

2016

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The Effects of Seed Mix Diversity on Soil Conditions and Nesting of Bees in Prairie Restorations

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ABSTRACT With the goal of conserving native bees, current recommendations for improving habitats include increasing available floral resources by planting diverse seed mixes. However, these recommendations only account for the nutritional needs of bees while the availability of equally important nesting resources is often ignored. Here we used a novel system to investigate the effects of seed mix diversity on abiotic factors previously associated with nest sites of ground-nesting bees—available bare ground and soil temperature, moisture, and compaction—and on the occurrence of nests. We used standard bee-collecting techniques and a newer method using soil emergence tents (E-tents) to assess how seed mix diversity affects the distribution of bees. Plots planted with the highest-diversity seed mixes had the greatest amount of available bare ground and the highest soil temperatures at the surface and depths commonly associated with bee nests. The observed changes suggest these areas should be preferred by ground-nesting bees, but nest occurrence did not vary significantly among treatments. However, foraging bee species richness and abundance was greatest in plots planted with the highest-diversity seed mixes. Failure to detect a response in nest occurrence to seed mix diversity may be the result of low bee nest density, manifested in only a few nests being detected and low statistical power. We conclude that the current recommendation of planting highly diverse seed mixes provides adequate nutritional resources and improves some of the key abiotic factors associated with selection of nest sites by ground-nesting bees.

KEY WORDS ground-nesting bees, habitat restoration, plant diversity, seed mix, soil

INTRODUCTION

Bee species richness and abundance are strongly linked to flowering plant diversity (Batáry et al. 2010, Carson et al. 2016, Mallinger et al. 2016). As such, recommendations for land managers for pollinator conservation focus on planting hyperdiverse seed mixes to best serve the nutritional requirements of bee communities (Harmon-Threatt and Hendrix 2015) while often overlooking nesting resources. For many animals (Newton 1994, Phelps et al. 2009, Pike et al. 2010), including ground-nesting bees (Potts et al. 2005), optimal nest sites are often a limited resource. However, we do not know if the currently recommended high-diversity plant assemblages provide access to preferred or even adequate nest sites—a potentially important detail if these conservation and restoration efforts are to succeed.

Solitary bees are central-place foragers and require access to suitable nesting sites and floral forage to successfully establish in a habitat (Orians and Pearson 1979, Plowright and Laverty 1984, Westrich 1996, Williams and Tepedino 2003). Bees are able to utilize multiple patches within their foraging range (Westrich 1996); however, there are likely costs associated with moving between patches to obtain resources (Morris 1992, Westrich 1996, Williams and Tepedino 2003, Neff 2008). If access to optimal foraging and nesting resources is limited, bees are forced to make decisions about which resource to prioritize—sacrificing access to higher-quality resources of one

type to ensure access to adequate quality of the other. Such tradeoffs have been previously observed for other Hymenoptera (Klein et al. 2004). Currently, little is known about this decision in bees and if areas with high flowering resources provide nest sites of high quality.

Many variables may affect the selection of nest sites by ground-nesting bees, a group that includes the majority of bees (O'Toole and Raw 1991). In particular, a number of abiotic factors have been repeatedly associated with nest site selection and are commonly thought to influence nesting bees' decisions. Bee nest site selection has been suggested to be positively correlated to the amount of available bare ground (Wuellner 1999, Potts et al. 2005, Donovan et al. 2010), soil temperature (Potts and Willmer 1997, Wuellner 1999), and soil moisture (Cane 1991 and Wuellner 1999) and negatively correlated with soil compaction or hardness (Potts and Willmer 1997, Sardiñas and Kremen 2014). Each of these factors is potentially influenced by the surrounding vegetation and could ultimately affect a habitat's suitability for bee nests (Potts et al. 2005). Plant communities that contain a diversity of forbs in addition to grasses have greater heterogeneity in their physical structure due to varied plant growth forms (Liira and Zobel 2000), which may alter amounts of bare ground and light penetration to the soil surface. However, the way diversity modulates these characters and those that depend on them, such as soil temperature, is still largely unknown. Similarly, the root systems of plant communities can alter additional soil properties. For example, the roots of high-diversity plant assemblages stabilize soil structure (Pohl et al. 2009), which

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reduces soil compaction (Angers et al. 1987), and the growth of these root systems form macropores in the soil that facilitate water movement and higher soil moisture levels (Angers and Caron 1998). Thus, in addition to their role in providing nutritional resources, diverse plant communities may increase a habitat's suitability for nest establishment by modifying abiotic conditions.

