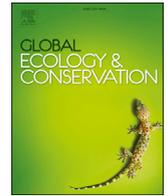




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Original Research Article

## Field-level characteristics influence wild bee functional guilds on public lands managed for conservation

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## ABSTRACT

Throughout the Midwestern US, many public lands set aside for conservation engage in management activities (e.g., agriculture) that may act as stressors on wild bee populations. Several studies have investigated how wild bees respond to large-scale agriculture production; however, there has been limited assessment of how wild bees may be impacted by agricultural activity on public lands or how local variables may influence bee communities in these same areas. In this study, we assessed the abundance and richness of wild bee floral and nesting guilds at 30 agricultural field margins located on five Conservation Areas in Missouri. Generally, regardless of guild, bee abundance and richness was greater in field margins with more floral diversity and taller vegetation. Bee guilds responded negatively to agricultural production in Conservation Areas with fewer soil- and cavity-nesting bees collected in margins adjacent to annually cropped fields. Although fewer diet specialists were collected, specialist bee abundance and richness was greater in margins near fields that were uncropped (i.e., vegetated, but not row-cropped) during the previous year. Overall, the percentage of trees and shrubs within 800 m of study fields (i.e., “woodland”) was negatively associated with abundance and richness of bees, but specifically, reduced richness of soil-nesters and diet specialists. Our findings indicate agricultural management activities on public lands may lead to decreased abundance and richness of wild bee guilds. If public lands are to be managed for species diversity, including wild bees, maintaining diverse plant communities with taller vegetation (>100 cm) near cultivated fields and/or modifying agricultural production practices on public lands may greatly improve the conservation of local bee communities.

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## 1. Introduction

Animal biodiversity is predicted to experience rapid losses across the globe (Ceballos et al., 2015), making it critical to conserve natural ecosystems for maintaining self-sustaining populations of native species (Rodrigues and Gaston, 2002). This trend is especially true of pollinators where wild bee abundance and diversity in Europe and North America have been

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declining (Biesmeijer et al., 2006; Cameron et al., 2011; Koh et al., 2016). Wild bees are critical for the provisioning of ecosystem services including insect pollination which maintains wild plant communities and global agricultural production (Kennedy et al., 2013; Potts et al., 2010). However, a range of stressors including climate change, habitat loss, pesticides, and/or agricultural intensification may negatively affect pollinator communities (Kennedy et al., 2013; Potts et al., 2010; Winfree et al., 2009).

Agricultural intensification has led to declines in agroecosystem biodiversity including regional pollinators (Spivak et al., 2011), and beneficial predatory insects (Douglas and Tooker, 2016). Throughout the United States, declines in native bee abundance are most associated with the conversion of natural habitats to row crop agriculture (Koh et al., 2016). In arable landscapes, conservation practices in agroecosystems (e.g., conservation buffers, prairie strips) have risen in popularity due to their ability to reduce soil erosion, filter agrochemicals, and limit runoff while reducing potential impacts on local biodiversity (Lovell and Sullivan, 2006; Schulte et al., 2017). Marginal lands are often the focus of pollinator conservation efforts as *field margins* (i.e., field edges) typically produce lower yields than other portions of cultivated fields, but may provide diverse wildflowers, nesting habitat, and refuge for wild bees (Schulte et al., 2017).

Conservation practices implemented on private and public lands are critical for the protection of native bee species. Programs such as the Conservation Reserve Program (CRP) provide subsidies to agricultural producers to convert highly erodible and/or sensitive cropland for conservation with ~179 thousand ha dedicated to pollinator habitat since 2012 (USDA, 2018). In the United States (U.S.), the federal government owns ~259 million hectares of public lands with the U.S. Fish and Wildlife Service managing 36.1 million hectares to conserve and protect animals and plants (Vincent et al., 2017). However, many federal and state managed lands are annually cultivated to row crops for wildlife food plots, wildlife cover (i.e., shelter), or used to initiate landscape disturbance (Carver and Caudill, 2013). These practices may either benefit or harm native pollinator communities depending on the individual wild bee species or specific habitat requirements of a functional guild (e.g., floral specialists). The loss of habitat to intensive farming is a major cause of bumble bee declines (Goulson et al., 2008), but it is unclear if the cultivation of public land acts as a stressor on other local bee populations.

Understanding the factors that shape pollinator communities can be achieved by exploring differences in biotic and abiotic features both within a habitat patch and the surrounding landscape (Grundel et al., 2010; Potts et al., 2003). For example, small-bodied social generalist (i.e., polylectic) species benefit from large habitat patches, whereas habitat specialists are more affected by local factors such as habitat quality and habitat area (Hopfenmüller et al., 2014). Landscape composition and configuration at a patch, or local scale (<250 m), can increase bee species richness (Steckel et al., 2014); bees further benefit from greater proportions of non-crop habitat (Holzschuh et al., 2010). Currently, a better understanding of species-specific bee and bee functional guild conservation needs is critical to maintaining diverse bee communities (Williams et al., 2010).

