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Title:

Dryland organic farming partially offsets negative effects of highly-simplified agricultural landscapes on forbs, bees, and bee-flower networks

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Running title:

Farming system effects on forbs and bees

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Dryland conventional farming, natural habitat, Northern Great Plains, small-and large-bodied bees, wild bees

Abstract

Industrialized farming practices result in simplified agricultural landscapes, reduced biodiversity, and degraded species-interaction networks. Thus far, most research assessing the combined effects of farming systems and landscape complexity on beneficial insects has been conducted in relatively diversified and mesic systems and may not represent the large-scale, monoculture-based dryland agriculture that dominates many regions worldwide. Specifically, the effects of farming systems on forbs, bees, and their interactions is poorly understood in highly-simplified dryland landscapes such as those in the Northern Great Plains, USA, an area globally important for conventional and organic small grain, pulse, forage, and oilseed production. During a 3-year (2013-2015) study, we assessed (i) the effects of dryland no-till conventional and tilled organic farming on forbs, bees, and bee-flower networks, and (ii) the relationship between natural habitat and bee abundance. Flower density and richness were greater in tilled organic fields than in no-till conventional fields, and forb community composition differed between farming systems. We observed high bee diversity (109 taxa) in this highly-simplified landscape, and bee abundance, richness, and community composition were similar between systems. Compared with tilled organic fields, bee-flower interactions in no-till conventional fields were poorly connected, suggesting these systems maintain relatively impoverished plant-pollinator networks. Natural habitat (11% of the landscape) did not affect small-bodied bee abundance in either farming system, but positively affected large-bodied bees within 2000 m of crop field centers. In highly-simplified agricultural landscapes, dryland organic farming and no-till conventional farming together support relatively high bee diversity, presumably because dryland organic farming enhances floral resources and bee-flower networks, and no-till management in conventional farming provides undisturbed ground-nesting habitats for wild bees.

Introduction

While modern industrialized crop production systems provide valuable agronomic and economic benefits to humankind, they are also major drivers of declines in local and regional biodiversity. For example, bees (Hymenoptera: Apoidea, Apiformes) provide billions of dollars of pollination services to crops globally, but a suite of direct and indirect anthropogenic stressors, including agricultural intensification, reduction of floral resources, landscape simplification, pesticide toxicity, and exposure to parasites and pathogens, are driving their declines (Goulson et al. 2015). Declines in bee abundance and diversity, in turn, influence bee-flower networks (e.g., Burkle et al. 2013), negatively impacting ecosystem functioning and food security (Gallai et al. 2009, Vanbergen 2013).

Organic farming relies on frequent crop rotation and a lack of synthetic off-farm inputs such as herbicides, resulting in greater weed abundance and diversity (Menalled et al 2001, Hole et al. 2005). Changes in weed abundance and composition could positively influence beneficial insects, including bees (Nicholls and Altieri 2013), via plant-mediated bottom-up effects (Scherber et al. 2010). Studies conducted in drylands of the Northern Great Plains (NGP), a key agricultural region of small grain, pulse, and oilseed crop production, have also shown higher weed abundance and diversity in organic systems compared to conventional ones (Pollnac et al. 2008). Nevertheless, how differing weed communities are associated with the abundance and diversity of bees and bee-flower networks across farming systems is unknown for this region.

Additionally, within crop fields, weedy forbs (i.e., broad-leaf plants) and mass-flowering crops (e.g., canola, *Brassica napus* L.) provide food resources to beneficial insects for a short time interval (Morandin and Winston 2006), but surrounding uncultivated natural habitats provide season-long food resources, nesting substrates and stable refugia (Landis et al. 2005, Requier

2015). Studies conducted in diversified agroecosystems worldwide have shown positive effects of natural habitat on farmland biodiversity (Rader et al. 2014), bee pollinators (Kennedy et al. 2013, Boscolo et al. 2017), and pollination networks (Moreira et al. 2015). However, the relationship between natural habitat and farmland biodiversity is poorly understood in the highly-simplified dryland landscapes. that rank high in net productivity and help meet the global food demand (Millennium Ecosystem Assessment 2005). Hence, understanding biodiversity and its functioning in drylands is key to supporting future crop production and food security, particularly because these ecosystems are projected to increase and occupy 48% of the global land surface by 2025 due to climate change (Huang et al. 2016).

