

The Effects of Crop Intensification on the Diversity of Native Pollinator Communities

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Abstract

Increases in agricultural conversion are leading to declines in native grasslands and natural resources critical for beneficial insects. However, little is known regarding how these changes affect pollinator diversity. Land use types were categorized within 300 m and 3 km radii of pollinator sampling locations in Brookings County, SD. Pollinator abundance and species richness were regressed on the proportion of the landscape dedicated to row crops, grass and pasture, forage crops, small grains, and aquatic habitats using variance components modeling. Row crops had a negative effect on bee abundance at 300 m, after fixed effects modeling accounted for outliers skewing this relationship. At 3 km, corn positively affected bee abundance and richness, while soybean acreage decreased species richness. The landscape matrix of outlying sites consisted of large monocultured areas with few alternative habitat types available, leading to inflated populations of *Melissodes* and Halictidae. Syrphids had a positive parabolic relationship between diversity and row crops, indicating potential for competitive exclusion from intermediate landscapes. Unlike other studies, landscape diversity within 300 m was not found to significantly benefit pollinator diversity. Within especially agriculturally developed areas of the region, high abundances of pollinators suggest selection for a few dominant species. There was no effect of forage crops or aquatic habitats on pollinator diversity, indicating that less highly managed areas still represent degraded habitat within the landscape. Incorporating pollinator-friendly crops at the farm level throughout the region is likely to enhance pollinator diversity by lessening the negative effects of large monocultures.

Key words: agrobiont, Cropland Data Layer, landscape simplification, *Melissodes*

Landscape simplification as a result of agricultural intensification is documented worldwide (Foley et al. 2005). The northern Great Plains of North America are no exception. A rapid increase in agricultural conversion of the Corn Belt occurred in the 1920s and 1930s with the wide-scale industrialization and mechanization of United States agriculture (Ramankutty and Foley 1999). Presently, a second great conversion of grasslands within the landscape into cropland is underway (Wright and Wimberly 2013, Johnston 2014), driven by high commodity prices in corn and soybean for biofuels as well as crop insurance programs (Claassen et al. 2011, Gallant et al. 2014, Fausti 2015). Grassland conversions in this part of the United States, which are occurring at annual rates of 1.0–5.4%, are comparable to deforestation rates in Brazil, Malaysia, and Indonesia (Claassen et al. 2011). This coincides with landscape simplification, with arable lands being planted mostly in continuous corn or corn-soy rotations (Wright and Wimberly 2013, Johnston 2014, Fausti

2015). Increases in land and land rental prices, combined with high commodity prices, have led to the removal of historic tree stands and field margins at the local farm level in order to maximize crop production areas.

Landscape simplification associated with agricultural intensification has been correlated with reductions in the abundance and diversity of many taxa (Tscharntke et al. 2012), including negative consequences to pollinators (Grixti et al. 2009, Kremen and Miles 2012, Vanbergen and the Insect Pollinators Initiative 2013). The loss of marginal habitat (defined in this manuscript as those areas of field margins containing weedy and native flowering vegetation) leads to the loss of ecosystem services provided by resident organisms, prompting the need to manage these margins for critical functions such as pollination (Tscharntke et al. 2005, Kremen et al. 2007). As the landscape is simplified, the role of marginal habitat for supporting diverse beneficial insect communities is enhanced

(Haaland et al. 2011, Tschardt et al. 2012, Anderson et al. 2013, Jha and Kremen 2013, Kennedy et al. 2013, Korpela et al. 2013).

Worldwide, native (Potts et al. 2010) and managed (Oldroyd 2007) pollinator populations are declining with numerous possible explanations, including parasites and pathogens, insecticides applied in-hive and in the foraging environment, changing cultural practices, and a loss of suitable foraging habitat, as well as combinations of these factors (Oldroyd 2007, Potts et al. 2010, Vanbergen and the Insect Pollinators Initiative 2013). Declines in floral resources resulting from expanding agricultural production are strongly implicated in decreasing overall health of honey bees, thereby making them more susceptible to other stressors (Alaux et al. 2010, Di Pasquale et al. 2013). There is also evidence that broad-scale landscape alterations have a negative effect on pollination services (Kremen et al. 2002, Ricketts et al. 2008, Garibaldi et al. 2011, Cariveau et al. 2013, Benjamin et al. 2014).

The northern Great Plains serve as the summering grounds for most of the honey bee hives in the United States (see Gallant et al. 2014). Other pollinators are also abundant in this part of the country, with a recent survey identifying 114 pollinator species on the USDA-ARS North Central Agricultural Research Laboratory research farm in Brookings, SD (J.G.L., last accessed 22 March 2014). Further, this region was recently identified for a pollinator conservation initiative in the 2014 Farm Bill to create and improve pollinator habitat. South Dakota specifically is one of the top corn- (ranked number 6 in 2013 in area harvested) and soybean- (ranked number 5 in 2013) producing states (NASS 2013). Because of the high diversity and abundance of pollinators and region-focused conservation initiatives, eastern South Dakota represents an ideal location for evaluating local and landscape-level diversity effects on native pollinators in an agriculturally dominated region.

The purpose of this study was to identify those features of the agricultural landscape in eastern South Dakota that contribute most to shaping native pollinator community diversity. This was driven by the hypothesis that increasing agricultural intensification as measured by a larger area planted with fewer crops will decrease pollinator diversity at local and landscape scales. Specifically, we predicted that increasing row crops (corn and soybeans) will have a negative effect on pollinator abundance and species richness, while flowering forage crops such as alfalfa will provide an overall diversity benefit.