Using a novel system that allows the direct examination of the effects of starting seed mix diversity on bee ecology, we investigated the relationship between plant community structure and soil abiotic factors associated with bee nesting and the effect on nesting rates. We hypothesized that increased plant diversity would enhance nest site quality via one or a combination of increased amount of bare ground, increased soil temperature, increased soil moisture, and decreased soil hardness—here measured as compaction—and that these improvements would result in a higher occurrence of bees nesting in these areas.

MATERIALS AND METHODS

Study Site

This study was conducted 22–25 July 2014 at The Nature Conservancy's (TNC) Platte River Prairies site (40.743587N, 98.590454W). During the study period, daytime high temperatures ranged from 28 °C to 37 °C ($\mu = 32$ °C) and there was no precipitation. The soil is composed of Caruso and Wann loam and has a slope of 0–2° (Soil Survey Staff NRCS USDA 2017). TNC actively manages this area and established the experimental plots used here in 2010—prior to which they were a single gravity-irrigated crop field for 70+ y (C. Helzer, personal communication). A total of twelve 0.3-ha (50 m × 60 m) plots, separated by 10-m-wide mowed areas, were established with 1 of 3 seeding treatments: big bluestem (*Andropogon gerardii* Vitman) monoculture (MONO), low-diversity forb and grass mix (LD), or high-diversity forb and grass mix (HD). The LD-treated plots were planted with grass and forb seeds harvested by combine from an existing prairie restoration—mainly warm-season grasses, Canada wild rye (*Elymus canadensis* L.), and a few forbs that were tall enough and adequately mature to be captured by the combine. The HD plots were planted with the LD mixture augmented with a seed mix containing 102 species of locally collected grasses and forbs (C. Helzer, personal communication). These plots were burned on 28 March 2013 and, since their establishment, invasive musk thistle (*Carduus nutans* L.) has been actively controlled (C. Helzer, personal communication). Management practices were applied evenly across all sites with the exception of the initial seed mix. This study site was chosen because the individual plots are located close enough together that we were justified in assuming that bees were able to move freely between them. When making nesting and foraging decisions solitary bees

can travel up to 1 km from their nests and regularly travel up to hundreds of meters during foraging bouts (Cane 2001, Gathmann and Tschardt 2002, Greenleaf et al. 2007). Under such circumstances, bees could theoretically forage on flowers in the HD plots, but nest in one of the MONO plots, thus semi-decoupling foraging and nesting decisions.

Plants

To establish that the initial seeding treatments (MONO, LD, and HD) had resulted in plant assemblages that differed substantially in their floristic quality and species richness, data on plant presence were collected by Chris Helzer on 31 July 2013 using 15 randomly stratified 1-m² quadrats within each plot (C. Helzer, unpublished data).

In 2014, available flowering resources were assessed for each plot via 3 equally spaced 2-m × 50-m transects. This sampling effort allowed us to survey 10% of the total plot area. Transects ran parallel to the short (50-m) edge of each plot at 15 m and 30 m from the edges. Flowers were identified to species and the number of individual flowers in bloom was counted—except for dense flowering heads and spikes where individual flowers are difficult to count efficiently, such as black-eyed-Susan (*Rudbeckia hirta* L.), purple prairie clover (*Dalea purpurea* Vent.), and wild bergamot (*Monarda fistulosa* L.), which were thus treated as a single flower. Flowers observed within plots, but not captured in one of the transects, were also identified to species and included in the measure of species richness.

Soils

The abiotic factors measured in this study were amount of bare ground, soil temperature, soil moisture, and soil compaction. With the exception of bare ground, these factors were measured at the soil surface (<2.5 cm) and at 30 cm immediately below the E-tents during their collection (23–25 July 2014). We chose these depths because they cover the likely microhabitat conditions bees assess when choosing nest sites and a substantial portion of common nest depths (Cane and Neff 2011). The amount of bare ground was measured immediately below E-tents and in five additional 0.25-m² quadrats in each plot ($n = 10$). The percentage of bare ground was estimated as a bare ground rating (0 = 0%, 1 = <25%, 2 = 25–50%, 3 = 50–75%, 4 = 75–100%, 5 = 100%). To measure soil temperature and moisture, we first took a 2-cm × 30-cm soil core (JMC Soil Samplers PN001 & PN007). Soil temperature was measured by inserting the probe of a digital thermometer (Cooper-Atkins DPP800W) into the surface and 30-cm ends of the extracted soil core. Soil moisture was measured in the same way with a soil moisture meter (Extech Instruments MO750). Five soil cores were taken per plot. Soil compaction was measured with a soil compaction tester (DICKEY-john). Raw readings were converted into a

