

Assessing wild bees in perennial bioenergy landscapes: effects of bioenergy crop composition, landscape configuration, and bioenergy crop area

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Abstract

Context Wild bee populations are currently under threat, which has led to recent efforts to increase pollinator habitat in North America. Simultaneously, U.S. federal energy policies are beginning to encourage perennial bioenergy cropping (PBC) systems, which have the potential to support native bees.

Objectives Our objective was to explore the potentially interactive effects of crop composition, total PBC area, and PBC patches in different landscape configurations.

Methods Using a spatially-explicit modeling approach, the Lonsdorf model, we simulated the impacts of three perennial bioenergy crops (PBC: willow, switchgrass, and prairie), three scenarios with different total PBC area (11.7, 23.5 and 28.8% of agricultural land converted to PBC) and two types of landscape configurations (PBC in clustered landscape patterns that represent realistic future configurations or in dispersed neutral landscape models) on a nest abundance index in an Illinois landscape.

Results Our modeling results suggest that crop composition and PBC area are particularly important for bee nest abundance, whereas landscape configuration is associated with bee nest abundance at the local scale but less so at the regional scale.

Conclusions Strategies to enhance wild bee habitat should therefore emphasize the crop composition and amount of PBC.

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Introduction

Wild bees are currently under threat, with agricultural intensification as one recognized cause of measured declines in their populations (Grixti et al. 2009; Potts et al. 2010; Deguines et al. 2014). A recent assessment of the status of wild bees in the United States found a

decline in bee abundance across 23% of the United States (U.S.) from 2008 to 2013 as estimated via a spatially explicit model (Koh et al. 2016). This decline is particularly evident in agricultural areas reliant on conventional commodity crops, including Illinois, which has experienced a substantial reduction in wild bee richness and diversity as measured by museum collections of bumble bees (*Bombus* sp.) (Grixti et al. 2009) and which exhibits a very low modeled bee abundance and a relatively high demand for pollination services (Koh et al. 2016).

In light of recent declines in bee populations, national and international strategies to enhance pollinator habitat are underway. In the U.S., a “National Strategy to Promote the Health of Honey Bees and Other Pollinators” was adopted in May 2015 (Pollinator Health Task Force 2015), which includes collaborative strategies with Canada and Mexico to develop a “pollinator corridor” throughout the Mississippi River basin and restore or enhance 7 million acres for pollinators over the next 5 years. Additionally, U.S. federal energy policies are beginning to promote the development of perennial crops for use in bioenergy production (e.g., the “biofuel mandate” in the Energy Independence and Security act of 2007, Public Law 110–140). Since most cropped land in the central U.S. is under annual cultivation, switching some land to perennial crops could increase available habitat for wild bees on agricultural land.

Even small increases in perennial vegetation can lead to increases in wild bees. Recent research has demonstrated that creating relatively small (e.g., 300–500 m) hedgerows can increase bee species richness (Morandin and Kremen 2013) and promote community spatial heterogeneity (beta diversity) of wild bees (Ponisio et al. 2016). Hedgerows can also increase the occurrence (Kremen and M’Gonigle 2015) and persistence (M’Gonigle et al. 2015) of specialist pollinators, including wild bees, and can promote crop pollination, sometimes leading to enhanced pollinator presence in neighboring crop fields (e.g., canola, Morandin and Kremen 2013). However, these positive effects on pollinators do not always occur (e.g., sunflowers, Sardiñas and Kremen 2015). The diversity of land cover types can also influence bee populations. Land cover diversity at the scale of the surrounding 1 to 2 km is positively correlated with bee abundance and richness, likely due

to variation in floral resources throughout the season when bees are active (Mallinger et al. 2016).

In north central Illinois, researchers are developing cropping systems that incorporate perennial bioenergy crops (PBC) in small subfield patches (e.g., ~1 to 10 ha) within larger commodity crop fields (~10 to 100 ha), with the goal of enhancing landscape multifunctionality by reducing field nutrient loss and enhancing ecological benefits, including biodiversity (Hamada et al. 2015; Graham 2016; Ssegane and Negri 2016). These efforts take into account both subfield edaphic conditions (soil type, slope, nutrient leaching, etc.) and farmers’ management preferences (Ssegane et al. 2015; Graham 2016; Ssegane and Negri 2016). However, depending on which edaphic conditions are targeted, planting PBC in subfield patches within fields of row crops can result in different landscape configurations and different total PBC area within the landscape. Similarly, the specific perennial crop chosen may vary from herbaceous monocultures (e.g., switchgrass, *Panicum virgatum*), to woody monocultures (e.g., willow, *Salix* sp.), to polycultures (e.g., mixed prairie species).

Understanding how the specific crop composition, the relative PBC area, and its configuration in the landscape influence bee nest abundance is important to assess the potential impacts of PBC cropping systems on wild bees. These characteristics can be investigated by using a spatially explicit model to predict the impact of landscape conditions on native bee nest abundance and diversity, such as one recently developed by Lonsdorf et al. (2011). The model (hereafter called the “Lonsdorf model”) is available as the Crop Pollination module, readily accessible and adaptable as part of the InVEST program (Kareiva et al. 2011), a standalone software package available from the Natural Capital Project (www.naturalcapitalproject.org/invest). The Lonsdorf model evaluates the abundance of bees visiting and nesting in each pixel of a landscape by using a land cover raster, a table of land cover attributes for each land cover class, and a table of bee species or guilds with nesting and foraging requirements and foraging distances.

The Lonsdorf model has been used to evaluate pollination services in landscape scenarios of bioenergy in Wisconsin (Meehan et al. 2013), and its projections have been compared to empirical data on bees in coffee plantations in Costa Rica and

watermelon fields in Pennsylvania and New Jersey (Lonsdorf et al. 2009). Kennedy et al. (2013) found that the model correlated with empirical results in coarse grained, homogeneous landscapes but lacks clarity in fine grained or complex landscapes. Olsson et al. (2015) explored the results of the model in simple and complex hypothetical landscapes and found that incorporating bee behavioral preferences enhanced the viability of the model results; however their revision has yet to be incorporated within the InVEST package. The Lonsdorf model was also the basis for Koh et al.' (2016) evaluation of wild bees in the United States.

