

Floral-Devoid Perennial Grass Seed Fields Harbor a Diversity of Native Bees

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ABSTRACT: Insect pollinators are critical for human food security and the proper functioning of natural ecosystems, but long-term declines of wild bee populations have necessitated a broader understanding of how different land cover types can support bee conservation. In contrast to regularly tilled agricultural crops that seldom provide nesting areas for wild bees, perennial grass seed fields experience long intervals between soil disturbance (5-15 y) and may provide suitable nesting habitat for ground-nesting bees. In this study we sampled wild bees in perennial grass seed fields planted to tall fescue (*Schedonorus phoenix*) that were devoid of bloom to assess the potential for perennial grass seed fields to support bee populations when floral resources were absent. We sampled bees at both near (50 m) and far (200 m) distances from field edges, capturing > 750 individual bees that represented 41 species/morphospecies in 12 genera and 3 families within grass seed fields. Most of the bees we captured were ground-nesting species, with several of the most abundant genera harboring species that are critical for crop pollination including bumble bees (*Bombus* spp.), long-horned bees (*Melissodes* spp.), and sweat bees (*Halictus* spp.). When considering females of nest-building species, we detected no differences in observed species richness or abundance at sampling locations that were near and far from field edges. We also found no strong differences in body size differences between near and far sampling locations, suggesting small bees with limited foraging distances nested within grass seed fields. Our results indicate that native bees use floral-devoid grass seed fields, perhaps because they serve as nesting areas for ground-nesting species, and that such bees have the potential to spill over into adjacent crops and enhance pollination when grass seed fields are embedded within a mixed crop landscape.

KEYWORDS: Agricultural crops, native bees, grass seed fields, pollination, spillover

Agricultural crops can support wild pollinator populations, and much research has focused on evaluating the extent to which crops provide the floral resources typically used by pollinating insects (i.e., nectar, pollen). In contrast, less attention has focused on how cropped fields may provide other critical resources to insect pollinators – such as nesting substrates (Requier and Leonhardt, 2020) – despite the importance of nest sites for long-term maintenance of pollinator populations. Grass seed crops are unique relative to other agricultural crops because they are typically managed to be devoid of the floral resources required by insect pollinators, and because they usually experience long intervals between disturbance events that may promote suitable nesting sites. For example, Rao and Skyrn (2013) found nests of the Nevada bumble bee (*Bombus nevadensis*) within untilled annual ryegrass (*Lolium multiflorum*) fields in western Oregon, USA. In that study, the use of grass seed fields appeared to be exclusively for nesting because

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grasses lack nectar and bees typically avoid foraging on grass pollen (Erickson and Atmowidjojo, 1997; but see Immelman and Eardley, 2009) and because individuals were observed after the grass seed crop was harvested (Rao and Skyrn, 2013).

Despite these observations, it remains unknown whether grass seed fields may support a broader array of bee species, and whether these areas may play a role in pollinator conservation within mixed-crop landscapes. In this study, we assessed whether floral-devoid perennial grass seed fields in western Oregon, USA were used by wild, free-ranging bees to evaluate their conservation potential. Perennial grass crops can experience a relatively large interval between soil disturbance depending on their management (e.g., tilling on 5-y interval for tall fescue [*Schedonorus phoenix*] and 15-y intervals for orchardgrass [*Dactylis glomerata*]; Anderson, pers. obs.), and such areas may provide temporally stable nesting sites for bees that nest underground, which represent the majority of wild bee species worldwide (Cane, 1991). Additionally, perennial grass fields in our study region co-occur with a range of other crops that require and/or benefit from bee pollination (Rao and Stephen, 2010), making it an ideal location to test whether grass seed fields support pollinators as part of a diverse agricultural landscape.

To quantify bee use of perennial grass seed fields, we placed commercially available, bee-attractive blue vane traps (Rao and Ostroverkhova, 2015; Packer and Darla-West, 2021) within fields that were devoid of floral resources during the summer flight season. Because bee foraging range decreases with bee body size (Greenleaf *et al.*, 2007; Kendall *et al.*, 2022), we sampled bees at two different distances from the field edge (i.e., 50 m and 200 m) to evaluate whether smaller-bodied bees were less likely to be captured deeper into the interior of grass seed fields relative to field margins. Thus, we predicted that (1) bee richness and abundance would be greater at sampling locations closer to field edges, and (2) sampling locations far from field edges would be dominated by large-bodied species because the foraging range of small-bodied bees, which we assumed to be nesting outside of grass seed fields, would limit their flights into fields given they harbored no floral resources.

MATERIALS AND METHODS

Experimental Design

In spring 2021, we selected 10 commercial fields that were planted with tall fescue (*Schedonorus phoenix*) grown for seed and located within Benton County, Oregon, USA. Oregon is one of the largest grass seed production areas in the world, with grass seed crops being valued at > US \$415 million annually (ODA, 2021), and the majority of production occurs in the Willamette Valley, including Benton County, where it is considered the dominant crop. The fields we studied were windrowed and combine-harvested in late June 2021, so they contained minimal vegetation when we sampled bees in July and August. After bee sampling was initiated, we discovered that a weed common to the Willamette Valley (sharpshoot fluevellin [*Kickxia elatine*]) was flowering throughout $n = 3$ fields. Therefore, we removed these 3 sites from all statistical analyses because our study required areas devoid of flowers; bee communities from fields containing *Kickxia elatine* are described in Parvin (2022). The remaining $n = 7$ fields we used for analysis had a mean size of 32.7 ha and a mean perimeter of 2,572 m, both of which are typical of the size and configuration of commercial grass seed fields in our region (N. Anderson, pers. obs.).