Few studies have evaluated wild bee communities on public lands beyond site inventories (Pascarella et al., 1999; Stephenson et al., 2018). Although public lands often provide heterogeneous habitat, bee floral and nesting guilds are potentially reduced on these lands due to row crop agriculture and/or the spatial extent and timing of active management practices (e.g., mowing, burning). To elucidate features that influence the late-spring and summer bee communities on public lands designated as Conservation Areas, we evaluated the relative importance of local and landscape scale metrics on wild bee floral and nesting guild abundance and richness in 30 agricultural field margins. Within the framework of our study, we addressed (1) how field-level and landscape factors impact abundance and richness of bee guilds at Conservation Areas and (2) whether pollinator guilds were influenced by agricultural cultivation on Conservation Areas. This study highlights findings relevant to other public lands of the Midwestern USA, but also draws conclusions that are transferable to a range of ecosystems prioritized for pollinator conservation.

## 2. Material and methods

### 2.1. Study area

We conducted our field study from mid-May to mid-September of 2017 at 30 agricultural fields located on five Missouri Department of Conservation Areas (CAs). The five CAs we selected were in central-northern Missouri, USA and included: Atlanta (39.88961°N, 92.49373°W), Fountain Grove (39.72338°N, 93.31714°W), Indian Hills (40.33749°N, 92.2492°W), Thomas Hill Reservoir (39.599477°N, 92.620690°W), and Whetstone Creek (38.96766°N, 91.71155°W). Missouri CAs are public lands that are managed to maintain wildlife habitat; however, CAs also include areas designated for the production of agricultural row crops such as corn, soybeans, and sunflowers. Agricultural crops are cultivated to provide food resources and cover for wildlife. For this study, we chose agricultural fields (mean area: 1.74 ha) with an existing field margin surrounding a cultivated field. We defined a field margin as an uncultivated area typically comprised of a mix of herbaceous (e.g., wildflowers) and grassy vegetation. The floral composition of a field margin varies throughout the season, but typically includes genera from the families Asteraceae (e.g., *Helianthus*, *Leucanthemum*, *Erigeron*, *Vernonia*), Rosaceae (e.g., *Rosa*, *Rubus*), and Fabaceae (e.g., *Chamaecrista*, *Lotus*, *Trifolium*). At each CA, we selected six fields for evaluation. All study fields were planted with soybeans during the 2017 study year.

## 2.2. Field-level and surrounding landscape characteristics

To assess the influence of field-level and surrounding landscape characteristics on local (i.e., study field) native bee communities, we measured a series of variables that are (1) ecologically important for pollinators and (2) could inform land management decisions on Conservation Areas. Selected metrics included field margin width (Nicholls and Altieri, 2013); vegetation height (Carvell, 2002; Milberg et al., 2016); plant cover (Holzschuh et al., 2006); number of floral species (Holzschuh et al., 2006; Potts et al., 2003); previous field use (Gathmann et al., 1994; Kennedy et al., 2013) and surrounding percentage of trees/shrubs (i.e., “woodland”; Watson et al., 2011).

At each study field, we measured margin width in triplicate using a 50 m measuring tape, with one measure in the center of the field margin and two subsequent measures ~50 m in either direction of this point. The majority of our study fields had only one complete field margin along the longest edge of the field. Using a 50 cm × 50 cm quadrat, we recorded plant cover (%), the dominant species, and number of flowering plant species (i.e., richness) at six random points within the field margin. Plant height (cm) was measured at each quadrat location using a standard measuring tape from the ground to the tip of inflorescence. Margin width, vegetation height, cover, and floral richness were each averaged per study field for inclusion in our statistical models. All field margin variables were enumerated every 28 d at each of the five sampling intervals (May to September 2017). Each study field's previous field use (year 2016) was recorded as either row cropped (e.g., corn, soybeans) or uncropped (e.g., old-field, hayfield) to determine if agronomic practices had an impact on local pollinator communities. Lastly, to determine the influence of surrounding landscape variables on pollinator abundance and richness, we calculated the percentage of surrounding cropland (cultivated crops), herbaceous/grassland (incl. pasture, hayfields, grasslands), and woodland/forest (incl. herbaceous and coniferous trees, shrubs) in ArcMap 10.3.1 (ESRI, Redlands, CA). Using the buffer tool, all percentages were calculated by developing an 800 m zone surrounding the study field with data extracted from the 2017 USDA National Agricultural Statistics Service crop data layer (USDA, 2016). We chose an 800 m buffer because it encompasses the foraging distance of most native bees in these areas (Benjamin et al., 2014; Greenleaf et al., 2007).

## 2.3. Wild bee surveys

At each site, we used SpringStar™ blue vane traps (SpringStar Inc., Woodinville, WA), to monitor bee communities. Compared to other trap methods, blue vane traps (BVT) capture a significantly greater species richness (Hall, 2018) and are useful for greater biodiversity studies (Gibbs et al., 2017). Beginning in mid-May of 2017, we measured wild bee abundance by sampling the Conservation Area field margins every 28 days over five discrete sampling periods (as above). In each field margin, six BVT were placed in a linear row >30 m apart to encompass the length of the field; however, as margin lengths ranged from 96 to 571 m (mean: 271 m), trap positioning was adjusted to maximize spacing. No traps were situated in the cultivated portion of the field. Following Kimoto et al. (2012), traps were hung ~1.2 m above the ground via metal coat hangers that were zip-tied to heavy-duty Vigoro™ green-colored stakes (Home Depot; H: 183 cm, D: 0.97 cm). BVT were always placed above the vegetation to limit accumulation of other insects. During each sampling period, BVT were deployed between 0700 and 0900 h Central Standard Time for 24 h. No liquids or euthanizing agents were placed in the traps. Due to the potential capture of queen bumblebees during May and June, traps were carefully monitored, and live queens were identified to species and released the following day.