In addition to its use to assess bee habitat in existing landscapes, the Lonsdorf model can be used to explore the effect of hypothetical alterations to a landscape resulting from “alternative future scenarios” that represent changes in policy, technology, or social conditions (Nassauer and Corry 2004). Alternative future scenarios can be visualized as future landscape patterns (FLPs). FLPs illustrate plausible landscape configurations derived from participatory scenario planning, and can be used to evaluate the effect of different scenarios (Nassauer and Corry 2004; Alcamo 2008; Das et al. 2012). For instance, FLPs that vary the amount or type of PBC can be compared to assess the relative differences in bee nest abundance produced under each set of conditions. FLPs can also be compared to neutral landscape models (NLMs). Patches in NLMs mimic the characteristics (size, shape, etc.) of patches in corresponding FLPs but they are randomly distributed across the landscape. The patterns in NLMs are therefore quantitatively derived, and are not driven by the selection of specific edaphic conditions. This random distribution decouples the effect of PBC patch configuration from total PBC area. The development of normative FLPs and associated, quantitatively derived NLMs allows for comparisons between clustered and randomly distributed landscapes (e.g., by comparing one FLP to its corresponding NLM), between different PBC composition (e.g., by comparing one landscape configuration with willow to the same landscape configuration with prairie), and between different total areas of PBC (e.g., by comparing a NLM created from one set of scenario conditions to a NLM created with a different set of scenario conditions). Together, a series of FLPs and NLMs allows analysis of the three variables in a single landscape and minimizes confounding factors.

The research question that guided our modeling investigation was this: How would regional pollinator habitat compare under a variety of alternative but plausible future scenarios of landscape composition and configuration? Our approach was to develop models of plausible future landscapes and to use the Lonsdorf model to quantitatively estimate the bee nest abundance index (NAI) at the regional level under each FLP. Another objective was to assess the degree to which landscape composition and configuration each played a role in determining bee nest abundance at the scale of the regional watershed. To address this objective we compared each FLP to a comparable NLM. We hypothesized that alternative PBC patterns would result in significantly different bee nest abundance across the watershed as estimated by the Lonsdorf model. Further, we hypothesized that patch layout would play an important role in determining bee habitat viability at the level of the regional watershed, and therefore that landscape configuration, in addition to landscape composition, would significantly affect bee nest abundance.

This investigation will help policymakers to understand the likely landscape-level effects on pollination services of different land-change drivers when they play out in a spatial manner in a large agricultural landscape. It will also help policymakers to understand the effects of landscape configuration, which could inform future zoning laws, development permits, or conservation reserve program policies.

Methods

As part of earlier work exploring the possibilities for perennial bioenergy crops in an Illinois landscape (Graham 2016), we developed three scenarios that incorporate PBC in the Indian Creek watershed, Illinois. The Indian Creek watershed covers ca. 20,700 ha and is located in Livingston, McLean, and Ford counties, Illinois (Fig. 1). The National Land Cover Database shows that in 2011 nearly 90% of the watershed was cultivated in annual crops and 7% was developed (Jin et al. 2013).

To test the hypotheses described above, we developed alternative landscapes that varied according to landscape configuration (two levels; NLM versus FLP), PBC composition (three levels; switchgrass, prairie, and willow), and total PBC area (three levels;

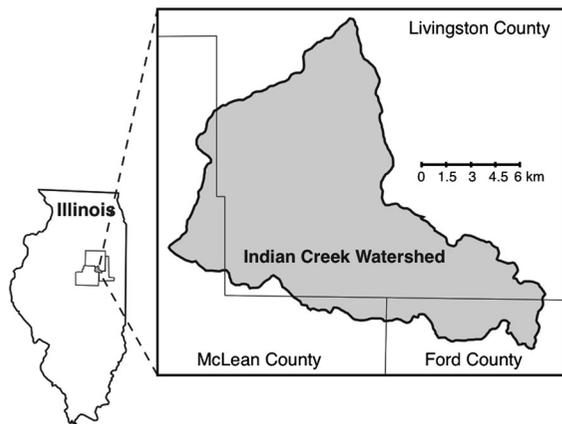


Fig. 1 The Indian Creek watershed, ca. 20,700 ha in north central Illinois, USA. The watershed is primarily located in Livingston County, with the southwestern corner of the watershed in McLean County and the southern tip in Ford County

11.7, 23.5, and 28.8% of the agricultural land in the watershed) (Table 1). Starting with three scenarios that target placement of PBC to sub-field locations that exhibit specific edaphic conditions (see below), we developed one base FLP and one corresponding NLM

for each set of scenario conditions. NLMs mimic the patch characteristics of each FLP but remove the spatial correlation and clustering that is present in the FLPs due to their association with existing edaphic conditions. We then evaluated each FLP and NLM with the bioenergy crops of switchgrass (S), prairie (P), and willow (W). This process resulted in a total of nine FLPs and nine NLMs, which we refer to according to their model type, scenario number, and bioenergy crop (e.g., FLP1P is the FLP resulting from Scenario 1 with prairie, while NLM1P is the corresponding NLM) (Table 1).

The three initial FLPs are based on scenarios that place PBC in small patches within fields where edaphic conditions (soil type, topography, frequent flooding, nutrient leaching, etc.) are less-suitable for annual row crops (Ssegane et al. 2015) as confirmed by local stakeholders (Graham 2016). Edaphic conditions used to develop each scenario are presented in Table 1. For FLP 1, PBC are allocated to areas where crop productivity limitations or nitrate leaching are concerns (11.7% of the agricultural land in the Indian Creek watershed). For FLP 2, PBC are allocated to areas where crop productivity limitations, nitrate or

Table 1 Factorial experimental design for modeling bee nesting in the Indian Creek watershed, Livingston County, Illinois