In each field, we affixed blue vane traps (BanfieldBio, Woodinville, Washington, USA) on

metal t-posts using wire in 3-5 sampling locations within each field, with the number of sampling locations scaling with field size. All sampling locations within and between fields were situated a minimum of 200 m from each other so they were as independent as possible while also maximizing the number of traps on each field; sampling locations alternated between near (50 m) and far (200 m) distance classes from the field edge. We determined the order of trap placement within each field by flipping a coin to determine which distance class would be assigned first beginning in the northwest corner of the field, and then we alternated to distance classes thereafter throughout the rest of the field; this resulted in a total of 24 sampling locations across all fields. Using the same process, at each sampling location we placed either a single trap or a combination of three traps affixed together, each capable of trapping insects, that were implemented as part of a broader investigation of bee use of perennial grass seed fields (Parvin, 2022).

Bee Community Sampling

We sampled bees in three sampling rounds during the 2021 summer flight season. In the first round, we placed traps in grass seed fields on July 2-3 and left them in place for 5 days due to uncertainty about the number of bee captures, which were expected to be low due to the lack of floral resources. After finding sufficient bees during the first round of sampling, we reduced the amount of time we left traps in place to 2 days during both the second (starting July 31) and third sampling rounds (starting August 19) to reduce sample degradation during hot weather. We set out traps from 0800–1730 local time and in all instances retrieved them within 30 min of the time they were placed out. In each trap we added a small amount of soapy water solution to facilitate capturing insects that entered traps. We emptied the contents of traps into a Whirl-Pak plastic bag that was filled with 70% ethanol solution prior to transport to the laboratory for washing, pinning, and identification. During the third round, three traps in a single field were damaged by farm equipment during field maintenance and thus were removed from subsequent analysis. Our sampling resulted in a total of 120 trap-days in the first round, 48 trap-days in the second round, and 42 trap-days in the third round. Importantly, we used an offset for sampling effort in our statistical models to account for the difference in trap-days across rounds that allowed us to make direct comparison of bee measures between rounds (see below).

All bee specimens were identified to species/morphospecies by an experienced taxonomist (L. R. Best, Oregon State University). Keys from Michener (2007) and Stephen *et al.* (1969) were used to identify specimens to the generic level, and both regional and synoptic collections and local keys were used to determine species-level identifications for *Agapostemon* (Roberts, 1973a), *Anthidium* (Gonzalez and Griswold, 2013), *Anthophora* (Brooks, 1983), *Halictus* (Roberts, 1973b), *Bombus* (Williams *et al.*, 2014), *Ceratina* (Daly, 1973), *Melissodes* (LaBerge, 1956a, 1956b, 1961) and to determine sub-genus and species/morphospecies-level identifications for *Lasioglossum* (McGinley, 1986; Gibbs *et al.*, 2013) and *Megachile* (Hurd and Michener, 1955; Grigarick and Stange, 1968). A reference collection made from a subset of specimens will be housed at the Oregon State Arthropod Collection at Oregon State University (<https://osac.oregonstate.edu/>).

A single individual (I.A.P.) measured intertegular distance (ITD), which is a strong and repeatable correlate of body mass that provides a comparative measure of size (Cane, 1987), from representative female specimens using a Leica S6D stereo dissecting microscope with a mounted Leica MC170 HD camera and the LAS v4.12 software package. Following calibration, each bee was mounted on a piece of modeling clay and three replicate measurements were taken from the middle of the inte-

rior margin of the left tegula to the interior margin of the right tegula; the average of the three measurements taken on each specimen served as its ITD for analysis. If > 10 specimens were available for each species we randomly selected 10 specimens to be measured; otherwise, if ≤ 10 were obtained for a single species, we measured all available specimens.

Statistical Analysis

We used the R statistical environment (v4.3.1; R Core Team, 2023) for all analyses. To assess how bee response variables were influenced by distance from field edge, we only considered female bees that create their own nests because, as central place foragers, they are constrained to a nest site and therefore restricted in their movement relative to males and cleptoparasitic species (Michener, 2007). We pooled bees that were captured in the multiple-trap sampling locations for each of the three sampling rounds, which resulted in a single measure of observed bee species richness and bee abundance for each sampling location in each sampling round. Next, we used the `glmmTMB` function of the `glmmTMB` package (Brooks *et al.*, 2017) to construct a model with a Poisson distribution and a log link that contained observed bee species richness as the response variable with distance to edge (2 levels: near, far) and sampling round (3 levels) as fixed effects, field and trap nested within field as random effects, and an offset for sampling effort (i.e., number of trap-days). We used the same approach and model structure to model bee abundance. We confirmed model fit using the `DHARMA` package (Hartig, 2020) and computed fixed effects tests using the `car` package (Fox and Weisberg, 2019). In addition, we used a Wilcoxon two-sample test to assess whether the ITD distribution of all bees captured differed between near and far sampling locations. We report estimated marginal means and associated 95% confidence intervals (CIs) from the `emmeans` package (Lenth, 2020) unless otherwise noted.