As the presence of bees in a trap does not always indicate local foraging, we concurrently collected sweep-net samples to complement the trap capture data and fully characterize the field margin bee fauna (Roulston et al., 2007). Using 38 cm diameter polyester mesh sweep-nets (BioQuip 7300 Professional Series), two researchers walked a ~200 m length of the field margin and actively netted bees for 40 min intervals at each site. Any bee that was within the researcher's immediate field of view (~2 m) was collected. An individual spent 40 min of targeted netting in each field, for a total of 80 min sweep-net sampling per field. Sweep-netting across all sites was initiated by 0800 h and completed by ~1330 h to avoid extreme temperatures later in the day. We acknowledge our sampling timeframe may have underestimated the net capture of some species that are more active in later parts of the day when temperatures may have cooled. The two observers started at different positions in the field margin to avoid missing potential bee foraging sites. During bee capture, the net-caught bees were placed in jars containing ethyl acetate.

Where possible, the trap and net sampling only occurred during suitable weather where winds were <10 km/h and initial temperatures were ~20 °C. However, in some instances, our 24 h total bee captures may have been influenced by evening rain events that followed the trap deployment. All bees collected in the traps and sweep-nets were transferred to 50 mL Falcon centrifuge tubes, stored in coolers during transport, and frozen at -20 °C until identification. The Missouri Department of Conservation (MDC) authorized collection of wild bees as part of this study under an MDC Wildlife Collector's Permit (#16916).

## 2.4. Bee identification

All bees preserved via freezing were processed in the laboratory by mounting specimens for identification and evaluating bees using a Nikon SMZ-2B microscope with a Nikon 10x/23 lens. Where possible, the collected bees were identified to the lowest taxonomic unit (i.e., species) using a key of tallgrass prairie bees (Arduser, 2016) in tandem with the Discover Life key (Ascher and Pickering, 2016). In contrast, individuals of *Ceratina* were identified to genus and the members of *Lasioglossum*

(*Dialictus*) were classified to morphospecies. During identification, the accuracy and consistency of identification were checked between observers and by a bee taxonomist where applicable. A representative voucher collection is stored in the School of Natural Resources at the University of Missouri (Columbia, MO).

### 2.5. Statistical analyses

We estimated the overall relative bee abundance by combining all field margin BVT and all timed margin sweeps per field. Similarly, the relative species richness was estimated cumulatively across BVT and sweeps due to a similar sampling efforts at every field (Main et al. *in review*). Species richness was calculated in R 3.4.4 (R Core Team, 2018) using the package ‘vegan’ (Oksanen et al., 2013). As we were interested in the influence of various field margin and landscape characteristics on bee communities, we further explored field-level factors on the abundance and richness of individual bee functional guilds. We determined the bee functional guilds by evaluating two traits: nesting specialization (e.g., soil-nester, carpenter, mason) and floral diet preferences (e.g., oligolectic or “specialist”, polylectic or “generalist”) from the existing literature (Table 1; e.g., Brittain and Potts, 2011; Otieno et al., 2015).

Using a series of generalized linear mixed-effects models (glmer, package: lme4) in R, each model was fit with the six explanatory variables and the inclusion of time (=sampling period) as a quadratic term. Time was included as a fixed effect and assumed to be quadratic as bee communities are likely to peak in the summer rather than linearly increase over time. Fixed effects were a mix of site-specific variables (field, field margin), and one surrounding landscape term. Functional guild (nest or floral specialization) was included as a covariate. Model terms included the means of field margin width (m), vegetation height (cm), plant cover (%), and floral spp.; previous field use (uncropped, row-cropped); nest or floral preference; and the percentage of forest/woodland within an 800 m buffer surrounding the study field (hereafter, “woodland”; Table A1). The models included all possible interactions with either floral or nesting functional guilds. To standardize, the predictor variables were converted to z scores (scaled, centered) and screened for correlations. As the percentage of woodland, grassland, and surrounding cropland were all highly correlated (>0.7, Dormann et al., 2013), we excluded the percentage of grassland and cropland from our models to limit the number of model predictors and further reduce over parameterization. Each model contained two random effects: (1) a random effect of ‘trap type’ to differentiate between the sweep-nets and BVT and (2) ‘FieldID’ nested in Conservation Area to account for the repeated sampling within fields over time. A mixed-effect model was developed for each of the four response variables including: abundance by nesting group, abundance by floral preference, richness by nesting group, and richness by floral preference (see Table A1). The model of wild bee nesting richness contained only soil- and cavity-nesters due to a lack of diversity in carpenter or cleptoparasitic bee species collected throughout the study. We selected a negative binomial distribution due to our count data being zero-inflated. Negative binomial models further reduce overdispersion, which may lead to biased parameter estimates and/or false conclusions. Model fit was assessed through visual inspection of residuals and a Shapiro-Wilk test to assess fit of residuals to a normal distribution. Finally, we conducted subset model selection using the dredge function in the package ‘MuMin’ (Barton, 2016), where candidate models are fitted through a repeated evaluation from the fully-parameterized (global) model. Candidate models are then ranked based on a comparison of Akaike information criterion (AICc) and model weights. We selected the top model, as it was the most parsimonious model. The proportion of the model variance explained by the fixed (marginal) and random-effects (conditional) of the top model was evaluated through the calculation of pseudo  $R^2$  values in package ‘piecewiseSEM’ (Lefchek et al., 2016). *Post hoc* testing to investigate the interactions between guilds was completed using Tukey tests corrected for multiple comparisons in package ‘lsmeans’ (Lenth and Hervé, 2015).