Scenario	Edaphic conditions replacing food crops with perennial bioenergy crops ^a	Amount of agricultural land in perennial bioenergy crops (%)	Perennial bioenergy crop		
			Switchgrass	Prairie	Willow
Scenario 1	Crop productivity limitations	11.7	FLP1S	FLP1P	FLP1W
	Nitrate leaching		NLM1S	NLM1P	NLM1W
Scenario 2	Nitrate leaching	23.5	FLP2S	FLP2P	FLP2W
	Pesticide leaching		NLM2S	NLM2P	NLM2W
	Crop productivity limitations				
	Ponding and drainage				
Scenario 3	Frequent flooding and drainage	28.8			
	Nitrate leaching		FLP3S	FLP3P	FLP3W
	Pesticide leaching		NLM3S	NLM3P	NLM3W
	Crop productivity limitations				
	Frequent flooding				
	Runoff				
	30 m stream buffers				

A future landscape pattern (FLP) and neutral landscape model (NLM) are developed for each combination of scenario conditions and perennial bioenergy crops

^a Edaphic conditions for each scenario include soil type, topography, areas with frequent flooding, nutrient leaching, and landscape conditions that are less suitable for cultivation of row crops, as discussed in Ssegane et al. (2015) and refined in a participatory scenario planning process with local stakeholders (Graham 2016)

pesticide leaching, combined ponding and drainage, or combined frequent flooding and drainage are concerns (23.5% of the agricultural land). For FLP 3, PBC are allocated to areas in which crop productivity limitations, nitrate or pesticide leaching, frequent flooding, or run-off are of concern, and 30 m buffer zones around streams (28.8% of the agricultural land). All alternative landscapes were based on 30 m resolution land cover data showing the 3-year crop rotation history as of 2012 (Ssegane and Negri 2016).

We then developed NLMs with PBC patch shapes that corresponded to each FLP, so that patch shapes were approximately equivalent between each FLP-NLM pair. The metric we used for patch shapes was a “related circumscribing circle,” which measures the ratio between patch area and the smallest circumscribing circle and provides a metric of overall patch elongation (McGarigal 2015). Bailey et al. (2007) examined 13 different landscape-level metrics and found that the mean related circumscribing circle best correlated with wild bee abundance in European agricultural landscapes. In cases where two or more potential NLMs had related circumscribing circle values close to those of the corresponding FLP, we chose the NLM that best matched the landscape means in “edge density” or “Euclidean nearest neighbor distance,” which have also been found to correlate with wild bee abundance (Bailey et al. 2007).

We created NLMs with the NLMpy PYTHON software package (Etherington et al. 2015) using the random cluster nearest-neighbor function. To control patch sizes, this function uses a proportional value (p : 0–1) determined by the proportion of elements randomly selected to form clusters. To define the clusters, the function uses a neighborhood value (n : 4-neighbor, 8-neighbor, or 6-neighbor diagonal), which controls the patch shapes. We chose p and n values to create NLMs that exhibit mean values for the class-level related circumscribing circle that were most similar to those exhibited in the corresponding FLPs, as calculated in Fragstats 4.2 (McGarigal and Ene 2013). For NLM1, we used $p = 0.45$ and the 4-neighbor clustering value. For NLM2, we used $p = 0.10$ and the 4-neighbor clustering value. For NLM3, we used $p = 0.10$ and the 8-neighbor clustering value. Landscape and PBC-class metrics potentially relevant for wild bees (Bailey et al. 2007) are provided for each FLP and NLM (Table S1).

In total, we evaluated the Lonsdorf nest abundance index for 19 landscapes: nine representing the three bioenergy crops for each of the three FLPs, nine representing the three bioenergy crops for each of the three NLMs (Fig. 2), and the current landscape that does not include PBC. The Lonsdorf model requires three inputs: a land cover map, a table of bee species, and a table of land cover attributes. Each FLP or NLM corresponds to a land cover map for that set of conditions. The bee species attribute table (Table S2) contains information on bee species, including species-specific nesting requirements, seasonal foraging activity, and maximum foraging distance. The land cover attribute table (Table S3) contains information for each land cover class present in the land cover map, including values for the relative availability of different categories of nesting habitat and values for the relative availability of floral resources in each season.

The bee species attribute table (Table S2) includes values recorded by Wolf and Ascher (2008) or used by Meehan et al. (2013) in prior Lonsdorf modeling in southern Wisconsin. To determine the species to use in the analysis, we reviewed the Illinois Natural History Survey records (www.inhs.illinois.edu/collections/insect) and identified 70 bee species that have been previously collected in Livingston, Ford, or McLean counties, Illinois, where the Indian Creek watershed is located. Of those, we selected the 50 species for which we were able to categorize nesting and foraging season (reported by Wolf and Ascher (2008) or Meehan et al. (2013)) and to obtain foraging distances. We calculated foraging distance estimates using an allometric equation (Greenleaf et al. 2007) based on the intertegular distance (distance between left and right wing bases) we measured from specimens in the University of Michigan Museum of Zoology Insect Collection. We were able to measure intertegular distances for 45 species; for the other five species (indicated with an asterisk), we used foraging distance estimates published by Meehan et al. (2013).

The land cover attribute table was based on work by Meehan and colleagues (Meehan et al. 2013). Nesting scores range from 0 to 1 and indicate the relative availability of particular nesting strata (soil, cavity, hive, or wood) in each land cover class. Foraging scores range from 0 to 1 and indicate the relative availability of floral resources during spring, summer, and fall for each land cover class. We used their values