Materials and Methods

Study Region

This study was conducted in Brookings County, located in east-central South Dakota. The daily high temperatures during sampling ranged from 26.1–33.3°C, and lows ranged from 9.4–22.2°C, with precipitation totals falling below the historical monthly average of 78 mm. Twelve field sites located along crop field margins at least 6 km apart (Fig. 1) were selected to reflect a range of landscape-level diversity conditions. Flowering species present in the immediate sampling region at the time of sampling are included in Supp. Table 1 (online only).

Pollinator Community Assessment

Pollinators were collected at each of the 12 study sites in August and September of 2013 when flowering vegetation was well established along field margins of mature crops, with sampling starting at 08:00 and lasting until 17:30 to encompass peak pollinator activity times. It has been previously demonstrated that sampling adults late in the

flight season effectively captures the most species with less sampling required (Grundel et al. 2011). Insects from each site were collected using two each of yellow, white, and blue pan traps (made from painted or white 100-ml Solo cups; Vrdoljak and Samways 2012) and one blue vane trap (SpringStar Inc., Woodinville, WA; Stephen and Rao 2005), which were deployed individually at the height of the surrounding vegetation in a transect 6.5 m apart. Multiple trap types were employed in order to maximize the diversity of trapped pollinators. Insects were collected from each site every 3–4 h and preserved in 70% ethanol in the field and transported back to the lab where they were pinned and identified. These passive collection methods largely excluded honey bees.

The Hymenoptera were identified to family using Borror and White (1998). Within this order, the Apoidea were identified to species using the Discover Life IDnature Guide (<http://pick4.pick.uga.edu/>, last accessed 22 March 2014), while the remaining hymenopteran specimens were identified to family and sorted to morphospecies. Syrphidae were identified to species, when possible, using Vockeroth and Thompson (1987), and references therein. All other dipterans and insect specimens were identified to family using Borror and White (1998) and sorted to morphospecies. Samples from the two sampling dates were combined and species abundance and richness were determined for each sampling site as measures of diversity.

Landuse Feature Analysis

Coordinates of the 12 field sites were imported into an ArcGIS 10.1 (ESRI 2010) database and mapped using ArcMap. A grid layer containing 2013 land cover data (USDA, National Agricultural Statistics Service Cropland Data Layer 2013; <http://nassgeodata.gmu.edu/CropScape/>, last accessed 23 May 2016) was added to the ArcGIS data base. Land cover was extracted in buffers surrounding each site at radii of 300 m to capture diversity effects of immediately adjacent land use types and 3 km to capture landscape-level effects. Within the foraging zones surrounding each sample site, the proportion of area in various cropping and other land use types was calculated. Cropped habitat included alfalfa, corn, flaxseed, hay, millet, oats, sorghum, soy, and wheat. Other landscape features included grass and pasture (a degraded habitat designation, often characterized by intense grazing in our region), herbaceous wetlands, and open water.

Data Analysis

Regression Analysis

Data were analyzed using Systat v.13.1 (San Jose, CA). Agriculturally relevant groupings of landscape features (row crops [corn and soybeans], forage crops [alfalfa and hay], small grains [flaxseed, millet, oats, sorghum, and wheat], grass and pasture, and aquatic habitats [herbaceous wetlands and open water]) were regressed against abundance and species richness as diversity metrics for bees and syrphids, the two most abundant pollinator groups. While bee metrics conformed to assumptions of normality and equal variances, syrphid abundance and richness for row crops at 3 km were best described using polynomial regression based on greater adj. R^2 values. Syrphid abundance was log transformed and analyzed using linear regression for grass and pasture at 3 km.

Mixed Modeling Analysis

To verify the results of regression modeling and to statistically validate outliers, a heterogeneous variance regression using a linear mixed model with variance component structure was used to estimate the fixed effect of landscape features on bee and syrphid abundance and species richness (SAS v.9.2, Cary, NC). Regression

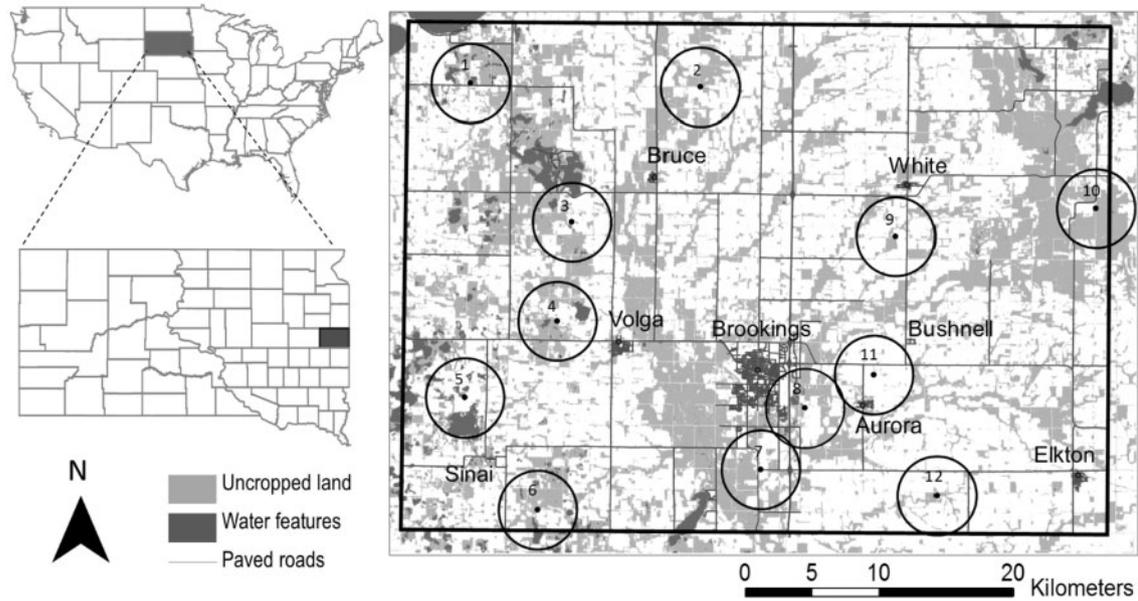


Fig. 1. Map of the study region with 3-km sampling buffers.