Farming systems and amount of natural habitat in agricultural landscapes influence bee communities (Holzschuh et al. 2007) and pollination (Nicholson et al. 2017), but the effects largely depend on landscape scale and complexity (Steffan-Dewenter et al. 2002). For instance, Holzschuh et al. (2007) found that, when compared to conventional fields, the effect of organic farming on bee diversity was stronger in simplified landscapes than in complex landscapes. Similarly, Nicholson et al. (2017) found that intensive farm management (i.e., large grain crop area and high pesticide use) exacerbates the negative effects of limited natural habitat on bee communities and pollination.

The effects of percent natural habitat on bee communities may vary as a function of species-specific bee body sizes (Benjamin et al. 2014, Forrest et al. 2015). The foraging ranges of small-bodied (intertegular width < 2.25 mm) bees are generally limited to a radius of less than 500 m from their nests (Gathmann and Tschardtke 2002, Greenleaf et al. 2007; but see Castilla et al. 2017). This limitation may make small-bodied bees more vulnerable to the impact of landscape simplification (Jauker et al. 2013, Benjamin et al. 2014) when compared to large-bodied

(intertegular width ≥ 2.25 mm) bees with larger flight capacities and foraging ranges (Westphal et al. 2006, Greenleaf et al. 2007).

Theoretically, a simplified agricultural landscape with limited natural habitat such as in the NGP should have stronger negative effects on small-bodied bees than on large-bodied bees (De Palma et al. 2015; but see Forrest et al. 2015). Hence, in highly-simplified landscapes, lower abundances of small-bodied bees are expected compared to abundances of large-bodied bees, but there is currently no empirical evidence testing this expectation. Previous studies on the interacting effects of farming system and amount of natural habitat on bee communities have mainly been conducted in relatively diversified and mesic agroecosystems and are lacking for highly-simplified dryland agricultural landscapes. Further, to our knowledge, no study has formally assessed the joint impact of farming systems and percent natural habitat on forbs, bees, and bee-flower networks in highly-simplified dryland agricultural landscapes.

To address these knowledge gaps, we tested the effects of no-till conventional vs. tilled organic farming on forbs, bees, and bee-flower networks in a three-year, on-farm study in drylands of the NGP. We also assessed how the percentage of natural habitat within various distances from crop fields might mediate the effects of farming system on the abundances of small- and large-bodied bees. We hypothesized that: (i) because of the higher crop rotation and avoidance of synthetic herbicides, organically-managed tilled wheat fields (hereafter, organic system) would have greater forb flower density and species richness, and different forb community composition than chemically-managed no-till wheat fields (hereafter, conventional system), (ii) greater floral density and species richness in organic fields would be associated with differences in bee community composition and dispersion, and positively correlated with the abundance and diversity of bees and the complexity of bee-flower networks, and (iii) percentage natural habitat

would be positively associated with the abundances of both small- and large-bodied bees, but the association would be stronger for small-bodied bees than for large-bodied bees, especially in conventional fields.

Materials and methods

Site description and cropping history

We conducted this three-year, on-farm study in conventional and organic wheat fields near Big Sandy, Montana, USA (Fig. 1; 48.036°N, 110.014°W; elevation 960 m). Located in an important dryland, small-grain producing region in the NGP, the Big Sandy area is relatively dry (i.e., the 94-year mean annual precipitation is 325 mm) and hot (i.e., mean annual minimum and maximum temperatures are -1.2°C and 14.8°C; see details in Adhikari et al., 2018). In each year from 2013 to 2015, we selected three conventionally-managed, no-till spring wheat (*Triticum aestivum* L.) and three adjacent organically-managed tilled “Kamut” wheat (*Triticum turgidum*, ssp. *duranicum* McKey) fields (Fig. 1). While conventionally managed farms follow no-till practices in this region, tillage is commonly used in organic farms to terminate cover crops, control weeds, and prepare for plantation. Different fields were chosen each year for a total of 18 fields, ranging from 25 ha to 70 ha and separated by a minimum of 500 m (see details of cropping history for each field in Adhikari et al. 2018 and Adhikari and Menalled 2018).