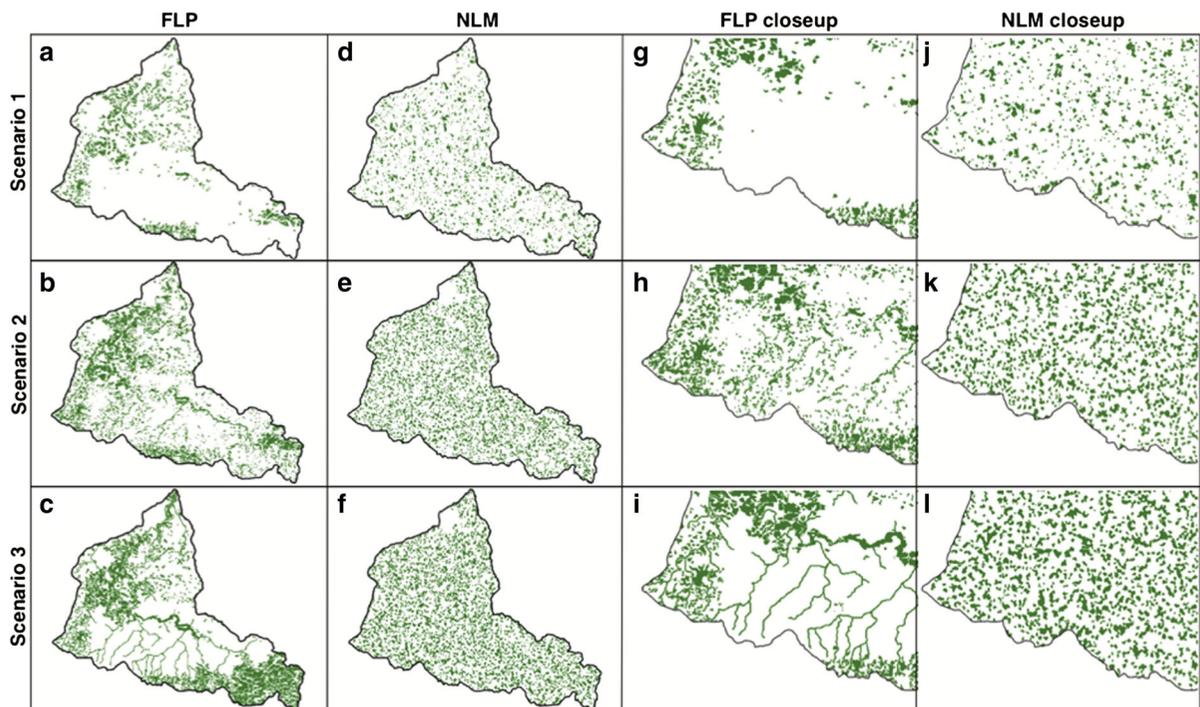


Fig. 2 Future landscape patterns (FLP) and neutral landscape models (NLM) for the Indian Creek watershed, Illinois. Areas shown in green represent perennial bioenergy crop plantings for FLP 1 (a), FLP 2 (b), FLP 3 (c), NLM 1 (d), NLM 2 (e), NLM 3 (f). Magnified images of the southwestern portion of the

watershed are provided for FLP 1 (g), FLP 2 (h), FLP 3 (i), NLM 1 (j), NLM 2 (k), and NLM 3 (l). Each FLP or NLM was independently evaluated with each perennial bioenergy crop: switchgrass, prairie, and willow

for land cover classes that were included both in their data and in ours. For land cover classes not represented in their published table, we used values for the individual nesting or foraging scores that were most comparable to the unrepresented cover class. For instance, for our land cover class of willow, we used the Meehan scores for soil nesting and spring foraging from their deciduous forest land cover class, the scores for cavity, hive, and wood nesting from their wetland land cover class, and the summer and fall foraging scores from their corn land cover class. Although these scores may not be perfect, they represent the general conditions present in each of the land cover classes not present in Meehan et al. (2013).

In order to compare the differences between FLPs, FLPs and NLMs, and NLMs, we calculated the 30 m pixel-level percent difference between different pairwise combinations of landscape configurations, and between alternative landscapes and the current landscape. Pixel-level percent difference in NAI illustrates the degree of difference between two alternative

landscapes, aggregated at the watershed level (via the mean percent difference) or at the fine scale (for instance, by highlighting areas with positive or negative percent difference on a map of the watershed). Pixel-level percent difference has been previously used to explore the impacts of different land use change scenarios on pollinators in the Upper Midwest (Meehan et al. 2013; Bennett et al. 2014) and provides an easily-interpreted metric.

In order to assess the three variables of landscape configuration (FLP or NLM), PBC area (Scenario 1, 11.7%, Scenario 2, 23.5%, or Scenario 3, 28.8% of agricultural land), and PBC composition (willow, switchgrass, or prairie) at the watershed scale, we conducted analysis of variance with post hoc Tukey tests on the watershed-level mean for the Lonsdorf NAI values in the R Statistical Computing Environment, version 3.2.3 (R Core Team 2015). Analysis of variance identifies which independent variables are significant influences on the overall landscape mean, and the post hoc Tukey tests conduct corrected

pairwise comparisons to determine which treatment groups show significant differences.

Results

The spatial arrangement of PBC for the three basic FLPs and corresponding NLMs are shown in Fig. 2. In total, the percentage of the agricultural land in the watershed converted to PBC ranged from 11.7 to 28.8% (Table 1; Fig. 2).

We calculated descriptive statistics for each FLP or NLM (Table 2). In all cases, alternative landscapes had greater NAI than the current landscape, which does not include PBC (Figure S.1). At the regional level of the watershed, crop composition was a significant predictor of NAI mean (Table 3). Specifically, landscapes with prairie have greater mean NAI than landscapes with switchgrass or willow, and landscapes with switchgrass have greater mean NAI than landscapes with willow. Assessed at the pixel level and aggregated over the landscape, NAI was always lower for willow as a perennial bioenergy crop than for either switchgrass or prairie (Fig. 3a; Table 4). Comparing landscapes with switchgrass to

landscapes with prairie shows an increased NAI at the pixel level and at the regional level of the watershed for both FLP (Fig. 3b) and NLM configurations.

Across the watershed, NAI was greater in scenarios with greater bioenergy crop area (Table 3). Specifically, Scenario 2 and Scenario 3 landscapes have greater mean NAI than Scenario 1 landscapes and Scenario 3 have greater NAI than Scenario 2 landscapes. Comparing landscapes with less PBC to landscapes with more PBC (e.g., FLP1S to FLP2S, FLP1S to FLP3S, and FLP2S to FLP3S, etc.) shows that more total PBC was associated with greater modeled NAI for NLMs (Table 4; Fig. 4a–c) and for FLPs (Table 4; Fig. 4d–f). However, a map of the comparison between FLP2 and FLP3 highlights lower NAI in some areas of FLP3 than FLP2 (Fig. 4f, red regions). This association is likely related to differences in the spatial configuration of FLP2 and FLP3: although FLP3 has an overall greater total PBC area, the distribution of PBC is different between these two FLPs. Some areas of the landscape in FLP2 have patches of PBC that are not present in FLP3 (Fig. 2g–i).