models with suppressed intercepts were estimated for abundance and species richness as the response levels. Collection site served as the treatment ($n = 12$), and because treatments were characterized by a continuum of landscape features, the study is not replicative. Pollinator types (bees or syrphids) were considered the subject of interest in the analysis with a group affect used to account for within-subject heterogeneity. For each metric, the covariate landscape features were from either the 300-m or 3-km radius. The regressions of landscape features and bee and syrphid diversity metrics (described in the previous section) revealed that three sites appeared to skew the relationships of diversity and land use. Thus, a dummy variable was created in the mixed model to assess their contribution as outliers.

The four models were estimated by the mixed modeling procedure in SAS. Given the limitations of the data, all models were estimated with the intercept suppressed. The general function for the regression models estimated is given by the equation:

$$D_{ijt} = \delta S_{ij} + \beta_k L_{kt} + \varepsilon_{ijt}$$

where D is the response (dependent) variable, with $i = 1$ to 4 for abundance and richness at 300 m and 3 km, respectively. The experimental unit is pollinator, as defined by S , where $j = 1$ for bees and 2 for syrphids; thus, when the response variable was for syrphids, $S_{ij} = 1$, and $S_{ij} = 0$ for bees. L is treatment effect associated with site location. A landscape feature is measured as a percentage of the total area, where $k = 1$ to 7 for corn, soy, forage crops, small grains, grass and pasture, wetlands, and open water. t denotes site location, 1 through 12. δ denotes the coefficient for the species dummy variable. β is the regression coefficient estimate for fixed effects associated with landscape features. The variable ε is the residual error that allows the variance-covariance matrix to be estimated using variance component structure. Analysis of the variance components of the residual variance-covariance matrix verified heterogeneity associated with species.

Results

Insect Diversity

The dominant land use types across the region were corn, soybean, and grass and pasture (Table 1), together accounting for nearly 75%

of all land use in the study region. A total of 763 Hymenoptera specimens representing 83 species and 826 Diptera specimens from 75 species were collected at the 12 sites, with the communities varying across the study region in insect richness (31 to 49 total species) and abundance (87 to 307 total specimens). Apidae and Halictidae were the two most abundant and speciose families within the Hymenoptera (Supp. Table 2 [online only]). The genus *Melissodes* was the most abundant group of bees, with *M. agilis* and *M. trinodis* together accounting for 73% of all Apoidea collected. Syrphidae was the most abundant and diverse family within the Diptera (*Toxomerus marginatus* accounted for 78% of all syrphids collected), which included pollinating species as well as species that may feed on pollen or nectar but with limited or no pollinating capabilities (Supp. Table 3 [online only]).

Mixed Model Analysis

The variance component analysis is provided in Tables 2 and 3, and fixed effects analysis is provided in Tables 4 and 5 for pollinator abundance and species richness, respectively. The results presented in these tables confirm heterogeneity between bees and syrphids. The random effect modeling assumption for pollinator type was rejected for pollinator abundance. A correlation table comparing correlation coefficients of the landscape factors is included as Supp. Table 4 (online only).

Abundance

300 m

There was a significant negative effect of row crops on abundance (corn: $t = 3.66$, $df = 14$, $P = 0.003$; soy: $t = 6.55$, $df = 14$, $P < 0.001$; Table 4), with corn and soy decreasing pollinator abundance by an average of 10.3 ± 2.80 and 15.9 ± 2.43 insects per site, respectively. Grass and pasture, forage crops, small grains, and open water all contributed positively to pollinator abundance, while wetlands had a negative effect. However, fewer than half of the sites had forage crops, small grains, wetlands, or open water within 300 m of the sampling locations. Regression analyses revealed no significant effect for area of corn, soybeans, or grass and pasture on bee or syrphid abundance.

Table 1. Percentage of the entire landscape composed of cropland and unmanaged areas across all the sampled sites, $N = 12$ for each

Land use type	300 m				3 km			
	Average \pm SE	Median	Range		Average \pm SE	Median	Range	
			Min.	Max			Min.	Max
Row crops	44.0 \pm 8.0	40.6	11.0	89.4	48.2 \pm 4.5	44.1	26.3	77.6
Grass and pasture	30.2 \pm 7.0	19.3	4.0	80.8	25.4 \pm 4.8	23.9	8.1	65.1
Forage crops	13.9 \pm 5.0	6.6	0	46.8	10.2 \pm 2.4	6.7	4.0	30.2
Small grains	1.0 \pm 0.7	0	0	6.6	1.93 \pm 0.4	1.9	0	4.1
Aquatic habitat	3.3 \pm 1.9	0	0	17.2	7.8 \pm 2.3	6.3	0.2	25.4