Forb and bee community sampling

Each year, we established a randomly-oriented, 55-m transect within each field, located at least 150 m from any field border. At three randomly selected points along this main transect, we established three perpendicular 25-m, sub-transects at each field. Each year, on three dates with

one each in June, July, and August, we quantified forb communities by visually estimating percent cover by species within a 0.5×1 m quadrat placed perpendicular to each sub-transect at every 1 m interval. Additionally, we estimated flower density by counting open flowers per individual forb plant within each quadrat. The naturally short growing season of the study area and logistical constraints precluded us from obtaining samples outside the June to August period.

On the same dates on which we sampled forb communities, we also assessed bee communities using pan traps (250 ml), one of the most efficient methods of sampling pollinator communities passively (Westphal et al. 2008, Lebuhn et al. 2013). We used blue, yellow, and white traps (i.e., cups) filled with diluted soapy water to break the surface tension; these colors are effective at passively capturing diverse bee groups (Lebuhn et al. 2013). We alternated traps (securely hanging on polyvinyl chloride poles) of each color, placing them 5 m apart at crop canopy height along the main transects described above ($n = 12$ pan traps per transect). After 24 hours in the field, bees were collected from traps and stored in a freezer until they could be processed. As above, seasonal and logistic constraints determined our sampling efforts.

Bees were identified using taxonomic keys, identification guides, and experts (Table S1). Eighty-five of 109 bee taxa were identified to species, while the remaining 24 were identified to subgenus only (mainly *Lasioglossum* (*Dialictus*) spp.) or morphospecies. Using digital calipers, we also measured intertegular width of up to 10 randomly-chosen bees of each species and used this variable as a proxy of overall bee body size and potential foraging distance (Greenleaf et al. 2007).

Bee-flower networks

To assess the impact of farming system on bee-flower interactions, we walked each of the 25-m

sub-transects used to evaluate forb communities for 20 minutes and recorded the identity and frequency of bees visiting flowers within 1 m of each sub-transect. Each year, we performed these observations three times between June and August (once each month; 54 h total). All observations were conducted between 0800 and 1625 h under sunny, warm (mean temperature: $29 \pm 0.3^{\circ}\text{C}$, $n = 231$), and calm-breeze (mean wind speed: $5 \pm 0.2 \text{ m s}^{-1}$, $n = 231$) conditions. During the observations, we collected all flower visiting bees using an insect net for later identification. In the rare cases (<10%) when it was not possible to capture bees during observations, we identified them to the lowest possible taxonomic level on the wing (usually genus).

Percent natural habitat and its relationship to small- and large-bodied bee abundance

For each field, we acquired cloud-free Landsat-8 images ($30 \times 30 \text{ m}$ resolution) from the United States Geological Survey and used ArcGIS 10.2 to analyze the images. Using ArcMap and V-LATE 2.0 beta (Vector-based Landscape Analysis Tools Extension), we classified the areas of land use types (“cropland,” “natural habitat,” “water,” and “others”) and calculated the percent natural habitat (all uncultivated semi-natural lands with forbs and grasses such as roadside margins, and grasslands with frequent grazing or non-grazing) within four concentric circles of 250 m, 500 m, 1000 m, and 2000 m radii from the center of each sampled field. We chose these radii, following Steffan-Dewenter et al. (2002), to determine the spatial scales at which percent natural habitat influences bee abundance. Additionally, we used ground observation, Google Earth, and USDA-National Agriculture Imagery Program to crosscheck the land use types.

Data analyses

After pooling data from all transects at each field, we first calculated forb flower density, bee abundance, species richness, and species evenness (following Pielou's evenness; Pielou 1966). We selected the most representative response variables to include in our analyses, after determining whether such variables were strongly correlated ($r_p > 0.6$; Table S2).

After removing strongly correlated variables (such as forb diversity and bee diversity), to test the effect of farming system on forb flower density, forb species richness, bee abundance, and bee species richness (i.e., for count data), we used generalized linear mixed-effects models ("glmer") with Poisson distributions. Diagnostic plots such as residual plots were used to check if the models met the assumptions of homogeneity of variance. Similarly, we used linear mixed-effect models ("lmer") to test the effects of farming system on forb and bee species evenness.

Diagnostic plots such as QQ plots and residual plots were used to check if the models met the assumptions of normality and homogeneity of variance, and response variables were log-transformed as required. In all models, farming system was treated as a fixed effect while year and field were treated as random effects, with month nested within field, and field nested in year.