NAI was lower in landscapes with a more clustered or spatially uneven distribution of PBCs, which occurred more frequently in simulated FLPs versus neutral landscape models with the equivalent

Table 2 Descriptive statistics for pixel-level nest abundance index, aggregated at the scale of the landscape for the current landscape and each alternative landscape

	Configuration	Mean	Minimum	Maximum	Standard Deviation
Neutral landscape model (NLM) or future landscape pattern (FLP); 11.7% of ag land in PBC (1), 23.5% of ag land in PBC (2), or 28.8% of ag land in PBC (3); switchgrass (S), prairie (P), or willow (W)	Current landscape	0.089	0.000	0.674	0.108
	NLM1S	0.136	0.000	0.697	0.155
	NLM1P	0.155	0.000	0.764	0.176
	NLM1W	0.120	0.000	0.687	0.129
	NLM2S	0.193	0.000	0.713	0.196
	NLM2P	0.244	0.000	0.863	0.247
	NLM2W	0.155	0.000	0.697	0.147
	NLM3S	0.222	0.000	0.726	0.213
	NLM3P	0.292	0.000	0.916	0.280
	NLM3W	0.173	0.000	0.705	0.155
	FLP1S	0.141	0.000	0.733	0.169
	FLP1P	0.165	0.000	0.892	0.206
	FLP1W	0.122	0.000	0.694	0.136
	FLP2S	0.197	0.000	0.778	0.213
	FLP2P	0.256	0.000	1.046	0.285
FLP2W	0.157	0.000	0.709	0.156	
FLP3S	0.223	0.000	0.785	0.228	
FLP3P	0.305	0.000	1.108	0.327	
FLP3W	0.170	0.000	0.681	0.159	

Table 3 Analysis of variance and Tukey comparisons for mean nest abundance index, aggregated at the scale of the landscape

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Analysis of variance					
Configuration ^a	1	0.00012	0.00012	0.36	0.561
Area ^b	2	0.026	0.013	37.58	6.81e−06
Composition ^c	2	0.023	0.011	33.21	1.28e−05
Residual	12	0.0041	0.00034		
Comparisons		Difference	Lower	Upper	<i>p</i> adjusted
Tukey multiple comparisons of means, 95% confidence level					
Configuration	NLM–FLP	−0.0052	−0.024	0.014	0.5609
Area	2–1	0.060	0.032	0.089	0.0003
	3–1	0.091	0.062	0.12	0.0000
	3–2	0.030	−0.0020	0.059	0.0359
Composition	S–P	−0.051	−0.080	−0.023	0.0012
	W–P	−0.087	−0.12	−0.058	0.0000
	W–S	−0.035	−0.064	−0.0070	0.0156

Landscape configuration, bioenergy crop composition, and bioenergy crop area were evaluated for their effect on nest abundance index

^a Neutral landscape model or future landscape pattern

^b 11.7% of ag land in PBC (1), 23.5% of ag land in PBC (2), or 28.8% of ag land in PBC (3)

^c *S* switchgrass, *P* prairie, or *W* willow

Table 4 Mean and standard deviation for pixel level percent difference in nest abundance index when comparing alternative landscapes to other alternative landscapes using the Lonsdorf model (Lonsdorf et al. 2011)

Starting	Ending	Mean	Standard Deviation
FLP1S	FLP1P	13.7	9.3
FLP2S	FLP2P	26.2	9.0
FLP3S	FLP3P	30.8	13.4
FLP1S	FLP1W	−5.7	8.6
FLP2S	FLP2W	−11.1	10.9
FLP3S	FLP3W	−13.3	12.1
FLP1P	FLP1W	−16.2	12.2
FLP2P	FLP2W	−28.9	11.7
FLP3P	FLP3W	−32.5	13.9
FLP1S	FLP2S	79.1	214.1
FLP1P	FLP2P	100.9	244.5
FLP1W	FLP2W	52.6	143.4
FLP1S	FLP3S	129.6	300.1
FLP1P	FLP3P	186.7	421.0
FLP1W	FLP3W	82.2	191.0
FLP2S	FLP3S	84.3	253.9
FLP2P	FLP3P	103.8	309.4
FLP2W	FLP3W	53.1	168.0
NLM1S	NLM2S	130.8	277.6

Table 4 continued

Starting	Ending	Mean	Standard Deviation
NLM1S	NLM3S	172.7	313.5
NLM1P	NLM2P	157.3	311.4
NLM1P	NLM3P	216.1	365.7
NLM1W	NLM2W	86.0	188.0
NLM1W	NLM3W	112.9	209.5
NLM2S	NLM3S	121.1	273.8
NLM2P	NLM3P	131.2	287.8
NLM2W	NLM3W	79.4	189.5
FLP1S	NLM1S	52.5	193.8
FLP1P	NLM1P	58.6	208.1
FLP1W	NLM1W	34.0	134.5
FLP2S	NLM2S	95.3	254.9
FLP2P	NLM2P	103.1	271.8
FLP2W	NLM2W	62.0	177.1
FLP3S	NLM3S	115.8	280.6
FLP3P	NLM3P	129.0	307.3
FLP3W	NLM3W	75.8	194.0

For each comparison, “starting” refers to the alternative landscape used as the basis for the comparison, and “ending” refers to the alternative landscape compared

Neutral landscape model (NLM) or future landscape pattern (FLP); 11.7% of ag land in PBC (1), 23.5% of ag land in PBC (2), or 28.8% of ag land in PBC (3); switchgrass (S), prairie (P), or willow (W)

composition. However, this difference was not statistically significant (Tables 2, 3). These results indicate that FLPs have more variability in NAI throughout the landscape than do NLMs. When comparing FLP configurations with NLM configurations, there is a positive mean percent difference in NAI for all FLP to NLM comparisons (Table 4). However, the mean values lie relatively close to 0, and the standard deviation for these comparisons is quite large, overlapping 0 in all cases. Furthermore, there are areas of the landscape that exhibit positive percent difference and areas that exhibit negative percent difference (Fig. 5). This variability is due to the clustered nature of PBC in the three FLPs. The concentration of PBC varies such that some regions have greater PBC concentrations in a FLP, and some regions have greater PBC concentrations in a NLM (Fig. 2g–l). Greater PBC concentrations tend to increase NAI in those regions of an alternative landscape, indicating that the effects of PBC distribution are scale dependent. Across the landscape, the uniform distribution of PBC in each NLM is associated with slightly greater NAI than the clustered distribution of each FLP.