Table 2. Variance components statistics (a) and model fit statistics (b) for pollinator abundance

a. Covariance parameter	300 m	3 km
	Covariance parameter estimate, Z-statistic ^a	Covariance parameter estimate, Z-statistic
Bees	111, Z = 2.26*	323, Z = 2.10*
Syrphids	783, Z = 2.26*	537, Z = 2.10*
b. LML fit statistics		
-2 Log likelihood	205	209
AIC	227	231
BIC	212	217
Likelihood ratio test: unrestricted (group effect) vs. restricted (no group effect) models	$\chi^2 = 5.59$, df = 1, $P < 0.02$	$\chi^2 = 1.08$, df = 1, $P > 0.10$

^a $P < 0.05^*$.**Table 3.** Variance components statistics (a) and model fit statistics (b) for species richness

a. Covariance parameter	300 m	3 km
	Covariance parameter estimate, Z-statistic ^a	Covariance parameter estimate, Z-statistic
Bees	2.92, Z = 2.00*	6.01, Z = 2.33**
Syrphids	0.801, Z = 2.00*	0.148, Z = 2.33**
b. LML fit statistics		
-2 Log likelihood	78.3	66.7
AIC	100	88.7
BIC	86.0	74.3
Likelihood ratio test: unrestricted (group effect) vs. restricted (no group effect) models	$\chi^2 = 1.65$, df = 1, $P > 0.10$	$\chi^2 = 16.3$, df = 1, $P < 0.01$

^a $P < 0.05^*$, $P < 0.01^{**}$.**Table 4.** Solutions for mixed model effects for pollinator abundance

Variable	300 m		3 km	
	Effect estimate	t-statistic ^a	Effect estimate	t-statistic
Corn	-0.46	3.66**	1.25	2.44*
Soy	-0.73	6.55***	-0.37	0.69
Grass/pasture	0.53	45.9***	0.38	5.87***
Forage	1.75	182***	0.65	1.40
Small grains	8.82	8.62***	-2.27	1.09
Wetlands	-9.48	34.9***	0.07	0.08
Open water	6.96	14.1***	0.15	0.76
Species	-21.3	1362***	-20.6	57.2*
Outliers	114	9.11***	52.9	4.90***

^a $P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$.**Table 5.** Solutions for mixed model effects for pollinator species richness

Variable	300 m		3 km	
	Effect estimate	t-statistic ^a	Effect estimate	t-statistic
Corn	0.048	45.8***	0.223	75.8***
Soy	0.069	3.46**	-0.031	1.75
Grass/pasture	0.120	38.1***	0.119	41.0***
Forage	0.134	21.2***	0.124	43.2***
Small grains	0.415	11.0***	-0.511	10.3***
Wetlands	-0.131	0.53	-0.115	31.3***
Open water	0.287	1.62	0.108	19.5***
Species	-6.59	139**	-6.17	11.7
Outliers	2.58	1.47	1.26	43.0***

^a $P < 0.01^{**}$, $P < 0.001^{***}$.

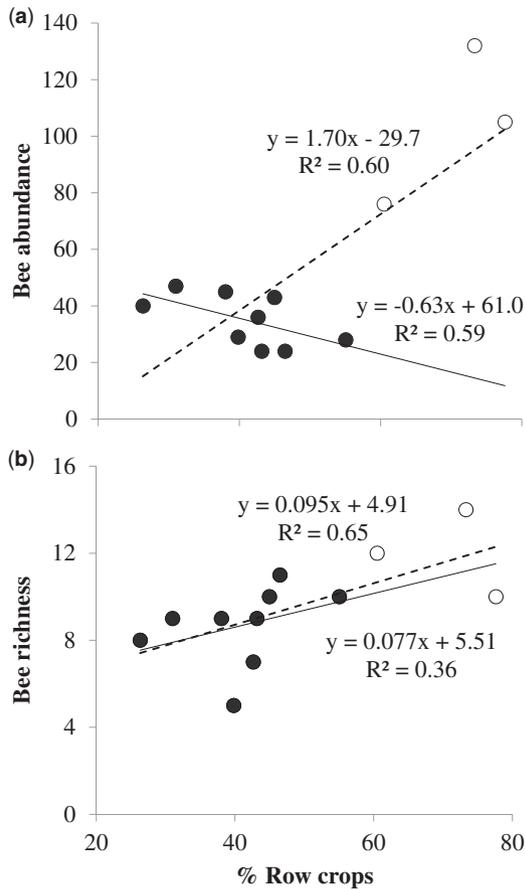


Fig. 2. (a, b) The effect of row crops on bee diversity before (white circles, dashed line) and after (dark circles, dark line) outliers were removed at the 3 km spatial scale.

3 km

Regression analysis revealed a significant positive effect of row crops on bee abundance ($F=15.3$, $df=1,10$, $P=0.003$; Fig. 2a). However, this relationship was driven by an overrepresentation of particular species dominating at only three of the sites, contributing significantly to the magnitude of this effect, as indicated by mixed modeling ($t=4.90$, $df=14$, $P<0.001$; Table 4). These species included the long-horned bees *Melissodes agilis*, *M. trinodis*, *M. druriella*, and *Svastra obliqua* (Apidae) and *Agapostemon virescens* and *Lasioglossum pruinosum* (Halictidae). The shift coefficient indicated an average of 52.9 ± 10.8 more bees at these three sites relative to the others. Controlling for this, the positive relationship between row crops and bee abundance was reversed to a negative tendency ($F=3.76$, $df=1,7$, $P=0.094$; Fig. 2a).