Finally, we used the `iNEXT` package (v3.0.0; Hsieh *et al.*, 2020) to construct rarefaction and extrapolation curves for three common Hill numbers (i.e., $q = 0$, $q = 1$, $q = 2$) that are used to assess biodiversity (Chao *et al.*, 2014; Hsieh *et al.*, 2016). Hill numbers represent the effective number of species for species richness ($q = 0$), the exponential of the Shannon index ($q = 1$; hereafter, Shannon diversity), and the inverse of the Simpson concentration ($q = 2$; hereafter, Simpson diversity), and they provide several advantages over other diversity measures including the ability to make “fair comparisons” based on sample coverage (Chao and Jost, 2012; Chao *et al.*, 2014; Hsieh *et al.*, 2016). For analysis, we constructed separate curves to compare between near and far distances from field edge; for each we created sample-sized-based rarefaction and extrapolation curves, coverage-based rarefaction curves, and sample-completeness curves with 95% confidence intervals (CIs; Chao *et al.*, 2014; Hsieh *et al.*, 2016). Additionally, we calculated asymptotic estimates of bee diversity for the first 3 Hill numbers for distance to edge categories.

RESULTS

We captured 758 bees overall, representing 41 species/morphospecies in 12 genera and 3 families (Table 1). The most frequently captured genera were *Melissodes* (36.2% of captures, 10 species), *Apis* (17.9% of captures, 1 species), *Bombus* (17.2%, 7 species), *Halictus* (10.8%, 4 species), and *Lasioglossum* (9.9%, 5 species; Table 1). We caught a total of 74 male bees in 16 species with most species represented by < 5 individuals (Table 1); their removal resulted in 684 female bees from 37 species used for statistical analysis. Considering females only, most species that were represented by > 1 specimens were trapped at both distance classes (88%; Table 1). Overall, most captured bees were classified as polylectic, ground-nesting species, with both solitary and eusocial species being well-represented in the dataset (Table 1).

Table 1. Classification, abundance, and life history characteristics of wild bees captured in fields of tall fescue (*Schedonorus phoenix* [Scop.] Holub) grown for seed and lacking floral resources in Benton County, Oregon through three sampling rounds undertaken during summer 2021. For each bee species, distance class of “Near” and “Far” denotes whether females were captured 50 m and 200 m from field edge, respectively. See Materials and Methods for details.

Family	Species/Morphospecies	Females captured	Males captured	Distance class (females only)	Social System	Nesting Location	Pollen Specialization
Apidae	<i>Anthophora bomboidea</i>	1	0	Near	Solitary ¹	Ground ²	Unknown
Apidae	<i>Anthophora urbana</i>	1	0	Far	Solitary ¹	Ground ²	Polylectic ¹
Apidae	<i>Apis mellifera</i>	136	0	Near, Far	Eusocial ²	Above Ground ²	Polylectic ²
Apidae	<i>Bombus appositus</i>	9	1	Near, Far	Eusocial ¹	Ground/ Above Ground ³	Polylectic ¹
Apidae	<i>Bombus caliginosus</i>	1	0	Far	Eusocial ¹	Ground/ Above Ground ³	Polylectic ¹
Apidae	<i>Bombus fervidus</i>	16	11	Near, Far	Eusocial ¹	Ground/ Above Ground ⁵	Polylectic ¹
Apidae	<i>Bombus griseocollis</i>	8	1	Near, Far	Eusocial ¹	Ground/ Above Ground ³	Polylectic ¹
Apidae	<i>Bombus mixtus</i>	2	0	Near	Eusocial ¹	Ground/ Above Ground ³	Polylectic ¹
Apidae	<i>Bombus nevadensis</i>	15	1	Near, Far	Eusocial ¹	Ground/ Above Ground ³	Polylectic ¹
Apidae	<i>Bombus vosnesenskii</i>	45	20	Near, Far	Eusocial ¹	Ground ⁷	Polylectic ¹

Family	Species/Morphospecies	Females captured	Males captured	Distance class (females only)	Social System	Nesting Location	Pollen Specialization
Apidae	<i>Eucera cordleyi</i>	24	0	Near, Far	Solitary ¹	Ground ¹	Unknown
Apidae	<i>Eucera edwardsii</i>	1	0	Far	Solitary ¹	Ground ¹	Polylectic ¹²
Apidae	<i>Melissodes agilis</i>	29	3	Near, Far	Solitary ¹	Ground ¹	Oligolectic (As-teraeae, Heliant-heae) ¹⁷
Apidae	<i>Melissodes clarkiae</i>	0	2	---	Solitary ¹	Ground ¹	Oligolectic (<i>Clarkia</i>) ¹
Apidae	<i>Melissodes communis</i>	15	9	Near, Far	Solitary ¹	Ground ¹	Oligolectic ¹
Apidae	<i>Melissodes lupinus</i>	56	14	Near, Far	Solitary ¹	Ground ¹	Oligolectic ¹
Apidae	<i>Melissodes metenus</i>	125	0	Near, Far	Solitary ¹	Ground ¹	Oligolectic ¹
Apidae	<i>Melissodes microstictus</i>	2	0	Near, Far	Solitary ¹	Ground ¹	Oligolectic ¹
Apidae	<i>Melissodes rivalis</i>	10	0	Near, Far	Solitary ¹	Ground ¹	Oligolectic ¹
Apidae	<i>Melissodes robustior</i>	0	4	---	Solitary ¹	Ground ¹	Oligolectic (As-teraceae) ¹⁸
Apidae	<i>Melissodes (Callimelissodes) sp. 1</i>	0	3	---	Solitary ¹	Ground ¹	Oligolectic ¹
Apidae	<i>Melissodes sp. 1</i>	2	0	Far	Solitary ¹	Ground ¹	Unknown
Halictidae	<i>Agapostemon texanus</i>	10	0	Near, Far	Solitary/Communal Nesting ¹	Ground ²	Polylectic ¹
Halictidae	<i>Agapostemon virescens</i>	9	1	Near	Solitary/Communal Nesting ¹	Ground ²	Polylectic ¹
Halictidae	<i>Halictus farinosus</i>	28	0	Near, Far	Primitively Eusocial ¹⁵	Ground ¹	Polylectic ¹