compaction rating (0 = <7 kg force [kgf] cm⁻², 1 = 7–8.7 kgf cm⁻², 2 = 8.8–10.4 kgf cm⁻², 3 = 10.5–12.2 kgf cm⁻², 4 = 12.3–14.0 kgf cm⁻², 5 = 14.1–15.7 kgf cm⁻², 6 = 15.8–17.5 kgf cm⁻², 7 = 17.6–19.2 kgf cm⁻², 8 = 19.3–21.1 kgf cm⁻², 9 = >21.1 kgf cm⁻²) because this instrument only provides rough estimates of compaction and a number of the measurements were outside the quantifiable range (<7 kgf cm⁻² or >21.1 kgf cm⁻²).

Bees

Bees were collected from each plot using 3 methods: hand netting, bee bowls, and E-tents. Hand netting bees on flowers occurred within each plot on 2 d for 20 min each day between 0800 and 1200. We excluded time spent handling captured bees from the 20 min of netting. Bee bowls are a standard passive sampling technique for bees (Roulston et al. 2007, Geroff et al. 2014) that consists of alternating fluorescent yellow, blue, and white pan traps filled with soapy water. Twenty-five 3.25-oz Solo bowls (P325W-0007) were placed on the soil surface with one bowl located every 3 m on a diagonal transect across each plot. We deployed bee bowls for 4 h on the same days that hand netting took place. E-tents (60 cm × 60 cm × 60 cm; 108 × 32 mesh polyester netting; Bugdorm BT2006) are a relatively new technique for assessing the occurrence of ground-nesting bee nests (Sardiñas and Kremen 2014). Over the course of 3 nights (22–24 July 2014), five E-tents total were placed in each plot. The date and location of each E-tent deployment was randomly determined and they were set up starting at 1900 and retrieved the following day at 1200 (i.e., for each night of sampling, plots had either one or two randomly distributed E-tents for a total of five across the study period). We assumed E-tents deployed in this manner would capture female bees in a container of soapy water located at the top of the trap when they attempted to leave their nests to forage for pollen and nectar in the morning. Female bees captured in E-tents were interpreted to be nesting in the ground immediately below the trap. Netted bees were immediately anesthetized in cyanide jars and pinned the same day. Bees trapped in bee bowls and E-tents were transferred to 70% ethanol until they could be pinned later. All bees were identified to species.

Statistical Analysis

One-way analyses of variance (ANOVAs), followed by Tukey's honestly significant difference (HSD) post-hoc tests were used to analyze the effects of the 3 seeding treatments on plant species richness and floristic quality index (FQI) in 2013 and flower and bee abundance and species richness in 2014. Plant species richness was measured as the total number of species identified within each plot by Chris Helzer in 2013 (C. Helzer, unpublished data). Utilizing the same data set, plants were assigned a coefficient of

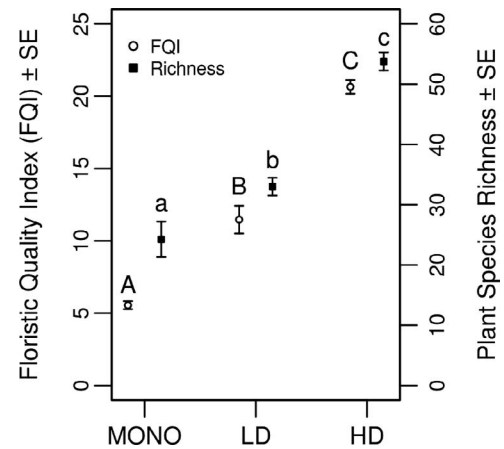


Figure 1. Floristic quality index (FQI) values and plant species richness for plots planted with seed mixes of different diversity. Data were collected on 31 July 2013 using 15 randomly stratified 1-m² quadrats within each plot (C. Helzer, unpublished data). Upper- and lowercase letters represent separate statistical analyses for FQI and plant species richness, respectively, while different letters indicate significant differences among groups ($P < 0.05$).