Regression analyses indicated that the long horned bees also skewed the relationships of bee abundance with small grains ($F=9.72$, $df=1,9$, $P=0.012$ vs. $F=0.01$, $df=1,9$, $P=0.916$; Fig. 3a), grass and pasture ($F=4.32$, $df=1,9$, $P=0.068$ vs. $F=0.30$, $df=1,7$, $P=0.604$; Fig. 3b), and aquatic habitats ($F=3.93$, $df=1,10$, $P=0.076$ vs. $F=0.03$, $df=1,7$, $P=0.871$; Fig. 3c). Of these variables, mixed modeling only found significance for grass and pasture ($t=5.87$, $df=14$, $P<0.001$). There was no effect of forage crops on bee abundance.

Syrphid abundance had a parabolic relationship with row crops, with low and high percentages of row crops positively affecting this metric ($F=10.7$, $df=2,9$, $P=0.004$; Fig. 4). This was driven by two dominant species (*Toxomerus marginatus* and *Syrphus* sp.) at

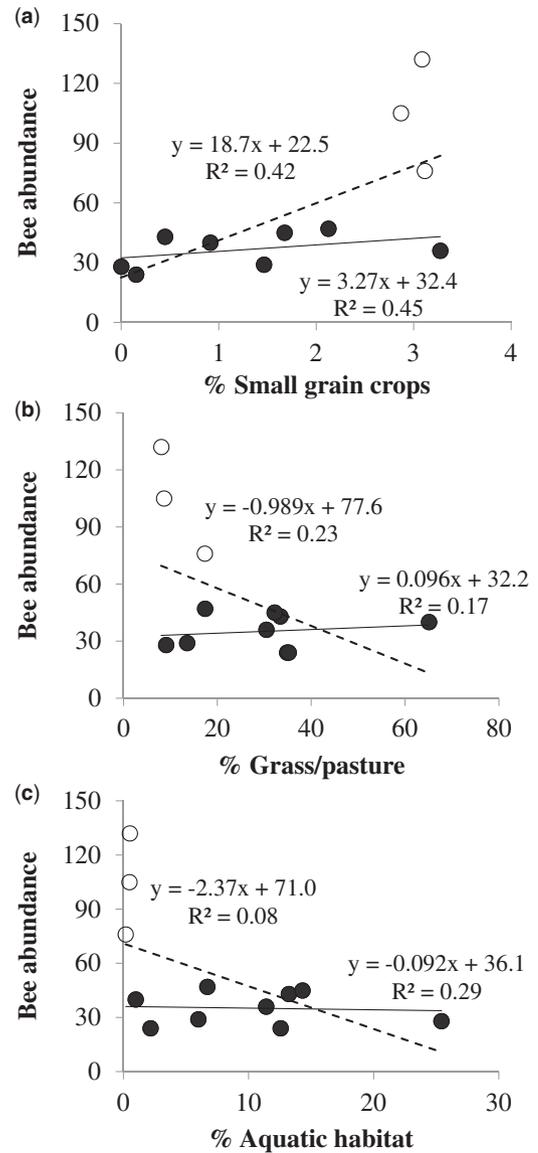


Fig. 3. (a–c) The effects of landscape variables before (open circles, dashed line) and after (dark circles, solid line) outliers were removed on native bee abundance at 3 km.

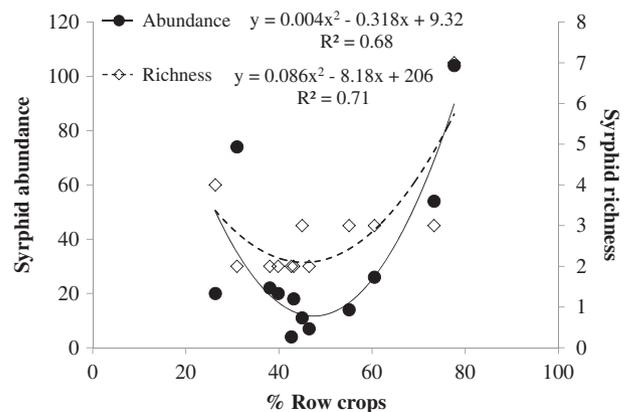


Fig. 4. The effects of row crops on syrphid richness and abundance at 3 km.

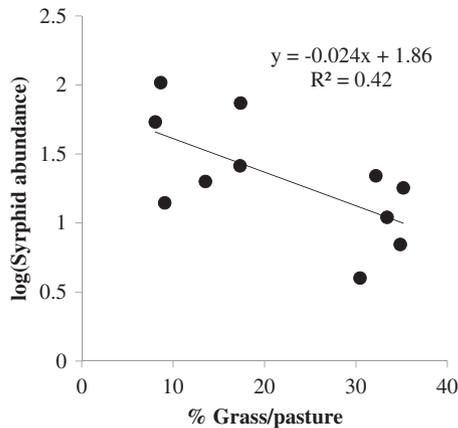


Fig. 5. The effects of grass and pasture on syrphid abundance at 3 km.

those sites where the proportion of row crops was higher or lower than the average across the region. Increasing grass and pasture percentage in the landscape reduced syrphid numbers as well ($F = 6.59$, $df = 1,9$, $P = 0.030$; Fig. 5).

Richness

300 m

None of the mixed model variables contributed significantly to the observed patterns in pollinator richness across sites. Regression analyses also revealed no significant effect for area of corn, soybeans, or grass and pasture on bee or syrphid species richness. As fewer than half of the sites had forage crops, small grains, wetlands, or open water within 300 m, these variables were not considered for regression analysis.