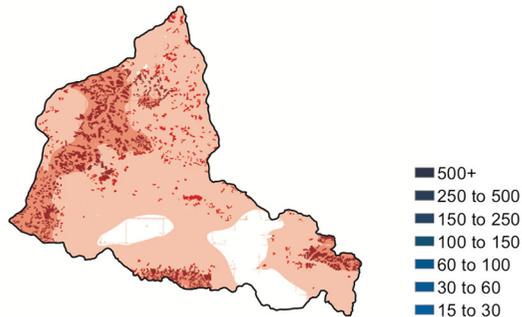
Discussion

The results of our simulation indicate that crop composition and the total area of PBC may shape the influence of PBC patches on native bee populations at both the fine scale (e.g., pixel) and the regional scale. Our results also indicate that the impact of spatial configuration is important at the fine scale but not necessarily at the scale of the entire watershed.

Bioenergy crop composition

Our simulation has several implications for the design and implementation of PBC landscapes. One implication is that the specific bioenergy crop will likely be an important factor in determining the impacts on wild bees. The model predicts that prairie may be associated with greater NAI than switchgrass, and both may be associated with greater NAI than willow. These results are similar to the findings of an empirical study of PBC plantings in Iowa, which found greater bee abundance in more diverse prairie plantings than in switchgrass (Ridgeway et al. 2015). This result is not

a FLP 1 Switchgrass to Willow



b FLP 1 Switchgrass to Prairie

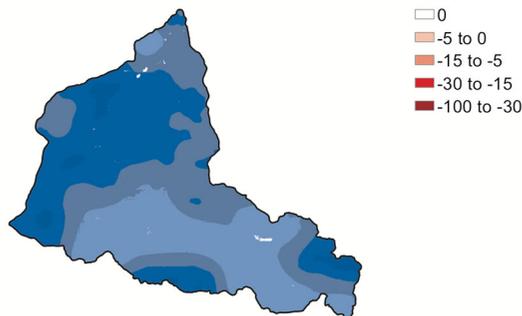


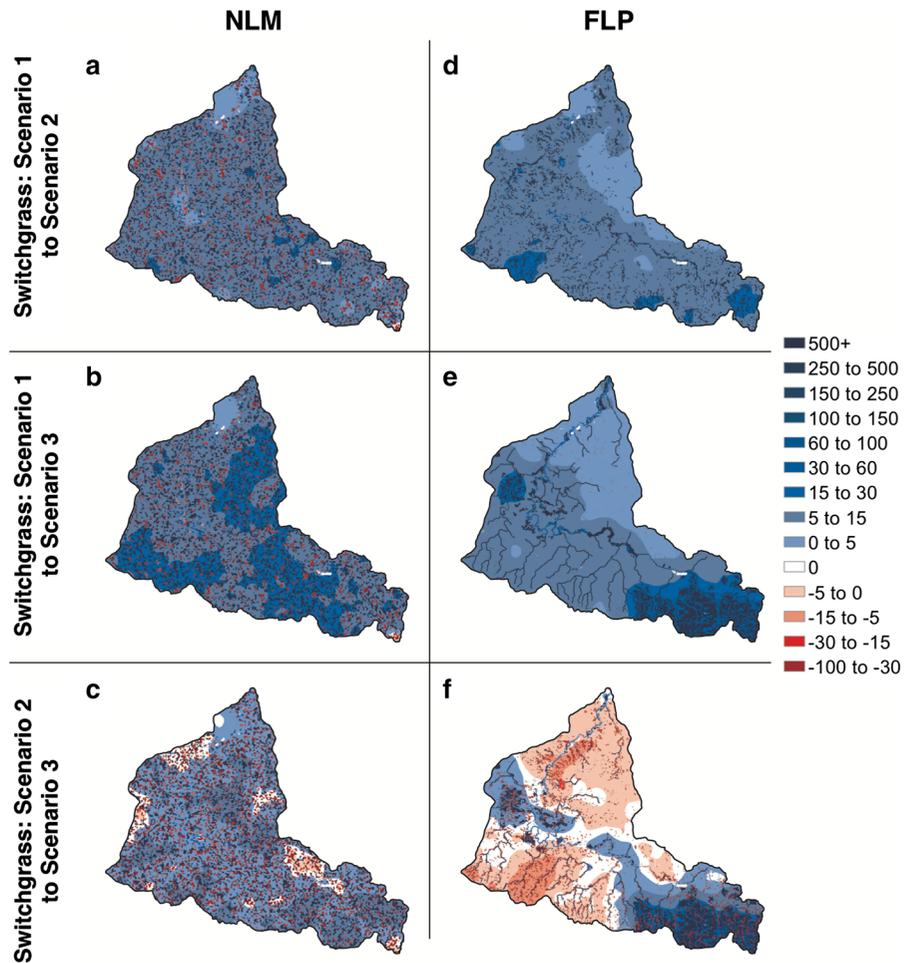
Fig. 3 Percent difference in nest abundance index for Composition. Pixel level percent difference and distribution for Lonsdorf nest abundance index (Lonsdorf et al. 2011), when comparing **a** FLP 1 with switchgrass to FLP 1 with willow, and **b** FLP 1 with switchgrass to FLP 1 with prairie

surprising, since diverse prairie plantings provide a greater variety of floral resources and nesting habitats, both of which are important for wild bees (Wray et al. 2014). Similarly, Stanley and Stout (2013) found that solitary bee abundance and species richness were greater in plantings of miscanthus (*Miscanthus x giganteus*) than in conventional wheat. These results are also consistent with the results of Lonsdorf modeling of PBC scenarios in Wisconsin (Meehan et al. 2013) and with empirical regression modeling of PBC scenarios in southern Michigan (Bennett and Isaacs 2014; Bennett et al. 2014). Although the Lonsdorf model may not predict the precise effects of each crop, the differences in floral resources, nesting habitat, and seasonality are important characteristics of PBC and should be investigated further.