conservatism (C) according to Rolfsmeier and Steinauer (2003) and used to calculate a FQI value for each plot. To calculate FQI, we pooled data from all quadrats within a plot and took the product of the arithmetic mean of C and the square root of the species richness (Swink and Wilhelm 1994). Flower abundance was measured as the total number of flowers sampled within a plot in 2014, flowering species richness was measured as the total number of plant species in bloom observed within each plot in 2014, and bees collected by hand netting and bee bowls were pooled for analyses of bee abundance and richness. Seeding treatment was the independent variable tested, with 3 levels: MONO, LD, and HD. The proportion of E-tents that captured bees per plot was analyzed with a Kruskal-Wallis test. To avoid pseudoreplication, soil characteristics were assessed using one-way mixed effects ANOVAs, where the independent variable was seeding treatment and the random factor was the individual plots sampled, followed by Tukey's HSD. We used the program R (R Core Team, version 3.1.1) to analyze these data.

RESULTS

FQI values measured in 2013 differed significantly among seeding treatments ($F_{2,9} = 141.1$, $P \ll 0.001$; Figure 1). HD plots had 4 and 2 times higher FQI scores than MONO ($P \ll 0.001$) and LD ($P \ll 0.001$) plots, respectively. LD plots had FQI scores that were 2 times higher than MONO plots ($P \ll 0.001$). Similarly, plant species richness measured in 2013 differed significantly

Table 1. Complete list of flowering species in bloom during the study period (22–25 July 2014) in the 3 seeding treatments. An asterisk indicates species that flowered in at least 3 of the 4 replicate plots for the corresponding initial seeding treatment. The mean number of flowers corresponds to those sampled in the belt transects. Species in bloom that were not captured within the sample area were given a value of 0.5.

Species	Mean number of flowers \pm SE
Big bluestem (<i>Andropogon gerardii</i>) monoculture (MONO)	
<i>Asclepias incarnata</i>	0.13 \pm 0.13
<i>Cicuta maculata</i>	0.13 \pm 0.13
<i>Desmanthus illinoensis</i>	2 \pm 1.68
<i>Erigeron strigosus</i> ^a	13.5 \pm 13.17
<i>Lythrum alatum</i>	2.63 \pm 1.38
<i>Melilotus albus</i>	10 \pm 10
<i>Monarda fistulosa</i>	2.13 \pm 1.96
<i>Ratibida pinnata</i>	1.25 \pm 1.25
<i>Rudbeckia hirta</i> ^a	8.75 \pm 4.85
<i>Solidago canadensis</i>	1.75 \pm 1.44
<i>Verbascum thapsus</i>	0.38 \pm 0.24
<i>Verbena hastate</i>	7.5 \pm 2.90
<i>Verbena stricta</i> ^a	38.75 \pm 21.61
Low-diversity grass and forb mixture (LD)	
<i>Asclepias incarnata</i>	0.75 \pm 0.75
<i>Astragalus canadensis</i>	2.5 \pm 2.5
<i>Coreopsis tinctoria</i>	0.63 \pm 0.47
<i>Dalea purpurea</i>	0.75 \pm 0.75
<i>Desmanthus illinoensis</i>	3 \pm 2.38
<i>Erigeron strigosus</i>	13.5 \pm 6.24
<i>Hypericum perforatum</i>	2.88 \pm 2.71
<i>Lythrum alatum</i>	4 \pm 1.15
<i>Melilotus albus</i>	7.5 \pm 7.5
<i>Monarda fistulosa</i> ^a	21.13 \pm 16.75
<i>Oligoneuron rigidum</i>	0.75 \pm 0.75
<i>Ratibida pinnata</i>	7.25 \pm 3.63
<i>Rudbeckia hirta</i> ^a	190.75 \pm 77.29
<i>Silphium integrifolium</i>	1 \pm 1
<i>Solidago canadensis</i>	7 \pm 2.68
<i>Verbascum thapsus</i>	0.25 \pm 0.14
<i>Verbena hastate</i>	0.5 \pm 0.5
<i>Verbena stricta</i> ^a	33.13 \pm 20.68
High-diversity grass and forb mixture (HD)	
<i>Astragalus canadensis</i>	19.5 \pm 10.97
<i>Calylophus serrulatus</i>	0.25 \pm 0.25

Table 1. Continued.