Family	Species/Morphospecies	Females captured	Males captured	Distance class (females only)	Social System	Nesting Location	Pollen Specialization
Halictidae	<i>Halictus ligatus</i>	32	0	Near, Far	Primitively Eusocial ¹⁴	Ground ²	Polylectic ¹
Halictidae	<i>Halictus rubicundus</i>	6	0	Near, Far	Primitively Eusocial ²	Ground ²	Polylectic ¹
Halictidae	<i>Halictus tripartitus</i>	16	0	Near, Far	Primitively Eusocial ¹⁴	Ground ²	Polylectic ¹
Halictidae	<i>Lasioglossum cooleyi</i>	10	0	Near, Far	Primitively Eusocial ¹⁰	Ground ²	Polylectic ¹
Halictidae	<i>Lasioglossum (Dialictus) sp. 1</i>	55	0	Near, Far	Unknown	Unknown	Polylectic ¹
Halictidae	<i>Lasioglossum olympiae</i>	1	1	Far	Unknown	Ground ²	Polylectic ¹
Halictidae	<i>Lasioglossum titusi</i>	1	0	Far	Unknown	Ground ²	Polylectic ¹
Halictidae	<i>Lasioglossum zonulum</i>	6	1	Near, Far	Solitary ¹¹	Ground ²	Polylectic ¹
Megachilidae	<i>Anthidium manicatum</i>	1	0	Near	Solitary ¹	Ground/ Above Ground ²	Polylectic ¹
Megachilidae	<i>Hoplitis producta</i>	1	0	Near	Solitary ¹⁶	Stem ²	Polylectic ¹⁶
Megachilidae	<i>Megachile angelarum</i>	0	1	---	Solitary ¹	Above Ground ¹	Polylectic ¹³
Megachilidae	<i>Megachile perihirta</i>	1	0	Near	Solitary ¹	Ground ⁴	Oligolectic (Asteraceae, Fabaceae) ⁴
Megachilidae	<i>Megachile rotundata</i>	1	1	Near	Solitary ¹	Above Ground ¹	Oligolectic ¹
Megachilidae	<i>Megachile sp. 1</i>	1	0	Far	Solitary ¹	Unknown	Unknown

Family	Species/Morphospecies	Females captured	Males captured	Distance class (females only)	Social System	Nesting Location	Pollen Specialization
Megachilidae	<i>Osmia (Melanosmia) sp. 1</i>	1	0	Near	Solitary ¹	Above Ground ⁶	Polylectic ¹
Megachilidae	<i>Osmia nemoris</i>	6	0	Near, Far	Solitary ¹	Ground/ Above Ground ⁶	Polylectic ¹
Total abundance		684	74				

References: ¹Wilson and Carril, 2015; ²Michener, 2007; ³Williams *et al.*, 2014; ⁴Hobbs and Lilly, 1954; ⁵Whelden, 1954; ⁶Cane *et al.*, 2007; ⁷Saifuddin and Jha, 2014; ⁸Richards *et al.*, 2010; ⁹Tonietto *et al.*, 2017; ¹⁰Packer and Owen, 1989; ¹¹Blitzer *et al.*, 2016; ¹²Cane and Love, 2016; ¹³Pow, 2019; ¹⁴Roberts, 1973b; ¹⁵Nye, 1980; ¹⁶Danforth *et al.*, 2019; ¹⁷Linsley, 1958; ¹⁸Traynor, 2019.