However, the Lonsdorf model parameters might not fully simulate the nesting or foraging resources provided by different types of PBC. Although we

based the land cover attribute table on previously published data (Meehan et al. 2013), these values may not reflect the actual effect of any one type of PBC or land cover. For instance, the model predicts a reduced NAI in landscapes with willow, as compared to landscapes with switchgrass. Willow has been shown to be an important source of high quality pollen and nectar for wild bees, particularly early in the season when other floral resources are not yet present (Ostaff et al. 2015), and short-rotation willow coppice systems have been demonstrated to have relatively high diversity and richness of arthropods, including wild bees (Rowe et al. 2011). Willow could also provide an early season pollen and nectar boost that complements later season floral resources in other land cover classes. Riedinger et al. (2014) reported that landscapes with both early- and late-season crops exhibited a “temporal spillover” that enhanced *Bombus* sp. density. The presence of willow could produce a similar effect in PBC landscapes. It is therefore conceivable that the impact of willow was underestimated in the model, resulting in a lower NAI for simulated willow landscapes than would occur in a biological system, particularly if willow plantings included mid- or late-season floral resources. Similarly, the nesting or floral resources provided by switchgrass or prairie could be over- or underrepresented in the model. In their study in Iowa, Ridgeway et al. (2015) assessed bee abundance and diversity under three types of PBC: switchgrass monoculture, a 16 species prairie mix, and a 32 species prairie mix. Their results showed that the 16 species prairie mix had greater bee abundances than switchgrass, and that the 32 species prairie mix resulted in substantially greater bee abundances than either the 16 species mix or the switchgrass. This result was likely related to there being consistently high floral resources in the high diversity treatment, fewer early-season floral resources in the 16 species mix, and the fewest floral resources in the switchgrass treatments. The model parameters used in our study may simulate what could occur in some prairie plantings (e.g., a more diverse species mix) but not in others (e.g., a less diverse mix). Thus, if policies are intended to promote prairie as a PBC, they should consider the diversity and composition of the species because not all polycultures provide the same range of flower morphological diversity and temporal patterning of blooming.

Fig. 4 Percent difference in nest abundance index for Area. Pixel level percent difference and distribution for Lonsdorf nest abundance index (Lonsdorf et al. 2011) when comparing **a** NLM 1 with switchgrass to NLM 2 with switchgrass, **b** NLM 1 with switchgrass to NLM 3 with switchgrass, **c** NLM 2 with switchgrass to NLM 3 with switchgrass, **d** FLP 1 with switchgrass to FLP 2 with switchgrass, **e** FLP 1 with switchgrass to FLP 3 with switchgrass, and **f** FLP 2 with switchgrass to FLP 3 with switchgrass



Area

A second implication of our simulation is that the area in the landscape converted to PBC likely influences wild bee abundance. Aggregated at the scale of the regional watershed, comparing a landscape with less PBC to a landscape with more PBC always shows significantly greater NAI in the latter case. At the pixel scale, comparing a landscape with less PBC (Scenario 1) to a landscape with medium (Scenario 2) or high (Scenario 3) always shows an increased NAI in landscapes with more PBC. However, when comparing S2 to S3 landscapes, some areas show higher NAI under S2 than under S3. This pattern may be related to the specific configuration of the landscape, or it may be related to the landscape reaching a NAI threshold. The Lonsdorf model gives more weight to floral resources in nearby cells than to those in more distant

cells—given the foraging distances of the bee species used in this study, the landscape may have reached a critical threshold for bee foraging. Indeed, empirical research on wild bee visitation rates in California almond fields has shown a threshold in bee visitation rates, with substantial increases when more than ~30% of the surrounding landscape at a 1 km radius is in natural or semi-natural habitat (Klein et al. 2012). Regardless, policies aimed at maximizing wild bee abundance need to consider the proportion of the landscape in PBC, with the general assumption that more is better, while considering socially acceptable levels of land use change.

Configuration

A third implication of our simulation is that the PBC configuration (NLM vs. FLP) is not particularly

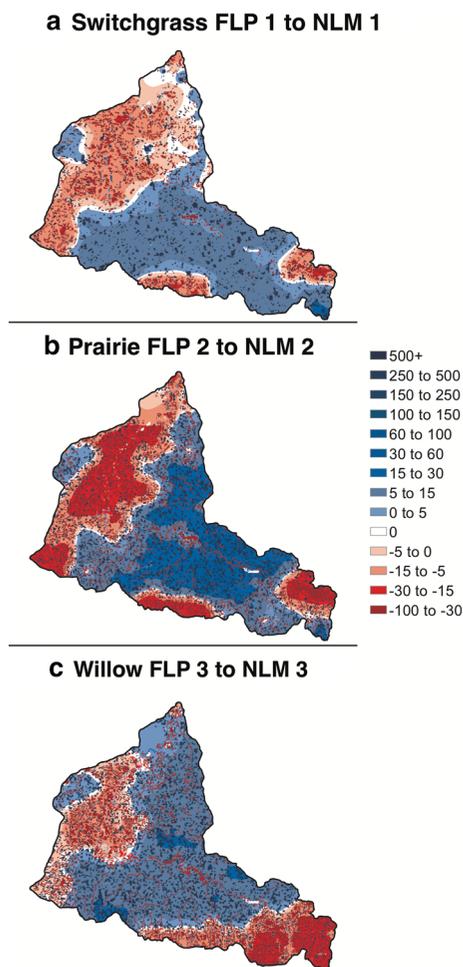


Fig. 5 Percent difference in nest abundance index for Configuration. Pixel level percent difference and distribution for Lonsdorf nest abundance index (Lonsdorf et al. 2011) when comparing **a** FLP 1 with switchgrass to NLM 1 with switchgrass, **b** FLP 2 with prairie to NLM 2 with prairie, and **c** FLP 3 with willow to NLM 3 with willow

important to NAI at the regional level (i.e., across the Indian Creek watershed), but is important at the fine scale. The greater variability in pixel-level NAI for FLPs than for NLMs (Table 2; Fig. 5) indicates that configuration is important at the local level (i.e., at the scale of 10 s or 100 s of meters), a finding that is consistent with empirical studies in German agricultural fields, where wild bee abundance decreased with the distance of the field to semi-natural grasslands (Jauker et al. 2009). The impact of landscape configuration is thus a scale-dependent phenomenon—at the scale of a 50 or 100 ha field, the presence or absence of