Species	Mean number of flowers \pm SE
<i>Coreopsis tinctoria</i>	7.25 \pm 4.94
<i>Dalea candida</i>	1.5 \pm 0.62
<i>Dalea purpurea</i>	2.5 \pm 1.04
<i>Desmanthus illinoensis</i>	3.88 \pm 3.04
<i>Erigeron strigosus</i>	3.75 \pm 3.75
<i>Helianthus maximilianii</i>	0.25 \pm 0.25
<i>Helianthus pauciflorus</i>	0.25 \pm 0.25
<i>Heliopsis helianthoides</i>	23.75 \pm 20.15
<i>Heterotheca villosa</i>	6 \pm 3.76
<i>Liatris squarrosa</i>	0.5 \pm 0.5
<i>Lythrum alatum</i>	1.38 \pm 0.69
<i>Melilotus albus</i>	131.75 \pm 76.77
<i>Monarda fistulosa</i> ^a	658.5 \pm 100.16
<i>Oligoneuron rigidum</i>	0.5 \pm 0.5
<i>Penstemon digitalis</i>	0.25 \pm 0.25
<i>Ratibida pinnata</i> ^a	102 \pm 8.66
<i>Rudbeckia hirta</i> ^a	1118 \pm 506.44
<i>Silphium integrifolium</i>	4.75 \pm 0.63
<i>Solidago canadensis</i>	19.88 \pm 16.84
<i>Verbena hastate</i>	15 \pm 9.41
<i>Verbena stricta</i>	65.5 \pm 10.65
<i>Vernonia fasciculata</i>	1.25 \pm 0.75

^a Species flowered in at least 3 of the 4 replicate plots for the corresponding initial seeding treatment.

among treatments ($F_{2,9} = 53.46$, $P < 0.001$; Figure 1). HD plots were 120% and 63% more species rich than MONO ($P < 0.001$) and LD ($P < 0.001$) plots, respectively. LD plots were 36% more species rich than MONO plots ($P = 0.033$).

Available flowering resources varied significantly among seeding treatments in 2014. Perhaps not unexpectedly, flower abundance ($F_{2,9} = 24.12$, $P < 0.001$) and the species richness of available flowers ($F_{2,9} = 11.08$, $P = 0.004$; Figure 2) differed significantly with seeding treatment. HD plots had 25 times more flowers in bloom ($P < 0.001$) and were more than twice as species rich ($P = 0.003$) compared to MONO plots. HD plots also had a 600% more flowers ($P < 0.001$) and 50% more species ($P = 0.038$) in bloom than LD plots. Flower resources did not vary significantly in terms of either species richness ($P = 0.265$) or abundance ($P = 0.809$) between MONO and LD plots. A list of blooming forb species during the study period is presented in Table 1.

The different plant communities resulting from the initial seed plantings significantly altered abiotic factors associated with bee nest site occurrence. Seeding treatment had a

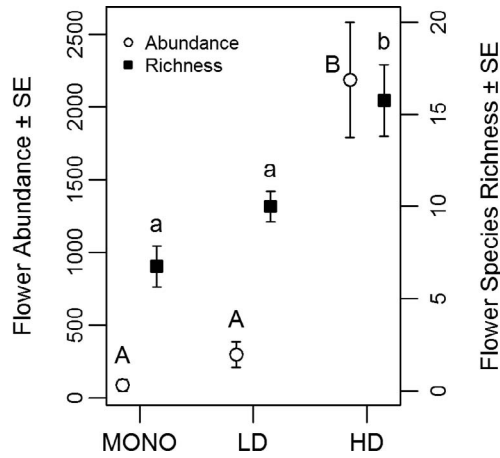


Figure 2. Flower abundance and species richness across seeding treatments. Upper- and lowercase letters represent separate statistical analyses for abundance and richness, respectively, while different letters indicate significant differences among groups ($P < 0.05$).

significant effect on the amount of available bare ground ($F_{2,9} = 8.721, P = 0.008$; Figure 3). HD plots had significantly more bare ground than MONO plots ($P = 0.006$). However, the amount of bare ground did not differ significantly between the MONO and LD ($P = 0.07$) or the LD and HD ($P = 0.307$) plots. Soil temperatures varied significantly in response to the different seeding treatments near the surface ($F_{2,9} = 5.97, P = 0.022$) and at 30 cm ($F_{2,9} = 9.743, P = 0.006$; Figure 4). Surface ($P = 0.020$) and 30-cm ($P = 0.004$) soil temperatures were 6.4% and 7% higher in HD plots compared to MONO plots, respectively. There was no significant difference in soil surface temperatures between the LD and HD ($P = 0.107$) and MONO and LD