When modeling diversity measures, we found that observed species richness was influenced by sampling round ($\chi^2 = 6.86$, $p = 0.032$, $df = 2$) but not distance to edge ($\chi^2 = 0.26$, $p = 0.613$, $df = 1$). When controlling for sampling effort, observed bee richness in the first sampling round was $1.9 \times$ higher (95% CI: 1.5, 2.5, $z = 5.19$, $p < 0.001$) and $2.9 \times$ higher (95% CI: 2.1, 3.9; $z = 6.96$, $p < 0.001$) relative to the second and third sampling rounds, respectively; observed bee richness was $1.5 \times$ higher (95% CI: 1.1, 2.2; $z = 2.42$, $p = 0.016$) in the second round relative to the third sampling round. Observed bee richness near field edges was very similar to measures far from field edges (ratio: 1.06 [95% CI: 0.84, 1.34], $z = 0.51$, $p = 0.613$; Figure 1A). We found that bee abundance followed a similar pattern as observed species richness in that it was influenced by sampling round ($\chi^2 = 11.94$, $p = 0.003$, $df = 2$) but not distance to edge ($\chi^2 = 0.56$, $p = 0.453$, $df = 1$). Abundance in the first round was $3.0 \times$ higher (95% CI: 2.4, 3.6; $z = 11.3$, $p < 0.001$) than the second round and $3.6 \times$ higher (95% CI: 2.9, 4.4; $z = 11.7$, $p < 0.001$) in the third round; abundance measures for the second and third sampling rounds were similar (ratio: 1.2 [95% CI: 0.9, 1.6]; $z = 1.51$, $p = 0.135$). Bee abundance at sampling locations near field edges was similar to sampling locations far from field edges (ratio: 1.2 [95% CI: 0.8, 1.7], $z = 0.75$, $p = 0.453$; Figure 1B). Finally, we found no evidence that the mean ITD size of bees captured differed between sampling sites located near (mean ITD = 2.71 mm [SD = 0.98]) and far from the field edges (mean ITD = 2.83 mm [SD = 1.06]; $W = 41342$, $P = 0.197$; Figure 2).

When comparing bee diversity measures between sampling locations that were near and far from field edges, we found that observed species richness was underestimated similarly at both distances relative to estimates of species richness (Table 2); however, estimated measures for both Shannon diversity and Simpson diversity were close to observed values (Table 2). For both near and far sites, curves for estimated species richness exhibited a slow increase beyond the reference sample (i.e., the number of specimens obtained from trapping), but not for Shannon or Simpson diversity (Supp. Figure S1A-C). In addition, sample coverage for the reference samples was high when comparing between near (98.3%, $n_{\text{reference}} = 423$) and far distance classes (96.6%, $n_{\text{reference}} = 261$; Figure S1D-F), indicating sample coverage deficit was $< 3.5\%$ for both groups. Applying the traditional rarefaction approach to standardize sample coverage to the smaller of the two sample sizes for distance to edge ($n = 261$) results in sample coverage of 98.6% for sampling locations near the edge with overlapping CIs for sample completeness curves (Supp. Figure S2).

DISCUSSION

The perennial grass seed fields we studied were devoid of floral resources due to intensive management that included herbicide application to remove competing vegetation, so the diversity and abundance of bees we found was unexpected given the critical role that floral resources play in supporting bee populations. Prior work in perennial grass crop systems has shown this crop type can support native bees (Larson *et al.*, 2017), but nearly all such studies have quantified bee diversity and abundance in locations where flowering plants are interspersed with perennial grasses and provide floral resources available to pollinators, making comparisons with our study difficult. One exception to this pattern is recent work by Campbell *et al.* (2021) that assessed community response to perennial grass management for cattle, including a treatment that included pastures with a mix of tall fescue and bermudagrass (*Cynodon dactylon*) and sprayed with herbicides to remove competing forbs. Although a direct comparison with that study is challenging due to differences in sampling methods, we detected more species in our

Figure 1. Estimated marginal means (\pm 95% CI) for (A) observed bee species richness and (B) bee abundance at sampling locations near (50 m) and far (200 m) from field edges. Neither observed species richness nor bee abundance varied as a function of the distance at which sampling locations were situated within fields.