nearby PBC is an important factor to nest abundance. However, at the scale of the landscape, the Lonsdorf model indicates that the specific arrangement of PBC is relatively unimportant to the overall impact on nest abundance. This result has implications for pollination services provided by wild bees to individual farmers and for the overall impact of PBC on bee nest abundance and diversity. If policies are intended to maximize pollination services across a landscape, then distributing PBC throughout the entire area will be necessary. In contrast, if policies are intended to enhance wild bee abundance or diversity, irrespective of pollination services, then the spatial distribution of PBC will be less critical. However, farmers may prefer to plant PBC in different configurations than those modeled by the FLPs. For instance, in a prior workshop in the Indian Creek watershed, farmers indicated that they tend to prefer managing whole fields under one management regime rather than subfields, like those represented in the FLPs (Graham 2016). As such, comparing the effects of entire-field PBC plantings with the effects of subfield PBC planting (as in the FLP) may show different results and should be explored further.

Model limitations, future research, and management implications

There are several important caveats to our findings. First, the model assumes that the bee species included in the simulation are currently present in the landscape or have the potential to disperse into the region. The Indian Creek watershed has been subjected to many decades of intensive agriculture, and now ~90% of the watershed is in agricultural land use. Wild bee visitation rates have been shown to be lower when there is less natural or semi-natural habitat in the surrounding landscape (Klein et al. 2012) and other studies of bee populations in the Corn Belt have shown that bee diversity is lower when maize and soy compose a greater portion of the surrounding landscape (Ridgeway et al. 2015). Possibly, few bee species remain in the landscape, and consequently, few species would be able to disperse into the landscape. Therefore, our model results should be taken as an estimate of what the different landscapes could provide, not what they necessarily would provide if PBC were developed in the watershed. Similarly, the model results indicate the relative

effects of crop composition, area, and configuration on a nest abundance index, not the actual effects of a real landscape on bees. However, in studies that have reported reductions in bee abundance or diversity with increasing agricultural intensification, bees were still found to be present in the landscape, even in relatively small PBC plantings in an otherwise agricultural landscape (Ridgeway et al. 2015). We recommend that future studies evaluate the current wild bee richness and diversity in the region, in order to better predict the effects of current conditions and bee populations.

A second caveat is that the Lonsdorf model does not directly evaluate bee mortality. If management techniques for either maize/soybeans or PBC include use of pesticides or herbicides, there may be high bee mortality. In the worst case, PBC patches could potentially function as population sinks, attracting bees from more protected areas but then exposing them to biocides. Systemic pesticides, such as neonicotinoids, that are currently widely used as seed treatments (Douglas and Tooker 2015) have been found to have lethal and sub-lethal effects on honeybees (Chensheng et al. 2014) and presumably wild bees as well. These pesticides are quite persistent in the landscape and have the potential of concentrating in bee nests, causing eventual colony death or hive abandonment (Chensheng et al. 2014; Sanchez-Bayo 2014). For herbicides or pesticides that are sprayed at ground level, incorporating 20' spray buffers can ameliorate some of the impacts on wild bees (Bentrup 2008). Efforts to enhance habitat for bees or other pollinators should consider the potential effects of biocides and should be combined with efforts to reduce the use of biocides or mitigate their effects. We recommend that future research evaluate the specific effects of biocides on wild bees in a PBC landscape and that future revisions to the Lonsdorf model consider the possibility of including a measure of mortality.

Finally, the current version of the Lonsdorf model does not incorporate behavioral patterns or preferences of bees in their foraging behavior. Unlike other pollinators including hoverflies (Jauker et al. 2009), bees are “central-place foragers” (Olsson et al. 2015), foraging across the landscape and then returning with pollen and nectar to a central nest location. In the Lonsdorf model, bees are assumed to diffuse across the landscape based solely on foraging distances and pixel-level floral resources, though the model does give more weight to floral resources that are closer to

the pixel being evaluated. In reality, bees exhibit some degree of preference, selecting floral patches based on landscape context and neighboring floral resources (e.g., Steffan-Dewenter et al. 2002; Heard et al. 2007; Olsson et al. 2015). This behavior, according to Olsson et al. (2015), may explain why the visitation index provided by the Lonsdorf model does not perform as well in complex landscapes. To account for landscape complexities, they developed a revised model that incorporates central-place foraging theory by assessing loading capacity, travel time, and harvesting rate to determine the metabolic costs of foraging and relative patch quality (Olsson et al. 2015). Although their revised model may improve predictions of pollination services in complex landscapes, the additional required inputs (e.g., loading capacity measurements for each bee species) may be difficult to determine or may involve complex calibration for each species. The revised model is not yet widely available, but we recommend that it be included in future editions of the InVEST package. For research that seeks to evaluate bee visitation across a landscape (i.e., pollination services), a central-place foraging model would provide a more accurate picture of bee behavior than does the Lonsdorf visiting index. However, the Lonsdorf and Olsson models are similar in their prediction of nesting behavior. Thus, for investigations related to bee conservation, the Lonsdorf NAI provides a reasonable estimate of overall habitat quality of the landscape.

Summary

The results of our modeling study suggest that perennial bioenergy cropping systems could be effective strategies to promote wild bee populations. Additional modeling techniques and revisions to the Lonsdorf model (e.g., Olsson et al. 2015) may provide more precise estimates of bee abundance, and we recommend further analysis with these revisions to InVEST. In light of international efforts to develop a pollinator corridor in the Mississippi River basin (Pollinator Health Task Force 2015), developing PBC that support wild bees is an important endeavor. Our modeling results indicate that, although the configuration of PBC is important to bee nest abundance at the fine scale, it is less important at the regional scale, unless the goal is to maximize pollination services

across the entire landscape. At the regional scale, the composition of bioenergy crops and the amount of PBC habitat are important considerations for the effects on wild bees, with diverse plantings (e.g., prairie) being particularly valuable for wild bees. As such, we recommend further research into the effects on wild bees of using different bioenergy crops, including more diverse, realistic combinations of multiple bioenergy crops. We also recommend research into the effects of different landscape configurations, such as those resulting from entire-field PBC planting strategies in contrast to the subfield plantings represented by the FLPs.

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