The effects of conventional and organic farming on forb and bee community composition were assessed using Permutational Multivariate Analysis of Variance (PERMANOVA) on a Bray-Curtis dissimilarity matrix (Bray and Curtis 1957) and visualized with Non-metric Multidimensional Scaling (NMDS) ordination. Also, PERMANOVA was used to assess any temporal shift or seasonal variation (i.e., across sampling months) in forb and bee communities. Community dispersion (β -diversity) between conventional and organic systems as well as among months was tested using the "betadisper" function. After the "adonis" test of PERMANOVA, if significant, we did post-hoc tests using "pairwise.perm.manova" function and reported the false discovery rate adjusted p-value (Hervé 2017). Following significant PERMANOVAs, we used

“simper” to determine which species contributed the most to the observed dissimilarity in community composition between farming systems or among months (Oksanen et al. 2016). We identified indicator species for both farming systems and for all months using “IndVal” (Cáceres and Legendre 2009), a procedure to detect key species in a particular site based on their relative abundance (specificity) and relative frequency (fidelity) (Dufrêne and Legendre 1997).

Rare bee-flower interactions in conventional fields (see Results) precluded quantitative analysis of the effects of farming system on network characteristics.

To compare the proportion of natural habitat surrounding conventional and organic fields within the circles with 500 m, 1000 m, and 2000 m radii described above, we utilized generalized linear mixed models - automatic differentiation model builder (“glmmADMB”) with beta distribution (Skaug et al. 2016). However, we did not include the 250 m radius in our analysis because the majority of crop fields (14 out of 18 fields) had 0% natural habitat within this radius. To evaluate the effects of percent natural habitat on large- and small-bodied bee abundances and following Benjamin et al. (2014), all sampled bees were divided into “large-bodied” (intertegular width ≥ 2.5 mm) bees and “small-bodied” (intertegular width < 2.5 mm) bees. Using generalized mixed-effects models (“glmer”), we tested the effect of percent natural habitat within a 500 m, 1000 m, or 2000 m radius from the center of each field on large- and small-bodied bee abundances. In the mixed-effects models, percent natural habitat, farming system, and their interaction (natural habitat $\times$ farming system) were treated as a fixed effect while field was treated as a random effect. To determine whether the effects of percent natural habitat on small- and large-bodied bees were stronger in conventional fields than in organic fields, we calculated marginal R^2 (variance explained by fixed factors alone) and conditional R^2 (variance explained by fixed and random factors) from mixed-effect models (Nakagawa and Schielzeth 2013), using “MuMIn”.

All statistical analyses and graphics were conducted with R 3.2.4 (R Core Team 2016). We used “lme4” (Bates et al. 2015), “glmmADMB” (Skaug et al. 2016), and “MuMIn” (Barton 2017) packages for mixed-effect models. Multivariate analyses, PERMANOVA post-hoc tests, and ordination graphics were conducted using “vegan” (Oksanen et al. 2017), and “RVAideMemoire” (Hervé 2017) packages. We produced all other graphics using the “ggplot2” (Wickham 2009) and ‘sciplot’ (Morales 2017) packages.

Results

Forb communities

Over the 3-year period of our study, we recorded 38 forb species, primarily non-native agricultural weeds. Of these, we observed 14 species in the conventional fields and 37 in the organic fields (Table S3). Flower density was 385% greater in organic fields than in conventional fields (Table 1). Forb species richness was 248% greater in organic fields than in conventional fields (Table 1). However, there was no effect of farming system on forb species evenness (Table 1).

Forb community composition differed between farming systems (Fig. 2; pseudo- $F_{1, 16} = 6.9$; $r^2 = 0.30$; $P = 0.001$). Also, forb community dispersion was greater across conventional fields than across organic fields ($F_{1, 16} = 35.2$; $P \leq 0.001$). There was no temporal shift in forb community composition (pseudo- $F_{2, 51} = 0.28$; $r^2 = 0.01$; $P = 0.311$) through the growing season (June, July, and August) in both farming systems. Together, *Thlaspi arvense* L., *Salsola kali* L., *Carthamus tinctorius* L., *Polygonum convolvulus* L., *Pisum sativum* L., *Chenopodium album* L., *Medicago sativa* L., and *Amaranthus retroflexus* L. contributed 72% to the observed dissimilarity in forb community composition between farming systems. These species were more abundant in organic

fields, and five of them were absent from conventional fields. Indicator species analysis did not reveal any forb associated with either system.