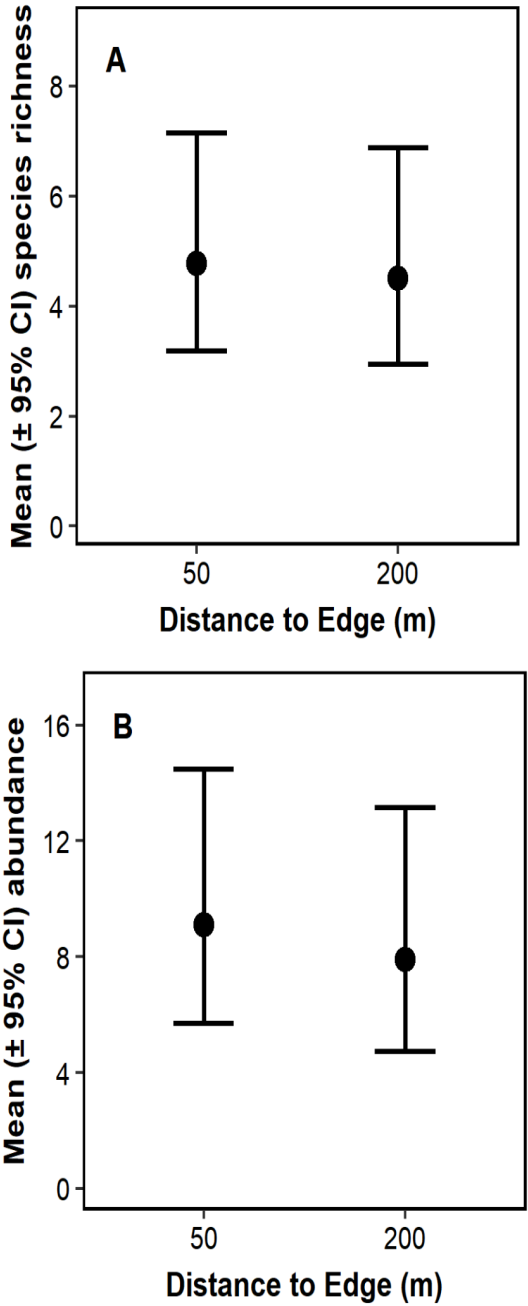


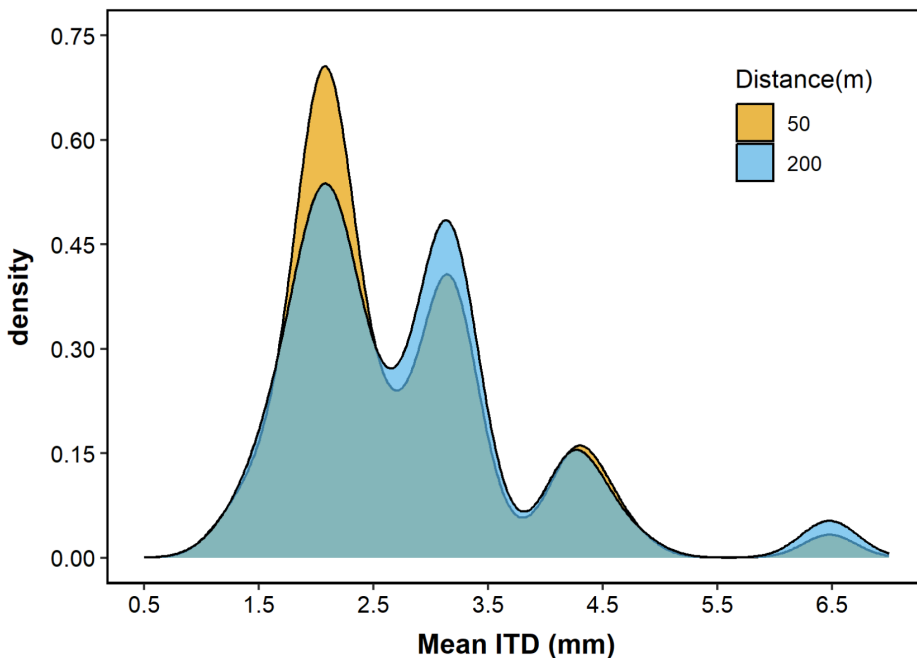
Table 2. Observed and asymptotic diversity estimates (95% confidence intervals [CI]) for bees captured at two distance classes (Near = 50 m; Far = 200 m) from field edges in commercial grass seed fields of western Oregon across three sampling rounds during summer 2021.

Distance class	Diversity measure	Hill number	Observed diversity	Estimated diversity	Estimated diversity (95% CI)
Near	Species richness	$q = 0$	30	42.2	30.0, 68.5
Near	Shannon diversity ¹	$q = 1$	14.7	15.5	13.9, 17.0
Near	Simpson diversity ²	$q = 2$	9.7	9.9	8.7, 11.0
Far	Species richness	$q = 0$	29	42.4	29.0, 75.7
Far	Shannon diversity ¹	$q = 1$	14.5	15.8	13.4, 18.1
Far	Simpson diversity ²	$q = 2$	9.4	9.7	7.7, 11.7

¹ equivalent to exponential of Shannon index and estimates the effective number of common species (Chao *et al.*, 2014)

² equivalent to inverse Simpson concentration and estimates the effective number of dominant species (Chao *et al.*, 2014)

Figure 2. Relationships between distribution of bee size, measured as mean intertegular distance (ITD) and sampling locations where bees were captured within grass seed fields. The limited difference between distributions indicates bees of similar sizes were found at both sampling distances within fields.



study (41 species) relative to what was found by Campbell *et al.* (28 species) despite the latter study implementing 5-6 months of continuous pan trapping across two summers. What led to these differences is unclear, but one possibility is that the diversity of crops in the landscape we studied, some of which are dependent on insect pollination (Rao and Stephen, 2010), provided nectar and/or pollen resources for bees that were lacking in the perennial grass fields and collectively these diverse crops promoted greater bee diversity at the landscape level.

Most of the bees we captured in our study were ground-nesting species representing several genera that are important crop pollinators, including the bumble bees (*Bombus* spp.), long-horned bees (*Melissodes* spp.), and sweat bees (*Halictus* spp.; Rao and Stephen 2009, 2010; Mallinger *et al.*, 2019; Esquivel *et al.*, 2021). In addition, the great majority of species captured in this study were classified as ground-nesting species, which is consistent with the idea that the exposed patches of soil and the small mammal burrows that we observed within grass seed fields (Parvin, pers. obs.) likely served as areas for bee nesting, paralleling prior research in our study region (Rao and Skyrn, 2013). We captured few bee species in our study that nest above ground, represented by several *Osmia* spp., and only one that is restricted to nesting in stems (i.e., *Hoplitis producta*; Michener, 2007). Of note, we had no captures of *Ceratina* or *Hylaeus*; both of these genera are characterized by nesting in stems with several species within each genus found in western Oregon in such varied crops and land cover types as highbush blueberry (*Vaccinium corymbosum*; Rao and Stephen, 2010), red clover (*Trifolium pratense*; Rao and Stephen, 2010), sunflower (*Helianthus annuus*; Stephen and Rao, 2007), and early seral Douglas-fir (*Pseudotsuga menziesii*) forest (Rivers and Betts, 2021; Zitomer *et al.*, 2023). Given that the fields we studied were managed for perennial grass seed production, it is not unexpected that they were devoid of pithy stems and lack the species that require these specific habitat elements for nesting, and instead were used by ground-nesting species that are able to exploit exposed soil and subterranean mammal burrows for nesting (Rao and Skyrn, 2013). It is also worth noting that many of the species we captured in perennial grass seed fields are common species that are present in a range of crops and land cover types in our region, including those noted above. Previous work has shown that the abundance of common of bee species can drive delivery of crop pollination services (Winfree *et al.*, 2015), bolstering the idea that grass seed fields that are devoid of floral resources may still boost ecosystem services by serving as nest sites for common species that ultimately use pollinator-dependent crops in the broader landscapes in which we worked.

