereby suggesting bee visitation data alone cannot explain forb preference. An alternative reason why high bee measures were observed in HD plots may be due to the close proximity of a dense riparian area and a cemetery. Riparian corridors have been correlated with high floral diversity and offer a wide variety of nesting resources from which pollinators benefit (Cole et al. 2017, Naiman et al. 1993) and cemeteries are known to support a high richness of bees (Normandin et al. 2017, Tonietto et al. 2017).

Although Remnant plots did not result in the highest average bee richness or abundance, it is important to note they did support wild bees consistently throughout all seasons unlike the large fluctuations seen in the HD plots. Further, Remnant plots filled a large foraging gap in the early season and showed that nonnative plants may be supplementing bee diets in the early season which aligns with Mallinger et al. (2016) and Seitz et al. (2020). Additionally, the consistent support may be due to the habitat composition of remnant prairies, specifically the availability of established floral and nesting resources throughout all growing seasons (Klein et al. 2012; Mallinger et al. 2016).

Our findings align with Sexton and Emery (2020) and Lane et al. (2020) in suggesting that maintaining both remnant prairies and high-diversity restorations may be a critical component to supporting diverse bee communities, especially in agriculturally dominated landscapes. As addressed in Schellhorn et al. (2015), an improved understanding of the collection of resources within these landscapes that are needed to support wild bees throughout all life stages (i.e. nesting, foraging, and overwintering habitat) may illuminate a path towards refined restoration tactics. As such, an assessment of available nesting habitat and variation in nutritional foraging habitat at remnant prairies and high-diversity restorations would lend further insight to their level of complementarity.

Management Implications

To address the early-season gap in forage availability seen in high-diversity restorations, we suggest a refinement of seed mixes to include more native, spring-blooming forbs and shrubs. Remnant prairies may also benefit from replacing nonnative, spring-blooming forbs with native, spring-blooming forbs and shrubs; though, as nonnative forbs were a vital source of food in the spring, it is imperative not to simply remove them without supplying new foraging resources.

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