Bee communities

We collected a total of 8,710 bee specimens, representing at least 109 species, 25 genera, and five families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae) from the pan traps (Table S4). Of the bees collected in our samples, all but 12 specimens (10 *Apis mellifera* and 2 *Bombus impatiens*) were wild (i.e., non-managed) bees (Table S4). The five most abundant bee taxa for both conventional and organic systems were *Lasioglossum* (*Dialictus*) spp., *Agapostemon texanus* Cresson, *Eucera hamata* (Bradley), *Agapostemon femoratus* Crawford, and *Agapostemon virescens* (F.). Bee intertegular widths ranged from an average of 0.7 ± 0.1 mm (*Perdita fallax* Cockerell) to 5.9 ± 0.4 mm (*Bombus nevadensis* Cresson). Approximately 81% of the bee taxa were ground nesting bees, representing 98.6% of the total individuals captured (Table S4). Approximately 79% of the total capture were small-bodied bees (intertegular widths < 2.5 mm).

We did not detect any differences between conventional and organic systems in bee abundance, species richness, or evenness (Table 2). Across years, we observed no differences in overall bee community composition between conventional and organic fields (pseudo- $F_{1, 52} = 1.35$; $r^2 = 0.03$; $P = 0.168$). However, bee community composition differed between farming systems in August (Fig. 3; pseudo- $F_{4, 48} = 2.2$; $r^2 = 0.27$; $P = 0.001$), with *Lasioglossum* (*Dialictus*) spp., *Melissodes agilis* Cresson, *Melissodes pallidisignatus* Cockerell, *Halictus ligatus* Say, and *Melissodes lupinus* Cresson contributing 75% of the total observed dissimilarity. In August, *M. pallidisignatus* was indicative of conventional farming, whereas *Andrena* sp.1 and *Anthidium*

porterae Cockerell were indicative of organic farming in (Table S5); all three taxa being ground-nesting bee species. Across fields, we observed a temporal shift in bee community composition (Fig. 3; pseudo- $F_{2, 51} = 7.75$; $r^2 = 0.23$; $P = 0.001$) over the growing season, with sampling months different from each other ($P = 0.001$, for all pairwise combinations). Twenty bee species were characteristic in June, two species were characteristic in July, and four species (all *Melissodes*) were characteristic in August (Table S5).

Bee-flower networks

Forbs and bee-forb interactions were so rare in conventional fields that bee-flower networks either could not be quantified, or they were extremely simplified (i.e., single forb species visited by a single bee taxon) (Fig. 4). In contrast, bee-flower interactions were more often observed in organic fields, hence the bee-flower networks were more complex (Fig. 4). Only six bee species (six individuals) were observed in the bee-flower networks of conventional fields over the three years, whereas 21 bee species (104 individuals) were recorded in organic fields. Because of its dominance in the landscape, *Medicago sativa* was the plant species most frequently visited by bees in both systems, and the unidentified *Halictus* spp. were observed on more plant species than any other bee taxa.

Percent natural habitat and its relationship to small- and large-bodied bee abundance

Since the landscape was primarily occupied by cropland, it had a low proportion of natural habitat ($11 \pm 2.2\%$ within 2000 m or $7 \pm 2.6\%$ within 1000 m of field centers; Fig. 1; Table S6). Percent natural habitat within 500 m and 1000 m from the center of the conventional fields was greater than those of the organic fields, but this difference was marginal within 2000 m (Table 3).

Percent natural habitat did not affect small-bodied bee abundance in either farming system for any of the analyzed distances from the field center (Fig. 5a-c; 500 m: $F_{1,16} = 0.27$; $P = 0.610$, 1000 m: $F_{1,16} = 0.21$; $P = 0.650$, and 2000 m: $F_{1,16} = 2.23$; $P = 0.150$). Similarly, we found no effect of percent natural habitat on large-bodied bee abundance in either farming system in the 500 m radius (Fig. 5d; $F_{1,16} = 0.15$; $P = 0.720$) or in the 1000 m radius (Fig. 5e; $F_{1,16} = 2.5$; $P = 0.141$). However, percent natural habitat within the 2000 m radius positively related to large-bodied bee abundance (Fig. 5f; $F_{1,16} = 11$; $P = 0.004$) in both conventional and organic fields; and the effect of natural habitat on large-bodied bee abundance was similar between conventional (conditional $R^2 = 0.93$, marginal $R^2 = 0.46$) and organic (conditional $R^2 = 0.93$, marginal $R^2 = 0.41$) fields.