We found similar bee diversity levels between sampling locations near (i.e., 50 m) and far (i.e., 200 m) from the field edge, counter to the prediction that lower bee diversity would be found at sampling locations far from field edges because few species would be unable – or unwilling – to move farther into grass seed fields. Because the grass seed fields in which we worked were devoid of floral resources, captured bees were either drawn to our sampling locations from outside of field margins or were occupying fields independently of our sampling. As noted above, previous research in our study area by Rao and Skyrn (2013) found at least one native bee species (*Bombus nevadensis* Cresson [Hymenoptera: Apidae]) using previously harvested grass seed fields as nesting sites, although it is worth noting this species is especially large relative to other native bees (Parvin *et al.*, unpubl. data) and is expected to have a larger foraging range based on its body size (Greenleaf *et al.*, 2007; Kendall *et al.*, 2022). In contrast, we captured a number of relatively small bee species (i.e., ITD < 1.2 mm) at sites located far (200 m) from the field edges; because bee foraging range scales with body size (Greenleaf *et al.*, 2007; Kendall *et al.*, 2022), such small bees would be expected to limit energetically expensive long-distance foraging excursions into grass seed fields and may instead have been nesting

within fields. The grass seed fields we studied are tilled on approximately 5-year intervals, and such timescales may provide temporally stable nest sites for ground-nesting bee species (Gardiner *et al.*, 2010), which may be used even when they lack floral resources if bees can access bloom in adjacent areas. Indeed, research from intensively managed forests found that experimental removal of forest floor duff and litter increased diversity and abundance of ground-nesting bees even when floral resources were sparse due to herbicide use (Rivers *et al.*, 2018), indicating suitable nest site availability alone may be sufficient to drive bee habitat use in managed sites. It is important to note that bees could not have been using tall fescue inflorescences for food resources given that fields had been harvested and sampling occurred well after tall fescue produced pollen (L.K. Parvin, pers. obs.), providing additional support for the hypothesis that bees used grass seed fields for nesting.

If the bees we captured in grass seed field were not using such areas as nesting sites, it could indicate that our traps were sufficient to draw bees to sampling locations across an apparently unsuitable landscape matrix as has been demonstrated in other agricultural settings (Rader *et al.*, 2011; Schmidlin *et al.*, 2021). However, this seems unlikely based on current bee vision models. The attraction of bees to blue vane traps relies on the chromatic visual system via the excitation of the blue photoreceptor type (Rao and Ostroverkhova, 2015; Ostroverkhova *et al.*, 2018), which is activated only when the target subtends at least 15° (Giurfa *et al.*, 1996; Giurfa and Vorobyev, 1998; Spaethe *et al.*, 2001). If our traps were viewed by bees outside of grass seed fields, their placement at distances of 50 m and 200 m from the field edge would subtend less than 1° . This would make it so that bees were unable to use their color vision to identify the target at such distances, and they would be required to be considerably closer to the traps before their chromatic system could be used. Thus, based on our current understanding of bee vision, it is most likely that the bees that we captured originated in grass seed fields, and were not drawn into them from adjoining areas.

As noted above, the grass seed fields we studied are embedded within a landscape with a diversity of agricultural crops across relatively small spatial scales (Rao and Stephen, 2010). Thus, it is possible that bees may use grass seed fields for nesting sites and commute into adjacent crops leading to a spillover of pollination services (Woodcock *et al.*, 2016). Although our study was not designed to evaluate this idea, it remains an important question that, when addressed, will improve understanding of the functional connectivity of grass seed fields and adjacent pollinator-dependent crops with respect to use by wild bees and their pollination services. In the meantime, it is clear that perennial grass seed fields support a diversity of wild bees – ostensibly by providing nesting sites that are unavailable in other agricultural crops – and therefore have the potential to contribute to bee conservation efforts. Thus, additional research to quantify how bees use grass seed fields in conjunction with adjacent pollinator-dependent crops is warranted, and such work should provide a more complete understanding of how floral-devoid grass seed fields support native bee populations.

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AUTHOR CONTRIBUTIONS

L.K.P. and J.W.R. designed the experiment with assistance from N.P.A. and O.O. L.K.P. conducted the field work, and L.K.P. and I.A.P. collected data. J.W.R. conducted data analysis, L.K.P. and J.W.R. prepared the original draft, and L.K.P., I.A.P., N.P.A., O.O., and J.W.R. edited and approved the final version of the manuscript.