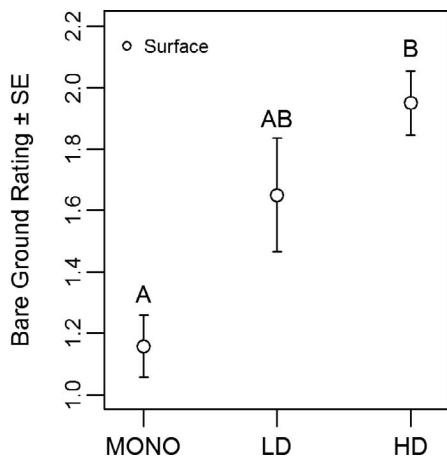


Figure 3. Bare ground availability in plots planted with different seed mix diversities. Different letters indicate significant differences among groups ($P < 0.05$).

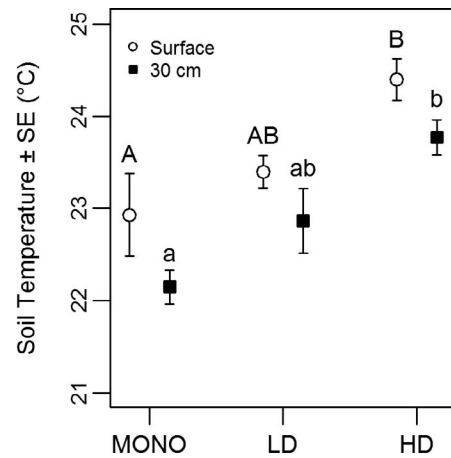


Figure 4. Soil temperature at the surface and 30 cm in plots with different seed mix diversities. Upper- and lowercase letters represent separate statistical analyses for surface and 30-cm samples, respectively, while different letters indicate significant differences among groups ($P < 0.05$).

($P = 0.548$) treatments. Similarly, there was no difference in the soil temperatures at 30 cm between the LD and HD ($P = 0.087$) and MONO and LD ($P = 0.168$) treatments. Soil moisture did not differ among the seeding treatments at the soil surface ($F_{2,9} = 0.572, P = 0.584$) or at 30 cm ($F_{2,9} = 1.865, P = 0.21$; Figure 5). Similarly, soil compaction did not differ among treatments at the soil surface ($F_{2,9} = 0.67, P = 0.537$) or at 30 cm ($F_{2,9} = 0.485, P = 0.631$; Figure 6).

A total of 15, 42, and 68 foraging bees belonging to 9, 25, and 41 species in MONO, LD, and HD treatments were captured, respectively, via hand netting and pan traps. The seeding treatments differed significantly in foraging bee abundance ($F_{2,9} = 175.58, P < 0.001$) and species richness ($F_{2,9} = 64.00, P < 0.001$; Figure 7). Bees were 350% and 60% more abundant in the HD treatment than they were in the MONO ($P < 0.001$) and LD ($P = 0.046$) plots, respectively. HD plots also had 360% and 60% higher bee species richness than either the MONO ($P < 0.001$) or LD ($P = 0.027$) treatments, respectively. LD-treated plots had nearly 3 times the number of individual bees ($P = 0.039$) and bee species ($P = 0.027$) compared to MONO plots. While there were statistically significant differences in 2 of the associated abiotic factors, the occurrence of bee nests did not differ significantly across treatments (Kruskal-Wallis $\chi^2_2 = 4.4, P = 0.1108$, Figure 8). However, overall capture rate was low, with E-tents capturing a single bee in 2 of the 4 HD plots.

DISCUSSION

Increasing flowering plant diversity is the most common recommendation for improving bee diversity in natural and restored areas. However, few studies have examined how

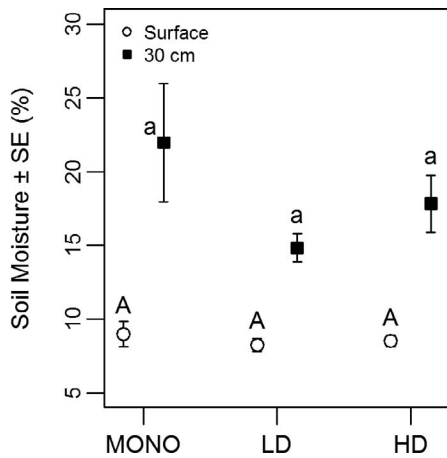


Figure 5. Soil moisture at the soil surface and 30 cm in response to initial seed mix diversity. Upper- and lowercase letters represent separate statistical analyses for surface and 30-cm samples, respectively, while different letters indicate significant differences among groups ($P < 0.05$).