Discussion

Prior to this study, little was known about wild bees and bee-flower networks in highly-simplified agricultural landscapes in dryland settings, like those that dominate the NGP. Although we found that organic fields supported greater forb flower density and species richness and more complex bee-flower networks, we observed no differences in bee abundance or richness from pan traps between organic and conventional fields. However, despite very limited natural habitat, there was surprisingly high bee diversity in both systems. Overall, our findings suggest that in highly-simplified dryland agricultural landscapes, the abundance and richness of flowers in organic farming enhances bee-flower interactions.

Forb communities

Consistent with Pollnac et al. (2008), organic fields had greater forb flower density and species richness than conventional fields, which likely provided food resources to beneficial insects,

influenced forb-insect interactions, and supported biodiversity and ecosystem services (Jordan and Vatovec 2004, DiTommaso et al. 2016). The observed differences in forb communities could result from the different ecological filters imposed by the two studied farming systems (Smith et al. 2015). Specifically, the continuous use of selective herbicides in conventional small grain fields excludes dicotyledonous species (Grossmann 2009), ultimately reducing floral resources for pollinators (Nicholls and Altieri 2013, Adhikari et al. 2019). Also, in agreement with Menalled et al. (2001), we found greater temporal variability in forb community composition in conventional fields than in organic fields, suggesting greater stability of resources for bees in organic fields.

Bee communities

While previous studies demonstrated that organic farming supports greater floral and bee diversity than conventional farming (Holzschuh et al. 2007), we failed to detect differences in the assessed bee community metrics between farming systems. One possible explanation is that while plant species are strongly affected by farming system at the within-field scale, mobile species like bees respond at larger scales with home ranges exceeding field size (Gabriel et al. 2010; but see Benjamin et al. 2014). For example, since the increased soil disturbance due to tillage in organic fields may reduce the habitat suitability for ground-nesting solitary (Shuler et al. 2005) and social (Williams et al. 2010) bees, these species may prefer un-tilled conventional fields for nesting and the adjacent flower-rich organic fields for foraging. However, our study found no differences in ground nesting bee abundance and diversity between no-till conventional and tilled organic fields, possibly because a vast majority of the bees in this system were solitary (vs. social and semi-social; Michener 2007, Table S1) and less sensitive to the disturbances imposed by tillage, compared with social bees (Williams et al. 2010). This hypothesis deserves

further consideration but assessing landscape-scale bee habitat use was beyond the scope of this study. Second, pan traps may have served as ‘magnets’ by luring bees that were flying through the fields searching for forage. This magnetic effect might be stronger (1) in landscapes with a low proportion of natural habitats, (2) in conventional fields with less floral resources, and (3) for bees with nests within the foraging range of pan traps. Hence, pan trap sampling may not allow us to distinguish resident or explicitly foraging bees from those flying further afield (but see Westphal et al. 2008).

Conventional and organic fields had surprisingly high bee diversity, given the extensive monoculture-based dryland cereal grains system (i.e., wind-pollinated) of the studied area, the limited abundance of natural habitat, and the consistently windy conditions that may have reduced bee movement. Though we lacked information from simplified dryland agricultural landscapes, other studies of bee communities done in natural and semi-natural systems in Montana have revealed similar or lower bee diversity. For example, Fultz (2005) reported 119 species of bees at the Tenderfoot National Experimental Forest in central Montana, whereas Pearce et al. (2012) found 48 species in south-central Montana on a floristically-diverse wildflower seed farm surrounded by natural and diversified agricultural areas. It is possible that rapid drainage in the sandy soil of the NGP landscape allows ground-nesting bees to thrive (Cane 1991), and the mosaic of weed-free no-till conventional fields and weedy but tilled organic fields that exist in the studied area provides required nesting habitat and resources to support diverse bee assemblages.