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SUPPLEMENTAL FIGURES

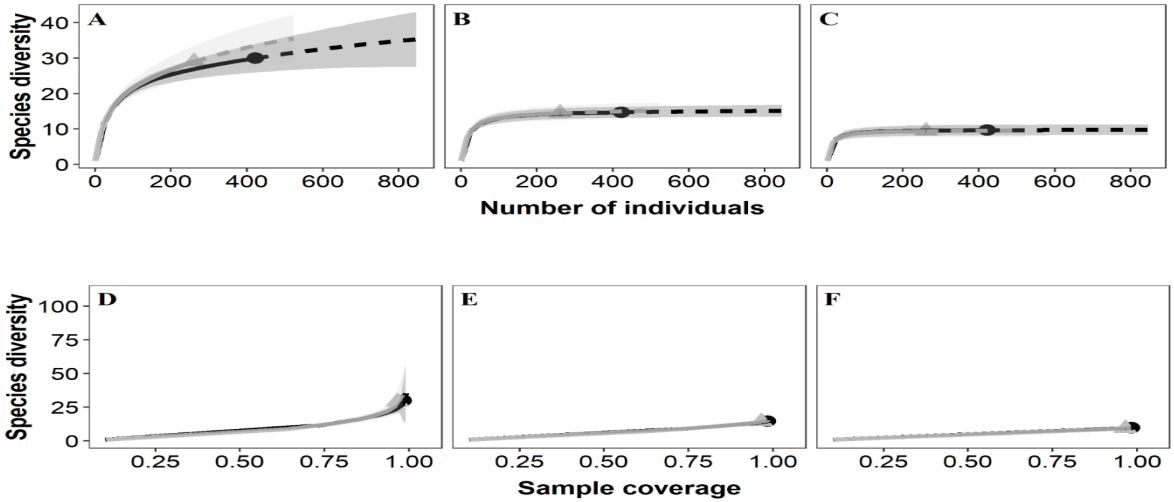


Figure S1. Sample size-based rarefaction and extrapolation curves for bees captured in grass seed fields at sampling locations situated near (i.e., 50 m) from field edge (black lines and circles) and far (i.e., 200 m) from field edge (gray lines and triangles) for three common Hill numbers used to assess biodiversity: (A) species richness ($q = 0$), (B) Shannon diversity ($q = 1$), and (C) Simpson diversity ($q = 2$). Coverage-based rarefaction and extrapolation curves for bees captured in grass fields near (black lines and circles) and far from field edge (gray lines and triangles) for (D) species richness ($q = 0$), (E) Shannon diversity ($q = 1$), and (F) Simpson diversity ($q = 2$). Reference samples (i.e., the sample size obtained from trapping) are shown by filled symbols, solid lines represent interpolation curves, dashed lines represent extrapolation curves, and shaded regions represent 95% confidence intervals. Curves in (A–C) for both groups were set to twice the sample size whereas coverages in curves in (D–F) were extrapolated to 98.6% for sampling locations near the field edge, and to 98.2% for sampling locations far from the field edge, both of which reflect a doubling of each reference sample.

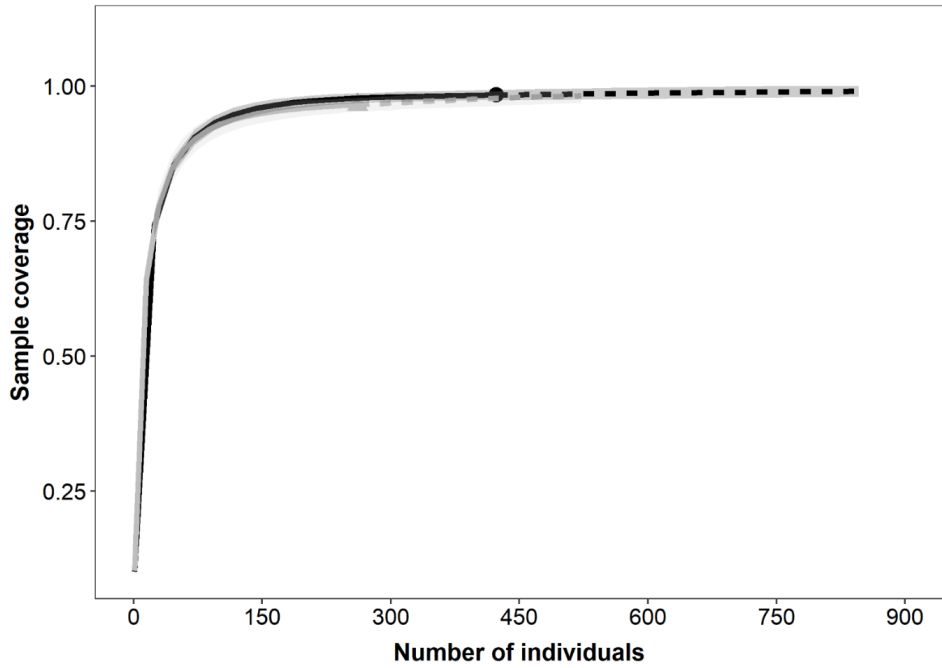


Figure S2. Sample completeness curves comparing sampling locations near (black line and circle) and far (gray line and triangle) from the field edge; solid lines represent interpolation curves, dashed lines represent extrapolation curves.