3 km

Regression analysis revealed a significant positive effect of row crops on bee richness ($F = 7.15$, $df = 1,10$, $P = 0.023$), which was again driven by high numbers of long-horned bees and halictids. This effect was neutralized when outliers identified by mixed modeling ($t = 43.0$, $df = 14$, $P < 0.001$; Table 5) were removed from the regression ($F = 1.07$, $df = 1,7$, $P = 0.335$; Fig. 2b). Mixed modeling identified significant effects of grass and pasture, small grains, forage crops, and aquatic habitats on bee richness, although the magnitude of these effects was very small (Table 5). These effects were not significant in regression models.

Syrphid richness was parabolically related to row crops, with low and high percentages of row crops again positively affecting these metrics ($F = 9.58$, $df = 2,9$, $P = 0.006$; Fig. 4b). There was no effect of grass and pasture, small grains, forage crops, and aquatic habitat on species richness.

Discussion

As expected, the dominant land use types in the study area consisted of corn and soybean crops and grasslands used predominantly for grazing livestock, together accounting for nearly 75% of all land use in the study region. Initially, it appeared that corn and soy had a positive effect on bee abundance and richness; however, this was driven largely by a few dominant bee species present in those areas containing particularly high proportions of row crops and correspondingly low proportions of other habitat types at 3 km. This suggests that a few species differentially benefit from, and dominate in, these highly developed agricultural landscapes. Cariveau et al.

(2013) found that while pollination services were stabilized by these dominant species, it was at the expense of pollinator diversity. As pollinators in the Northern Great Plains evolved with native flowering prairie species, an overabundance of certain species may contribute to a decrease in pollination of these wildflowers in prairie remnants in agricultural areas (Blaauw and Isaacs 2014). Native bees also decreased in abundance when agricultural cover of corn and soybeans increased at the 300 m spatial scale, which can compromise adjacent crop pollination (Benjamin et al. 2014), though in our agricultural system crops do not rely on pollination services (but see Danner et al. (2014) and Gill and O'neal (2015)).

Changes across spatial scales further disrupt local plant–pollinator interactions (Ferreira et al. 2013). While increasing agricultural landscape homogeneity may inhibit crop pollination, this may be recovered with conservation plantings (Benjamin et al. 2014). Potts et al. (2003) found that the overall structure of bee communities was dependent on floral diversity, with bee richness being closely linked to annual floral diversity. Similar strong positive effects of local vegetation have also been reported elsewhere (Jha and Kremen 2013, Scriven et al. 2013, Shackelford et al. 2013).

The parabolic relationship between syrphid abundance and richness and row crops could indicate potential competitive exclusion (Pulliam 2000) from niches shared with other pollinators or predators that are present when there are intermediate levels of row crops in the landscape. *Toxomerus marginatus* larvae have been identified as a potentially important predator of soybean aphids in the upper Midwest, with populations peaking in late summer (Eckberg et al. 2015). The distributions of adult syrphids could therefore be mediated by larval food sources such as soybean aphids and other prey items in row crops as opposed to floral resources used by adults. Syrphids may also concentrate on relatively diverse field margins in more structurally simple landscapes, such as where sampling occurred, as these resources make the greatest difference to diversity in an intensively managed landscape (Haenke et al. 2009).

Forage crops, including hayland and alfalfa, while agricultural, were expected to contribute somewhat to pollinator diversity by providing flowering resources. In our study region, alfalfa is grown largely as feed for dairy cows and thus must be mowed regularly, preventing flowering (Jennings 2013), though there may be low rates of flowering on field margins. However, there was no effect of forage crops on pollinator diversity at 300 m or 3 km, indicating that floral resources may not be the only important limiting resource for pollinators in this region. Similarly, aquatic habitats (herbaceous wetlands and open water) appeared to provide no benefits to native pollinator diversity.

The use of pan traps, or bee bowls, is common when sampling pollinator communities. However, certain species may be preferentially drawn to these traps while others are excluded, such that their use may skew capture results from bee communities (Joshi et al. 2015). We sought to overcome this by including blue vane traps, which are highly attractive to bumblebees (Stephen and Rao 2005, Joshi et al. 2015). Only one species of *Bombus* was recovered in our study region (*B. pensylvanicus*), with very few representative specimens (Supp. Table 2 [online only]). This is not unexpected given the documented declines in *Bombus* throughout North America, particularly as a result of agricultural intensification in the Midwest (Grixti et al. 2009), though historic records are lacking for eastern South Dakota. *Melissodes agilis* and *M. trimodis* were captured at much higher frequencies than any other Apoidea across the study region. The males of long-horned bees from these species form sleeping aggregations, though nearly all captured specimens were female. Parker et al. (1981) did not note aggregative nesting of *M. agilis*, but

very little biological information on nesting is available for *Melissodes*.

In addition to a consistent source of forage throughout the season (Carvell et al. 2007), pollinators also require habitat for nesting (Potts et al. 2003, Stanley and Stout 2013) and refuge from environmental extremes (Isaacs et al. 2009). Tilling is a common practice in our region, and given that ~70% of native bees in the United States are solitary ground nesting species, the high abundance of *Melissodes* sp. and halictids may be due to loose soil that is suitable for nesting, a phenomenon observed by Potts et al. (2003) and Kim et al. (2006). Parker et al. (1981) note that *Melissodes agilis* specialize on *Helianthus* sp. (a common weed in agricultural areas of eastern South Dakota), and *Melissodes* as a genus are considered pollen specialists of Asteraceae (Dickinson and McKone 1991), which includes many species native to the northern Great Plains. However, Kim et al. (2006) reported that *Melissodes* rarely nested in cropland and the genus has elsewhere been deemed likely to be disrupted by tillage practices (Parker et al. 1981). In contrast, halictids are floral generalists (Dickinson and McKone 1991) and are commonly observed nesting on farms (Kim et al. 2006).