Bee community composition did not differ between the two farming systems in June or July but did in August when *Melissodes pallidesignatus* was more abundant in conventional fields while *Andrena* sp.1 and *Anthidium porterae* were associated with organic fields. There are limited

studies on the biology, ecology, or phenology of these species, so it is not clear why these species were unequally distributed across systems. For example, *M. pallidisignatus* is reported to prefer sandy soil for nesting and is known as an oligolege (collecting pollen from a limited set of genera) in Asteraceae (Thorp and Chemsak 1964). But, Asteraceae were rare in the conventional fields and soil structure was not noticeably different between these dryland conventional and organic fields (Adhikari, *Pers. Obs.*). Similarly, the biology of *Andrena* sp. 1 (or, *Andrena* genus) and *A. porterae* is largely unknown, but are likely ground nesters, with oligolectic to polylectic habits (Gonzalez and Griswold 2013, Ascher and Pickering 2014). Association of these bees with organic fields could be due to the availability and diversity of floral resources.

Bee-flower networks

Due to low forb flower density and richness in conventional fields, we recorded fewer bee-flower interactions and less connected bee-flower networks compared to those in organic fields. Our results are partly consistent with Kehinde and Samways (2014), who compared insect-flower networks between conventional and organic vineyards in South Africa, where the higher number of interactions in organic vineyards was due to their greater forb abundance. Power and Stout (2011) also found more connected and “larger” insect-flower networks in Irish organic dairy farms with greater floral and bee abundance than in conventional farms. Yet, compared with networks observed in more botanically diverse and mesic systems (Power and Stout 2011, Kehinde and Samways 2014, Tucker and Rehan 2017), bee-flower networks in the organic fields we assessed were far less connected, suggesting that highly-simplified dryland agricultural landscapes maintain relatively impoverished bee-flower networks, despite the high diversity of bee taxa.

Percent natural habitat and its relationship to small- and large-bodied bee abundance

Previous studies assessing bee abundance and diversity in farmlands have been primarily conducted in diversified systems and heterogeneous landscapes (Kennedy et al. 2013, Boscolo et al. 2017) with more mesic settings, and little knowledge existed about how percent natural habitat impacts bee communities in highly-simplified dryland landscapes. The studied fields had only 11% natural habitat within 2000 m of their centers (or only $7 \pm 2.6\%$ within 1000 m). However, Morandin and Winston (2006) reported that 30% of the land within 750 m of field edges in Alberta, Canada is required to remain uncultivated to sustain pollinators and maximize *Brassica napus* L. production. This suggests that the natural habitats in the studied, resource-constrained dryland system are too limited to be the sole support of pollinators.

In both farming systems, the abundances of small-bodied bees were not related to natural habitat at either field or landscape scales, probably because these bees had short foraging ranges (Benjamin et al. 2014) that prevented them from moving across habitat boundaries. Studies have shown that the foraging range of small-bodied bees is limited to less than 500 m from their nests (Gathmann and Tschardt 2002, Greenleaf et al. 2007) and can be as low as 90 m (Wright et al. 2015; but see Castilla et al. 2017). These studies also suggested that with a short-distance flight capacity, small bees are confined near field edges making them more vulnerable to the impact of dryland landscape simplification (Jauker et al. 2013). In our study, most of the sampled bees (79%) were small-bodied and were collected at the centers of large conventional and organic fields. How these bees are sustained in the center of large, resource-constrained fields with little nearby natural habitat is unknown and requires further research.

By contrast, the abundances of large-bodied bees increased with increasing natural habitat 2000 m from crop-field centers in both farming systems. These results agree with previous research showing that large-bodied bees, due to their greater foraging range, respond positively to increases in natural habitat (Westphal et al. 2006, Greenleaf et al. 2007). Large-bodied bees in the highly-simplified dryland landscape of the NGP may have become adapted to fly greater distances, as they have shown extreme foraging plasticity to visit consistent floral patches in the landscape (Jha and Kremen 2012). Even though, there were differences in the amount of natural habitat between organic and conventional fields within 500 m and 1000m of their centers, natural habitat was not significantly different at the scale of 2000 m. Also, due to extremely limited natural habitat, the biological impacts of these differences could be negligible in the smaller spatial scales, particularly for the large-bodied bees with longer foraging distances (Steffan-Dewenter et al. 2002).

Conclusions

This study indicates that in a highly-simplified dryland agricultural landscape, the greater forb flower density and richness of organic fields was associated with more connected bee-flower networks when compared to conventional fields. However, both farming systems contained equally high bee diversity. Our results raise questions about how such diverse bee communities can be sustained in highly-simplified and seemingly depauperate dryland agricultural landscapes. For instance, the extent to which the simple bee-flower networks observed could be resilient in the face of agricultural intensification and climate change is largely unknown. Overall, our results suggest that practicing organic methods in the drylands of the NGP and intermixing natural habitat with crop fields may help to maintain or improve bee-flower network complexity and potentially better sustain these bee communities.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at.....