## 3. Results

A total of 6,629 bees were collected in 2017 over the five sampling periods (May to September; Table 2). For the purposes of this study, bees were categorized by their functional traits including nesting specialization and floral preference (Table 1). Though both “miners” and “soil-nesters” nest in the ground, we differentiated between these categories as mining bees are typically representative of species from the family Andrenidae. Soil-nesting bees (72.9%) were the most abundant bees

**Table 1**

Descriptions of the functional traits used for analyses of field margin bee abundance and richness by listed categories of nesting specialization and floral preference.

Functional trait <sup>a</sup>	Categories	Description
Nesting guild	Carpenters	Drills nests in wood and/or stem pith
	Cavity-nesters	Nests aboveground in tunnels and cavities (e.g., trees, fallen logs, boxes)
	Cleptoparasites	No nest; occupy nests of other bees; parasitic
	Mason	Constructs nests with mud
	Miners	Excavates nests in the ground (e.g., Andrenidae)
	Soil-nesters	Nests in cavities and/or tunnels in the soil
Floral preference	Specialist	Forages on limited resources; requires specific habitat (i.e., oligolectic)
	Generalist	Forages on a broad range of floral resources (i.e., polylectic)

<sup>a</sup> Information presented above adapted from descriptions in Otieno et al. (2015).

**Table 2**

Abundance of wild bees collected in the agroecosystems located on Missouri Conservation Areas. Bees were collected in the field margins surrounding agricultural fields in 2017 (Species-level information are presented in Table A3.).

Family Genera	Count
<b>Andrenidae</b>	<b>44</b>
<i>Andrena</i> spp.	36
<i>Calliopsis</i> spp.	8
<b>Apidae</b>	<b>4510</b>
<i>Anthophora</i> spp.	15
<i>Apis</i> sp.	87
<i>Bombus</i> spp.	1015
<i>Ceratina</i> spp.	489
<i>Eucera</i> spp.	371
<i>Melitoma</i> sp.	2
<i>Melissodes</i> spp.	2293
<i>Nomada</i> spp.	3
<i>Ptilothrix</i> sp.	40
<i>Svastra</i> sp.	29
<i>Triepeolus</i> spp.	36
<i>Xenoglossa</i> spp.	1
<i>Xeromelecta</i> sp.	1
<i>Xylocopa</i> sp.	128
<b>Colletidae</b>	<b>81</b>
<i>Hylaeus</i> spp.	81
<b>Halictidae</b>	<b>1690</b>
<i>Agapostemon</i> spp.	250
<i>Augochlora</i> sp.	183
<i>Augochlorella</i> spp.	168
<i>Augochloropsis</i> sp.	82
<i>Dieunomia</i> sp.	5
<i>Halictus</i> spp.	400
<i>Lasioglossum</i> spp.	599
<i>Nomia</i> sp.	3
<b>Megachilidae</b>	<b>304</b>
<i>Coelioxys</i> spp.	13
<i>Heriades</i> spp.	11
<i>Hoplitis</i> spp.	9
<i>Megachile</i> spp.	258
<i>Osmia</i> spp.	13
<b>Overall total</b>	<b>6629</b>

collected in field margins (Fig. A1), followed by cavity-nesters (16.1%), carpenters (9.43%), cleptoparasitic bees (0.82%), miners (0.55%), and masons (0.20%). Overall, diet generalists (82%) were far more common than specialists (18%). A specialist was defined as a species that foraged on limited resources (e.g., only flowers from the genus *Helianthus*). In addition to the genera *Ceratina* and *Lasioglossum*, we collected 97 distinct species in 2017 (Table A2). The most abundant genera (and number of individuals collected) were *Melissodes* (2,293), *Bombus* (1,015), *Lasioglossum* (599), and *Ceratina* (489). Of the bees collected, 11.3% were rare (i.e., represented by a single individual). Bees of the genera *Melitoma* (*Ipomoea* [morning glory] specialist), *Xenoglossa* (*Cucurbita* [squash] specialist), and *Xeromelecta* (host: *Anthophora abrupta*) were the most rare.

### 3.1. Influence of field-level and landscape characteristics on nest guild abundance and richness

Our top model evaluating nest guild abundance retained six variables and one interaction that explained 66% (marginal  $R^2 = 0.66$ ) of the variation. This model included previous field use, nest type, woodland, and means of margin width, vegetation height and floral richness (Table 3A). Previous field use and vegetation height had an influence on bee abundance with more bees collected from the field margins surrounding previously uncropped fields and the margins containing taller plants (Table 3A). Though nest type explained the greatest variation in abundance, there was a significant interaction between nesting groups and the previous field use on nest guild abundance ( $P = 0.03$ ). Although soil-nesters and cavity-nesters were more abundant in the field margins surrounding fields that were previously uncropped, differences among the same guilds were not significant (Fig. 1). No other interactions were retained in our top model. Regardless of nest preference, the wild bee abundance in field margins decreased as woodland increased ( $\beta = -0.20 \pm 0.08$ ,  $P < 0.01$ ).