In conclusion, most studies evaluating pollinator diversity in cropland are targeting the effects of landscape-level changes on food crop pollination services (Shackelford et al. 2013). Here, we found that increasing intensification of corn and soybean in the landscape has mixed effects on native pollinator groups, with bees having a reduced diversity skewed toward agrobiont species. This is expected to continue as more and more marginal habitats are converted for agricultural production (Claassen et al. 2011).

In order to conserve diversity of native pollinators in the northern Great Plains, incorporating flowering crops into the landscape, such as flowering oilseeds, will provide a mutual benefit to producers and pollinators by bolstering critical resources throughout the summer in this highly developed agricultural landscape while still providing a source of income to farmers. Studies show that flowering oilseeds specifically increase abundance of pollinators (Westphal et al. 2003). However, this approach should be balanced with the simultaneous incorporation of noncropped areas containing native and naturalized species to reduce the risk of further selection of pollinator generalists and agrobionts and to encourage maximum native bee diversity (Diekoetter et al. 2010, Holzschuh et al. 2011).

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References

- Alaux, C. F., F. Ducloz, D. Crauser, and Y. LeConte. 2010. Diet effects on honeybee immunocompetence. *Biol. Lett.* 6: 562–565.
- Anderson, A., T. Carnus, A. J. Helden, H. Sheridan, and G. Purvis. 2013. The influence of conservation field margins in intensively managed grazing land on communities of five arthropod trophic groups. *Insect Conserv. Divers.* 6: 201–211.
- Benjamin, F. E., J. R. Reilly, and R. Winfree. 2014. Pollinator body size mediates the scale at which land use drives crop pollination services. *J. Appl. Ecol.* 51: 440–449.
- Blaauw, B. R., and R. Isaacs. 2014. Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wild flowers. *Basic Appl. Ecol.* 15: 701–711.
- Borror, D. J., and R. E. White. 1998. A field guide to insects: America north of Mexico, Houghton Mifflin Company, Boston.
- Cariveau, D., N. Williams, F. E. Benjamin, and R. Winfree. 2013. Response diversity to land use occurs but does not consistently stabilize ecosystem services provided by native pollinators. *Ecol. Lett.* 16: 903–911.
- Carvell, C., W. R. Meek, R. F. Pywell, D. Goulson, and M. Nowakowski. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J. Appl. Ecol.* 44: 29–40.
- Claassen, R., R. Carriazo, J. C. Cooper, D. Hellerstein, and K. Ueda. 2011. Grassland to cropland conversion in the Northern Plains: the role of crop insurance, commodity, and disaster programs. In U. D. o. A. E. R. Service (ed.), *Economic Research Report No. ERR-120*. Washington, DC.
- Danner, N., S. Haertel, and I. Steffan-Dewenter. 2014. Maize pollen foraging by honey bees in relation to crop area and landscape context. *Basic Appl. Ecol.* 15: 677–684.
- Di Pasquale, G., M. Salignon, Y. LeConte, P. Belzunces, A. Decourtye, A. Kretzschmar, S. Suchail, J. Brunet, and C. F. Alaux. 2013. Influence of pollen nutrition on honeybee health: Do pollen quality and diversity matter? *PLoS ONE* 8: e72016.
- Dickinson, J. A., and M. J. McKone. 1991. Insect floral visitors to four species of tall-grass prairie composite (Asteraceae: Heliantheae). *Prairie Nat.* 24: 159–174.
- Diekoetter, T., T. Kadoya, F. Peter, V. Wolters, and F. Jauker. 2010. Oilseed rape crops distort plant-pollinator interactions. *J. Appl. Ecol.* 47: 209–214.
- Eckberg, J. O., J. A. Peterson, C. P. Borsh, J. M. Kaser, G. A. Johnson, J. C. Luhman, D. L. Wyse, and G. E. Heimpel. 2015. Field abundance and performance of hoverflies (Diptera: Syrphidae) on soybean aphid. *Ann. Entomol. Soc. Am.* 108: 26–34.
- Fausti, S. W. 2015. The causes and unintended consequences of a paradigm shift in corn production practices. *Environ. Sci. Policy* 52: 41–50.
- Ferreira, P. A., D. Boscolo, and B. F. Viana. 2013. What do we know about the effects of landscape changes on plant-pollinator interaction networks? *Ecol. Indic.* 31: 35–40.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, et al. 2005. Global consequences of land use. *Science* 309: 570–574.
- Gallant, A. L., N. H. Euliss, and Z. Browning. 2014. Mapping large area landscape suitability for honey bees to assess the influence of land-use change on sustainability of national pollination services. *PLoS ONE* 9: e99268.
- Garibaldi, L. A., I. Steffan-Dewenter, C. Kremen, J. M. Morales, R. Bommarco, S. A. Cunningham, L. G. Carvalheiro, N. P. Chacoff, J. H. Dudenhofer, S. S. Greenleaf, et al. 2011. Stability of pollination services decreases with isolation from natural areas despite honeybee visits. *Ecol. Lett.* 14: 1062–1072.
- Gill, K. A., and M. E. O'neal. 2015. Survey of soybean insect pollinators: Community identification and sampling method analysis. *Environ. Entomol.* 44: 488–498.
- Grixti, J. C., L. T. Wong, S. A. Cameron, and C. Favret. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biol. Conserv.* 142: 75–84.
- Grundel, R., K. J. Frohnapple, R. P. Jean, and N. B. Pavlovic. 2011. Effectiveness of bowl trapping and netting for inventory of a bee community. *Environ. Entomol.* 40: 374–380.
- Haaland, C., R. E. Naisbit, and L. F. Bersier. 2011. Sown wildflower strips for insect conservation: A review. *Insect Conserv. Divers.* 4: 60–80.
- Haenke, S., B. Scheid, M. Schaefer, T. Tschardtke, and C. Thies. 2009. Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. *J. Appl. Ecol.* 46: 1106–1114.
- Holzschuh, A., C. F. Dormann, T. Tschardtke, and I. Steffan-Dewenter. 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proc. R. Soc. B Biol. Sci.* 278: 3444–3451.
- Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Front. Ecol. Environ.* 7: 196–203.