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Figure legends

Figure 1: Study area in Big Sandy, MT, USA. (a) All 18-field shown (9 conventional: red triangles and 9 organic: blue filled circles). (b) Example of highly-simplified agricultural landscape in the Northern Great Plains. The picture was taken in 2015 during field sampling at one of the organic wheat fields. (c) Percent cropland, semi-natural habitat, other, and water (mean $\pm$ SE) within each of the four circles across all conventional and organic fields combined.

Figure 2: Non-metric multidimensional scaling ordination of forb communities observed in conventional and organic wheat fields. Dotted ellipses encircle communities in 2013, dashed ellipses encircle communities in 2014, and solid ellipses encircle communities in 2015. Each point represents a conventional (red) or organic field (blue).

Figure 3: Non-metric multidimensional scaling ordination of bee communities observed across June, July and August in conventional (red triangle) and organic (blue filled circles) fields. Dotted ellipses encircle communities in June, dashed ellipses encircle communities in July, and solid ellipses encircle communities in August. Due to the non-significant effects of year, values were pooled across three years (2013-2015). Each point represents a month at each field across three years.

Figure 4: Comparison of bee-flower networks between conventional and organic wheat fields across three years. The top yellow horizontal bars represent bee taxa and the bottom green horizontal bars represent forb species. Black lines connecting bee taxa and forb species represent interaction links (visits) and the thickness of these lines corresponds

to the frequency of interactions. To show general patterns between bee and forb species, all observation data were pooled across months and fields.

Figure 5: (a-c) Small bee (< 2.5 mm intertegular width) and (d-f) large bee (≥ 2.5 mm intertegular width) abundance versus percent natural habitat within 500 m, 1000 m, and 2000 m ($* = P < 0.05$). Circles were drawn from the centers of each conventional and organic wheat field, where transects were established to trap bees. Shaded bands around lines are the 95% confidence interval.

Table legends

Table 1: Floral density, species richness, and evenness in conventional and organic fields between 2013 and 2015 in Big Sandy, MT. Values were pooled across three years. Significant P-values ($P \leq 0.05$) are bolded.

Table 2: Bee abundance, species richness, and evenness in conventional and organic fields collected between 2013 and 2015 at Big Sandy, MT. Values were pooled across three years. Significant P-values ($P \leq 0.05$) are bolded.

Table 3: Percent natural habitat within 500 m, 1000 m, and 2000 m from the centers of conventional and organic fields in Big Sandy, MT. Significant P-values ($P \leq 0.05$) are bolded.

Table 1:

Variables	Conventional	Organic	Analysis		
	Mean $\pm$ SE	Mean $\pm$ SE	DF	F-statistic	P value
Floral density	88 $\pm$ 83	426 $\pm$ 128	1,16	16.8	<0.001
Richness	9.8 $\pm$ 2.1	34 $\pm$ 3.0	1,16	44.3	<0.001
Evenness	0.57 $\pm$ 0.1	0.65 $\pm$ 0.03	1,16	0.69	0.420

Table 2:

Variables	Conventional	Organic	Analysis		
	Mean $\pm$ SE	Mean $\pm$ SE	DF	F-statistic	P value
Abundance	158 $\pm$ 31	165 $\pm$ 33	1,16	0.56	0.47
Richness	25 $\pm$ 2	27 $\pm$ 3	1,16	0.19	0.67
Evenness	0.85 $\pm$ 0.02	0.80 $\pm$ 0.02	1,16	3.55	0.08

Table 3:

Distance from	Conventional	Organic	Analysis		
the field centers	Mean $\pm$ SE	Mean $\pm$ SE	DF (n)	χ^2 - statistic	P value
500 m	4.9 $\pm$ 1.8%	1.3 $\pm$ 0.9%	1 (18)	4.5	0.040
1000 m	9.9 $\pm$ 1.5%	4.7 $\pm$ 2.2 %	1 (18)	10.6	0.001
2000 m	13.1 $\pm$ 2.2%	8.6 $\pm$ 2.4%	1 (18)	3.04	0.080