the flower community directly affects nesting resources or nesting despite the known importance that flowering plant diversity has on bee diversity (Potts et al. 2005). As expected, areas planted with the most diverse seed mixes provided the greatest abundance and species richness of blooming flowers in addition to having higher floristic quality and overall plant species richness. Additionally, the diverse plant assemblages that resulted from the HD seeding treatment had the most bare ground and highest soil temperatures, conditions associated with increased bee

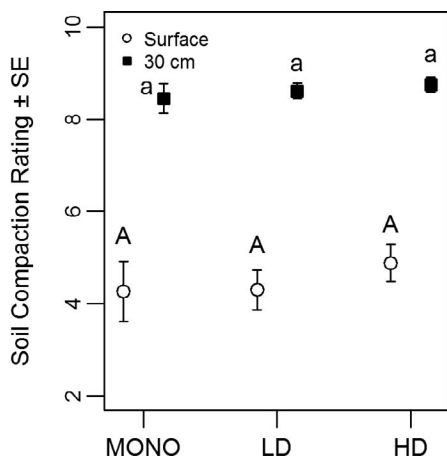


Figure 6. Soil compaction rating at the soil surface and 30 cm in plots planted with seed mixes that varied in diversity. Upper- and lowercase letters represent separate statistical analyses, for surface and 30 cm, respectively, while different letters indicate significant differences among groups ($P < 0.05$).

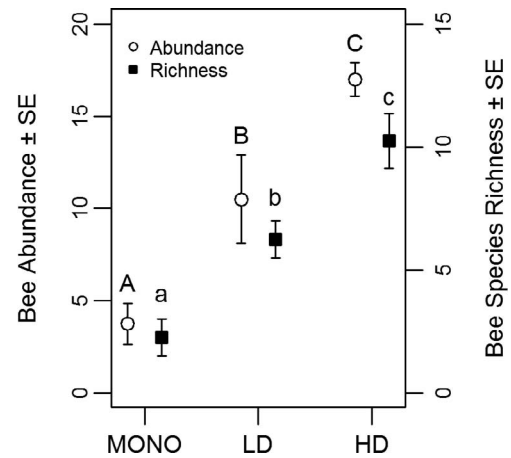


Figure 7. Foraging bee abundance and species richness across seeding treatments. Upper- and lowercase letters represent separate statistical analyses for abundance and species, respectively, while different letters indicate significant differences among groups ($P < 0.05$).

nesting frequency (Wuellner 1999, Potts et al. 2005, Donovan et al. 2010). While these changes to the plant community seemingly improved these areas for ground-nesting bees with regard to their nutritional and nesting requirements, we only observed a strong response from foraging bees and did not detect a significant response in terms of nesting. However, this is likely due to the low catch rate of E-tents—0 in 20 traps each for MONO and LD and 2 bees in 20 traps for HD—and the resulting low statistical power. Our data weakly imply that incidence of nesting is

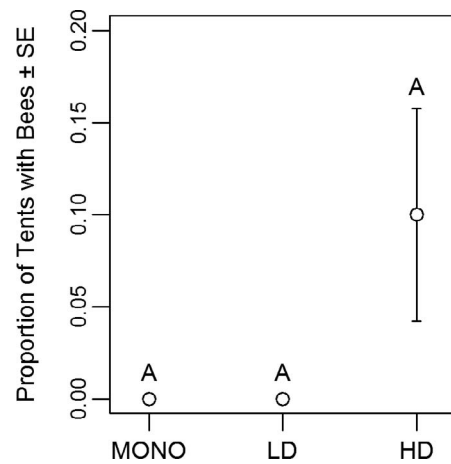


Figure 8. Bee nest occurrence in response to initial seed mix diversity. The response variable is the proportion of soil emergence tents (E-tents) within a single plot that captured a nesting bee (5 E-tents per plot, 4 plots per seeding treatment). Different letters indicate significant differences among groups ($P < 0.05$).

highest in plots planted with the most diverse seed mixes (see Sardiñas and Kremen 2014 and Pane and Harmon-Threatt 2017, for suggestions on increasing catch rate). Supporting this suggestion is a previous study that used the same E-tent methodology in high-quality remnant prairies and had a similar capture rate to the 10% observed in our HD plots (Buckles 2015).