**Table 3**

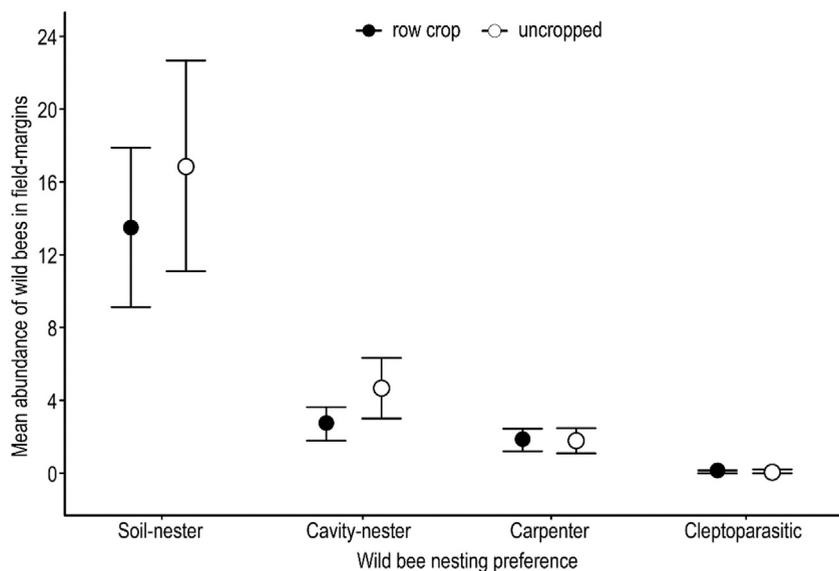
Results of generalized linear mixed-effects models analyzing wild bee abundance and richness by (A) nest and (B) floral guilds in response to field margin, field, and landscape characteristics. The table includes only the data from top models presented as model estimates ( $\beta$ ), standard errors (SE), and  $P$  values. Marginal  $R^2$  values indicate the amount of variation explained by fixed-effects alone.

A. Nest guild	Fixed effects	Response					
		Abundance			Richness		
Type	Variables	$\beta$	$\pm$ SE	$P$	$\beta$	$\pm$ SE	$P$
Field margin	Mean width (m)	0.10	0.06		–	–	
	Mean veg. height (cm)	0.21	0.04	***	0.17	0.03	***
	Mean floral richness	0.18	0.04	***	0.14	0.03	***
Field	Prev. field use (uncropped)	0.53	0.19	**	0.24	0.12	
Landscape	% Woody (800 m)	–0.20	0.08	**	–0.08	0.07	
Nest guild <sup>a</sup>	Carpenter	–0.37	0.11	***	not tested		
	Soil-nester	1.58	0.10	***	1.04	0.05	***
	Cleptoparasitic	–2.81	0.19	***	not tested		
Interactions	Prev. field use x Nest guild	–		*	–		
	Woody x Nest guild	–			–		*
Marginal $R^2$ (fixed effects)		0.66			0.39		
B. Floral guild		Abundance			Richness		
Type	Variables	$\beta$	$\pm$ SE	$P$	$\beta$	$\pm$ SE	$P$
Field margin	Mean width (m)	0.13	0.07		–	–	
	Mean veg. height (cm)	0.21	0.06	***	0.16	0.03	***
	Mean cover (%)	0.11	0.06		–	–	
	Mean floral richness	0.20	0.05	***	0.14	0.03	***
Field	Prev. field use (uncropped)	0.64	0.21	**	0.79	0.15	***
Landscape	% Woody (800 m)	–0.28	0.08	***	–0.29	0.07	***
Floral guild <sup>b</sup>	Generalist	1.77	0.11	***	1.32	0.08	***
Interactions	Prev. field use x Floral guild	–		*	–		***
	Woody x Floral guild	–			–		**
Marginal $R^2$ (fixed effects)		0.36			0.38		

– model variable not included in top model; Significance: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

<sup>a</sup> Reference level = cavity-nester.

<sup>b</sup> Reference level = specialist.



**Fig. 1.** Difference in mean ( $\pm$ SE) wild bee nest guild abundance in the field margins surrounding previously row cropped and uncropped fields (2016). Row cropped fields are represented by closed symbols and uncropped fields are represented by open symbols.

In our evaluation of wild bee richness, six variables explained 39% (marginal  $R^2 = 0.39$ ) of the variation in field margin bee richness by nesting guild. Overall bee richness was greater in the field margins with taller plants ( $\beta = 0.17 \pm 0.03$ ,  $P < 0.001$ ) and those field margins with more diverse floral species ( $\beta = 0.14 \pm 0.03$ ,  $P < 0.001$ ). Individually, the effects of field use and woodland were not significant. However, the interaction between nest guild and woodland was significant ( $P = 0.04$ ) with fewer soil-nesting species collected from the field margins adjacent to woodland (Table 3A; Fig. A2).