- Jennings, J. 2013. Alfalfa for dairy cattle. University of Arkansas Cooperative Extension Service, FSA4000-PD-10RV. (<http://www.uaex.edu/publications/pdf/FSA-4000.pdf>) last accessed 23 May 2016.
- Jha, S., and C. Kremen. 2013. Resource diversity and landscape-level homogeneity drive native bee foraging. *Proc. Natl. Acad. Sci. USA*. 110: 555–558.
- Johnston, C. A. 2014. Agricultural expansion: Land use shell game in the US Northern Plains. *Landscape Ecol.* 29: 81–95.
- Joshi, N. K., T. Leslie, E. G. Rajotte, M. A. Kammerer, M. Otieno, and D. J. Biddinger. 2015. Comparative trapping efficiency to characterize bee abundance, diversity, and community composition in apple orchards. *Ann. Entomol. Soc. Am.* 108: 785–799.
- Kennedy, C. M., E. Lonsdorf, M. C. Neel, N. Williams, T. H. Ricketts, R. Winfree, R. Bommarco, C. Brittain, A. L. Burley, D. Cariveau, et al. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16: 584–599.
- Kim, J., N. Williams, and C. Kremen. 2006. Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. *J. Kans. Entomol. Soc.* 79: 309–320.
- Korpela, E. L., T. Hyvonen, S. Lindgren, and M. Kuussaari. 2013. Can pollination services, species diversity and conservation be simultaneously promoted by sown wildflower strips on farmland. *Agric. Ecosyst. Environ.* 179: 18–24.
- Kremen, C., and A. Miles. 2012. Ecosystem services in biologically diversified versus conventional farming systems: Benefits, externalities, and trade-offs. *Ecol. Soc.* 17: 40.
- Kremen, C., N. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. USA*. 99: 16812–16816.
- Kremen, C., N. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, T. Roulston, I. Steffan-Dewenter, et al. 2007. Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecol. Lett.* 10: 299–314.
- NASS. 2013. Annual report on acreage. (<http://www.nass.usda.gov>) last accessed 23 May 2016.
- Oldroyd, B. P. 2007. What's killing American honey bees. *PLoS Biol.* 5: e168.
- Parker, F. D., V. J. Tepedino, and G. E. Bohart. 1981. Notes on the biology of a common sunflower bee, *Melissodes (Eumelissodes) agilis* Cresson. *N. Y. Entomol. Soc.* 89: 43–52.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology* 84: 2628–2642.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.* 25: 345–353.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecol. Lett.* 3: 349–361.
- Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: Croplands from 1700–1992. *Glob. Biogeochem. Cycles* 13: 997–1027.
- Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, S. S. Greenleaf, A. M. Klein, M. M. Mayfield, et al. 2008. Landscape effects on crop pollination services: Are there general patterns? *Ecol. Lett.* 11: 499–515.
- Scriven, L. A., J. Sweet, and G. R. Port. 2013. Flower density is more important than habitat type for increasing flower visiting insect diversity. *Int. J. Ecol.* 2013: 237457.
- Shackelford, G., P. R. Steward, T. G. Benton, W. E. Kunin, S. G. Potts, J. C. Biesmeijer, and S. M. Sait. 2013. Comparison of pollinators and natural enemies: A meta-analysis of landscape and local effects on abundance and richness in crops. *Biol. Rev.* 88: 1002–1021.
- Stanley, D. A., and J. C. Stout. 2013. Quantifying the impacts of bioenergy crops on pollinating insect abundance and diversity: A field-scale evaluation reveals taxon-specific responses. *J. Appl. Ecol.* 50: 335–344.
- Stephen, W. P., and S. Rao. 2005. Unscented color traps for non-*Apis* bees (Hymenoptera: Apiformes). *J. Kans. Entomol. Soc.* 78: 373–380.
- Tscharntke, T., A. M. Klein, A. Kreuss, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecol. Lett.* 8: 857–874.
- Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batary, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, et al. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.* 87: 661–685.
- Vanbergen, A. J., and the Insect Pollinators Initiative. 2013. Threats to an ecosystem service: pressures on pollinators. *Front. Ecol. Environ.* 11: 251–259.
- Vockeroth, J. R., and F. C. Thompson. 1987. Syrphidae, pp. 713–743. *In* J. F. McAlpine (ed.), *Manual of Nearctic Diptera*, vol. 2. Canada Communication Group, Ottawa.
- Vrdoljak, S. M., and M. J. Samways. 2012. Optimising coloured pan traps to survey flower visiting insects. *J. Insect Conserv.* 16: 345–354.
- Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Mass-flower crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* 6: 961–965.
- Wright, C. K., and M. C. Wimberly. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *Proc. Natl. Acad. Sci. USA*.