We did not observe changes in soil moisture or compaction in response to seed mix diversity in our study sites for a number of possible reasons. While a previous study found that plant roots can fragment compacted soil (Tri 1968), the time scale over which such changes occur may be longer than the 4 y between planting and sampling used here (Kay 1990). Additionally, the close proximity of our sites to the Platte River (approximately 25 m from riverbank to nearest plot edge) may mask differences in soil moisture caused by our seeding treatments, as the water table is likely high here. Soil moisture can affect soil compaction (Lafond et al. 1992); the homogeneity of soil moisture values across our plots may further explain why we did not see differences in compaction. However, these factors are still likely important in determining bee nest site occurrence (Cane 1991, Potts and Willmer 1997, Wuellner 1999, Sardiñas and Kremen 2014), and additional studies are needed in areas without the potential confounding factors that may be present at our study site. Also, other measures of soil compaction and hardness may be better able to detect differences even in the presence of high, homogeneous soil moisture levels.

One interesting implication of this study is that increasing seed mix diversity could affect immature bee development via increased soil temperatures. The increase in soil temperature at 30 cm—a depth associated with many belowground nests (Cane and Neff 2011)—has the potential to accelerate bee development (Yocum et al. 2014). However, it is unknown how such a change in temperature affects the synchrony, and thus the strength, of plant–pollinator mutualisms (Rafferty and Ives 2011, Scaven and Rafferty 2013, Martins et al. 2015). If such an increase in temperature is determined to be deleterious for these important interactions, this knowledge could be used to fine-tune recommendations for restoration and conservation projects targeting native bees. For example, the species composition of seed mixes could be modified to compensate for shifts in phenology and ensure adequate overlap of flower bloom and bee activity. Additional research is necessary to determine if the effects on plant–pollinator synchrony will be biologically significant, and if the negative consequences can be mitigated by adjusting seed mixes.

One limitation of this study, and practically every previous study on the occurrence of bee nests, is that while we measured nesting within our experimental plots, it is likely that the unsampled matrix and surrounding habitat

could provide adequate or even preferred nesting conditions (Mandelik et al. 2012). In particular, the proximity of our study site to river banks, a forest patch, mowed walkways, and gravel roads, all areas associated with nesting in at least some species (Kukuk et al. 1977, Wuellner 1999, Winfree et al. 2007), could have resulted in bees nesting in these sites while still foraging within the experimental area. Further studies are needed on the role of matrix quality on bee nesting, and how this might facilitate bee resource acquisition in fragmented habitats such as the one in the current study.

Future work should focus on monitoring the bee, floral, and abiotic variables of habitat patches across the growing season. Actively foraging bees (Mandelik et al. 2012), prairie plant communities (Mallinger et al. 2016), and the interactions between them (CaraDonna et al. 2017) vary greatly throughout the spring, summer, and fall. As the growing season progresses, the strength and directionality of the influence of the physical structure of the plant community on the abiotic factors measured here may change in addition to differences in the availability, composition, and spatial distribution of flower resources (Carson et al. 2016, Mallinger et al. 2016). These seasonal changes make it likely that plant assemblages differ in their influence of abiotic factors affecting nesting decisions over the course of the growing season and that associated bee communities have different sensitivities to the resulting conditions. The changing impacts of the plant community and the variable sensitivities of bee communities to these factors likely interact in complex ways that cannot be elucidated with the data presented here. Such differences may prove to be important for achieving conservation and restoration goals.

In addition to their widely accepted role in providing foraging resources for bees, our research has shown that plant communities with diverse flower resources also alter abiotic factors associated with nest occurrence of ground-nesting bees. In particular, these communities offer more bare ground and increased soil temperatures. As central-place foragers with relatively limited foraging ranges, the selection of a habitat or set of habitat fragments that provide access to adequate food and nesting resources is critical for bees. We report here that, while we did not observe a significant difference in nesting between treatments, restoration practices incorporating diverse seed mixes aimed at providing bees access to a wide variety and abundance of nutritional resources may also provide nesting resources thought to be preferred by ground-nesting bees.

ACKNOWLEDGMENTS

We would like to thank The Nature Conservancy for allowing us to conduct this research on their property, C. Helzer for his help throughout the project, D. Blankenship

and J. Cutter for their help in the field, M. Arduser and B. Buckles for their help in identifying bees, and R. Anderson, T. Burk, A. Pane, B. Decker, S. Clem, E. Moscoso Anderson, and an anonymous reviewer for comments that improved the manuscript. This research was funded by the University of Illinois at Urbana-Champaign.

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