### 3.2. Influence of field-level and landscape characteristics on floral guild abundance and richness

Floral guild abundance was positively associated with floral richness, vegetation height, and the previously uncropped fields (Table 3B). By comparison, fewer bees were collected in the field margins areas adjacent to woodland ( $\beta = -0.28 \pm 0.08$ ,  $P < 0.001$ ). Additionally, the interaction between floral guild and the previous field use was significant ( $P = 0.04$ ) with fewer generalists and fewer specialists collected in the field margins surrounding row-cropped fields (Fig. 2). Although no other interactions were significant, this model explained 36% of the variation in floral guild abundance.

Four variables explained 38% (marginal  $R^2 = 0.38$ ) of the variation in field margin floral guild richness including positive effects of the uncropped fields, floral richness, and vegetation height with a negative impact of woodland (Table 3B). There were significantly more generalist bee species collected than specialist bee species in field margins throughout the study ( $\beta = 1.32 \pm 0.08$ ,  $P < 0.001$ ). There were two significant interactions with floral preference including an interaction with the previous field use ( $P < 0.001$ ) and an interaction with woodland ( $P = 0.002$ ). There were significantly fewer specialist bee species in the field margins surrounding row-cropped fields compared to the uncropped field margins (Fig. 3). Additionally, specialist bee species were fewer in the field margins adjacent to woodland ( $\beta = -0.21 \pm 0.07$ ,  $P = 0.002$ ).

## 4. Discussion

The 97 distinct species collected in this study represent 22% of the ~450 species of ground-nesting, cavity-nesting, and parasitic bees found throughout Missouri (White, 2016). Therefore, it is important to improve our understanding of which factors influence bee abundance and diversity, especially on publicly managed lands as pollinator communities are known to be locally diverse and vary across space and time (Williams et al., 2001). In this study, wild bees benefited from less area being annually cropped with greater abundance (nesting and floral guild) and richness (floral guild only) of wild bees in the field margins adjacent to the fields that were uncropped the previous year. Additionally, field margin vegetation height (>100 cm) and floral richness benefited wild bee communities regardless of guild. In contrast, the only variable to have a negative impact on the abundance and richness of both bee floral and nesting guilds was woodland. Therefore, field margins that (a) have low local floral diversity, (b) surround continuously cultivated fields (c) experience regular mowing and/or (d) are surrounded by a high percentage of woodland area may create unfavorable local conditions for wild bee guilds on public lands during the late-spring and throughout the summer.

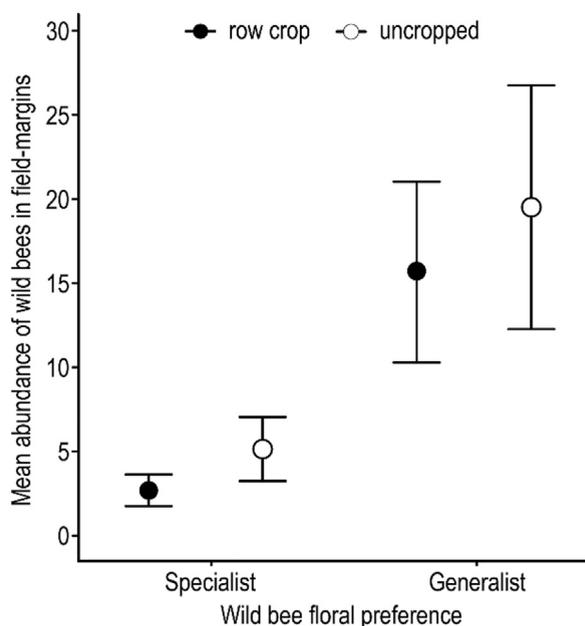
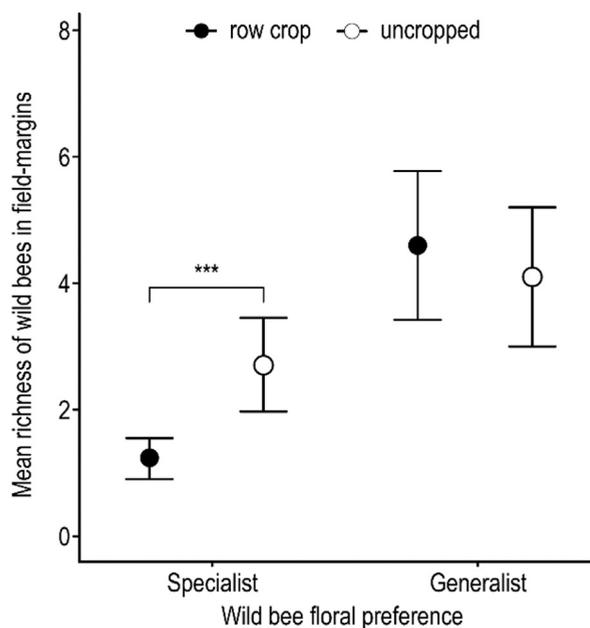


Fig. 2. Differences in mean ( $\pm$ SE) floral guild abundance of specialist and generalist wild bees collected from the field margins surrounding previously row cropped (closed circles) or uncropped fields (open circles).



**Fig. 3.** Differences in mean ( $\pm$ SE) floral guild richness of specialist and generalist wild bees collected from the field margins surrounding previously row cropped (closed circles) or uncropped fields (open circles). An asterisk over a symbol indicates significant differences between the groups with the same floral preference. Significance based on Tukey tests corrected for multiple post hoc comparisons. Significance: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

#### 4.1. Influence of local field-level characteristics on wild bee abundance and richness

At the local scale, mean floral richness and vegetation height in field margins benefited overall bee abundance and richness regardless of bee nesting preferences or diet specialization. The majority of our study Conservation Areas contained field margins with relatively diverse plant communities (incl. Fabaceae, Asteraceae and Apiaceae). Floral richness is known to influence bee visitation and overall wild bee richness (Blaauw and Isaacs, 2014; Hannon and Sisk, 2009; Potts et al., 2003), and abundance of some genera (e.g., *Bombus*) is explained by the temporal availability of suitable floral resources (Carvell, 2002; Martins et al., 2018). Maintaining a diversity of native flowering plants can provide resources in the form of pollen, nectar, and shelter throughout the growing season and sustain overall populations and wild bee diversity (Blaauw and Isaacs, 2014). While honeybees and bumblebees benefit from diverse plantings of the family Fabaceae, non-corbiculate species favor plants from the Asteraceae and Apiaceae families (Wood et al., 2015). Throughout our study, 18% of the bees collected were designated as floral specialists. To our knowledge, no comparable data from these areas exist making it unclear as to whether this number is considered low. We cannot rule out the fact that fewer specialists may be found on Conservation Areas due to the existence of agricultural activity including tillage, spraying, or destruction of semi-natural habitat; other studies have found habitat specialists are less likely to be found on agricultural landscapes (Forrest et al., 2015; Le Féon et al., 2013).

In our study system, regardless of plant species, the field margins containing taller plants (>100 cm) had more abundant and species-rich wild bee communities. In grassland communities, invertebrate assemblages benefit from diverse, taller vegetation that likely provide microhabitats, refugia, nesting areas and shelter, landscape connectivity, and food resources (Milberg et al., 2016; Reid and Hochuli, 2007). Similarly, in urban landscapes, overall bee richness and abundance were correlated with floral abundance and taller vegetation (Pardee and Philpott, 2014). Generally, wild bees and other hymenoptera benefit from management practices that minimize vegetation disturbance such as reduced grazing on pasture and grasslands (Sjödén, 2007) and delaying the initial mowing date in locations where floral resources may be limited (Meyer et al., 2017). However, mowing events can be positive as they can increase the overall species richness of herbs (Steffan-Dewenter and Leschke, 2003) that benefit wild bee communities. Therefore, management practices (e.g., maintaining field boundaries) are likely to be more effective in low-diversity, simple landscapes (Tscharntke et al., 2005) with wild bee populations directly benefiting from more undisturbed habitat availability on public lands managed for a range of species and activities (e.g., hunting, grazing, farming).

#### 4.2. Impact of agricultural activity on adjacent field margin bee guilds

Our results demonstrate agricultural management activities on public lands influence wild bee communities. We observed that the margins adjacent to annually cultivated fields contained fewer soil and cavity-nesting bees, and similarly, fewer floral specialists and generalists than found in the margins near recently uncropped fields. Depending on

the species, bees exhibit a wide range of nesting requirements and preferences including soil hardness, vegetation cover, substrate (e.g., stem/twig, leaves, wood, soil), and moisture (Grundel et al., 2010; Julier and Roulston, 2009; Kim et al., 2006; Potts and Willmer, 1997). We accounted for some field margin metrics that evaluated local habitat quality (see methods), therefore, the greater abundance and richness of bees near recently uncropped fields could be a result of crop rotation or field abandonment. In the previous year (2016), many fields classified as “uncropped” were sown to grasses, legumes, or left fallow between years. Crop rotations, including the use of cereals and temporary grasses, had a positive effect on solitary bee communities in France with greater bee abundance and richness as the proportion of mixed fields increased at the 400 m–800 m scale (Le Féon et al., 2013). Species richness and abundance of solitary wild bees increased with greater percentages of semi-natural habitat within a 750 m radius of experimental plots in Germany (Steffan-Dewenter et al., 2002). Alternatively, row-cropping may lead to a decrease in the nesting density for ground-nesting bees due to annual disturbance, changes in soil hardness, and/or secondary floral resources (e.g., weeds) being less available for bees near cropped fields where herbicides are applied (Kim et al., 2006). In our study, ~44% of all floral specialists collected were ground-nesting species. The margins surrounding annually row-cropped fields had significantly fewer floral specialists, which may be due to losses of oligoleges nesting in fields, greater levels of soil disturbance, and/or due to the soil composition. Studies of squash (*Cucurbita*) specialist bees (*Peponapis* and *Xenoglossa*) have found nesting sites preferentially located within fields (Julier and Roulston, 2009). Although there was no impact of tillage, the soil clay content negatively affected the *P. pruinosa* abundance in fields (Julier and Roulston, 2009). Two of our sites were situated on claypan soils that exhibit properties such as poor drainage, shrink-swell and cracking behavior, and where the claypan horizon occurs at depths from 20 to 62 cm (Veum et al., 2012). For some species, these soils may prove too difficult for nesting. As we did not evaluate tillage or soil composition, we cannot rule out that this may have influenced the local bee communities via destruction caused by cultivation or limiting nest initiation in some areas, respectively. Conversely, the recently uncropped fields may also contain a range of ground-nesting and other bee species utilizing permanent nesting locations.

#### 4.3. The effect of woodland on adjacent field margin wild bee floral and nesting guilds

A number of studies have identified landscape characteristics such as landscape composition, connectivity, and configuration (Le Féon et al., 2013; Steckel et al., 2014; Steffan-Dewenter et al., 2002) as critical to pollinator conservation management. Further, studies have demonstrated a benefit for wild bee communities by preserving semi-natural areas such as forests, grasslands, and riparian habitat near agricultural sites (Grundel et al., 2010; Hannon and Sisk, 2009; Öckinger and Smith, 2006). Regardless of guild, at our field sites, we found a negative relationship between woodland and bee abundance during the late-spring through the summer. This negative trend was more pronounced for soil-nesters and floral specialists, with the mean richness of soil-nesting and floral specialist bees lowest in the field margins surrounded by a greater percentage of woodland. Comparative studies have presented mixed conclusions when evaluating forest cover as a predictor of bee communities. Bee abundance and density were negatively related to greater tree canopy cover in Indiana; in more forested sites, however, most bees were caught during early spring before tree leaf out (Grundel et al., 2010). An increasing percentage of forest cover within 1600 m influenced strong declines in both bee abundance and richness in New Jersey's pine barrens (Winfree et al., 2007). In the studies conducted by Grundel et al. (2010) and Winfree et al. (2007), the sampling of bee communities was initiated a full month before our own study and therefore captured a potentially greater suite of early season species. For example, we collected only 44 individuals from the family Andrenidae which typically contains a greater number of early spring-flying species that forage predominantly on woody plants (Wood and Roberts, 2018). As we began sampling in mid-May, our results may be more indicative of woodland creating unfavorable conditions for the later spring- or summer-flying bee communities.

Our results of declining soil-nester richness with increasing woodland may be due to some species of bee being limited by suitable nesting substrates with fewer bees found to nest in clay or silt (Cane, 1991). More common species (e.g., *Halictus rubicundus*) select sites based on slope and aspect (e.g., south facing sites) to maximize the sunlight, soil thermal temperature, and steeper slopes for improved drainage (Potts and Willmer, 1997). In study sites adjacent to woodland, it may be that the soils contain excessive organic matter, coarse fragments or clay content, are poorly drained, or that limited sunlight leads to temperatures unfavorable for nesting. Similarly, many of our more treed sites contained less diverse floral communities within ~6–10 m of the field edge, likely limiting the potential pollen and nectar resources. Grundel et al. (2010) found that specialist bees declined with increased tree canopy cover, suggesting that diet specialists were more likely to find preferred floral plants in open areas. In New York, mid-summer wild bee abundance, richness, and diversity were shown to increase when greater percentages of wood were removed from the landscape (Romey et al., 2007). However, oligoleges are driven by the presence of their host plant species (Roberts et al., 2017) indicating that forested areas may simply act as a proxy for the sites lacking their required plant host. Some woody vegetation (e.g., hedgerows) is likely beneficial to wild bee communities near agricultural sites at certain times of the year due to presence of flowering shrubs and trees in late spring and early summer (Hannon and Sisk, 2009). As the focus of our study was on the late-spring and summer bee communities, some caution is advised in the extrapolation of our results to other early season or spring-flying bees.

#### 4.4. Conservation management

Our results indicate that maintaining high floral richness, taller field margin vegetation, and reducing the cultivation of agricultural crops will likely encourage greater abundance and richness of wild bee communities on public lands. Further, identifying functional guilds based on species traits can be useful when evaluating bee community response to management practices (Williams et al., 2010). We found annual cropping across Conservation Areas was associated with the reduced abundance and richness of bee floral and nesting guilds despite agricultural row crops acting as cover or food resources that benefit other wildlife (e.g., songbirds, game species). Our results have particular relevance for conserving bee floral guilds, as diet specialists were more abundant and diverse in the field margins surrounding recently uncultivated fields. However, several studies have demonstrated agricultural production can also encourage bee communities through improving habitat heterogeneity or allowing for successional change (Kennedy et al., 2013; Winfree et al., 2009, 2007). Rather than an “either/or” approach, a balance of agricultural activity and conservation goals is likely important or at least an understanding of potential trade-offs associated with maintaining the *status quo* is necessary. As specialist bees are often of greater conservation concern, returning to multi-year crop rotations that include more fallow periods may simply allow for more habitat availability and/or maintain limited host floral resources (Le Féon et al., 2013). In turn, this may broadly improve conservation efforts for a range of pollinator species. As we found that woodland adjacent to the study field negatively impacted soil-nesters and specialists, summer-flying wild bee communities would likely benefit from larger, more open field margins in areas dominated by extensive woody cover. However, this is likely to be context specific. To improve our knowledge of wild bee conservation and management on public areas, additional pollinator studies are needed that evaluate local, landscape, and management variables on public lands in other geographic regions outside of Missouri, especially studies conducted on a longer time scale.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00598>.

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