

Complementary habitat use by wild bees in agro-natural landscapes

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Abstract. Human activity causes abrupt changes in resource availability across the landscape. In order to persist in human-altered landscapes organisms need to shift their habitat use accordingly. Little is known about the mechanisms by which whole communities persist in human-altered landscapes, including the role of complementary habitat use. We define complementary habitat use as the use of different habitats at different times by the same group of species during the course of their activity period. We hypothesize that complementary habitat use is a mechanism through which native bee species persist in human-altered landscapes. To test this idea, we studied wild bee communities in agro-natural landscapes and explored their community-level patterns of habitat and resource use over space and time. The study was conducted in six agro-natural landscapes in the eastern United States, each containing three main bee habitat types (natural habitat, agricultural fields, and old fields). Each of the three habitats exhibited a unique seasonal pattern in amount, diversity, and composition of floral resources, and together they created phenological complementarity in foraging resources for bees. Individual bee species as well as the bee community responded to these spatiotemporal patterns in floral availability and exhibited a parallel pattern of complementary habitat use. The majority of wild bee species, including all the main crop visitors, used fallow areas within crops early in the season, shifted to crops in mid-season, and used old-field habitats later in the season. The natural-forest habitat supported very limited number of bees, mostly visitors of non-crop plants. Old fields are thus an important feature in these arable landscapes for maintaining crop pollination services. Our study provides a detailed examination of how shifts in habitat and resource use may enable bees to persist in highly dynamic agro-natural landscapes, and points to the need for a broad cross-habitat perspective in managing these landscapes.

Key words: agriculture; agro-natural landscape; Apoidea; bees; complementarity; deciduous forest; habitat use; old fields; pollination.

INTRODUCTION

Agriculture is globally the major form of anthropogenic land use and the leading cause of habitat conversion and fragmentation (Defries et al. 2004). Agricultural landscapes have changed over time due to increases in the area of crop habitat, fragmentation of remaining natural areas, and regeneration of natural vegetation on abandoned farmland (MEA 2005). Past research has demonstrated that the abundance of ecosystem service-providers within agricultural patches is affected by the area of seminatural habitats in the surrounding landscape (Tscharntke et al. 2005), and that many taxa appear to persist well in non-intensively agricultural landscapes (Daily et al. 2001, Mayfield and Daily 2005, Tscharntke et al. 2005). However, few studies have examined the mechanisms allowing species to persist in agricultural landscapes (Mendenhall et al. 2011). Movement of organisms between habitats over

time to track changing resources across the landscape is a mechanism that may enhance species persistence in agricultural landscapes, as demonstrated for natural enemies and pests moving between crop and non-crop depending on resource availability and needs (Duelli et al. 1990, Wissinger 1997, Tscharntke et al. 2007). However this mechanism is as yet little explored for other functionally important organisms, especially for maintaining their diversity in agricultural landscapes. Understanding how species move between habitats over time could provide a more complete and mechanistic understanding of how landscape structure affects key organisms, allowing us to manage landscapes to conserve them.

Habitats differ in their temporal distribution of resources for consumers. Agricultural landscapes are mosaics of crop and seminatural patches (Westphal et al. 2003). As a consequence of different plant species with different phenologies, there are significant temporal shifts in the amount and diversity of resources provided through the growing season (Tscharntke et al. 2005). Crops provide “pulsed” resources during short periods

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after planting and before harvest, while less managed seminatural and natural habitats display more gradual seasonal changes in phenology of the flora. As a result, no single habitat may provide all the resources that a species needs to persist. Instead, mobile organisms may move between habitats, tracking shifting resources as they become sequentially available in them. Hence, different habitats may provide resources that are “complementary” in time. Such complementarity would provide a mechanism that could explain observations of species occurrence in fragmented landscapes (Daily et al. 2001, Mayfield and Daily 2005, Cane et al. 2006) and their spatiotemporal abundance patterns (Lonsdorf et al. 2009). Previous studies acknowledge that many plant and animal species utilize resources in the natural habitats as well as the cultivated and otherwise disturbed areas in agricultural landscapes (e.g., Daily et al. 2001, Mayfield and Daily 2005). However, these studies are mostly describing patterns of species occurrence, and few as yet delve into the mechanism that promotes species persistence in agricultural landscapes and shapes their diversity patterns (Mendenhall et al. 2011). Hence, despite the potential role of complementary habitat and resource use in maintaining biodiversity in agro-natural landscapes, it is largely unexplored.

Bees provide an important service by pollinating wild plants (Ashman et al. 2004, Ollerton et al. 2011) and crops (Free 1993, Klein et al. 2007), worth billions of dollars per year (Gallai et al. 2009). Species-rich communities of wild bees in agricultural landscapes provide a higher magnitude (Klein et al. 2003, 2009, Hoehn et al. 2008) and stability (Garibaldi et al. 2011) of pollination services; hence it is important to explore mechanisms that may facilitate their persistence in agricultural landscapes. Bees are relatively mobile organisms and are thus affected by both local and landscape scale land-use practices (Kremen et al. 2007, Ricketts et al. 2008, Winfree et al. 2009, Williams et al. 2010). They are central place foragers that disperse from their nests to gather floral resources from the surrounding landscape and change resource use based on floral resource levels (Westrich 1996, Williams and Kremen 2007, Pitts-Singer and James 2008). As floral resources show different temporal availabilities in different crop and natural habitats, we hypothesize that bee communities may persist in the agricultural landscape by moving between different habitats to access floral and nesting resources. Bee communities may thus serve as an important model taxon for studying the role of complementary habitat use as a mechanism for persistence in fragmented agricultural landscapes. Few studies have examined how bees use the different habitats across agricultural landscapes throughout a growing season. Past studies have shown correlations between bee abundance and diversity within fields and the distance to or area of key habitats in the surrounding landscape (e.g., Klein et al. 2003, Kremen et al. 2004, Ricketts et al. 2004) or compared bee diversity patterns between

habitats using data taken across the flight season (e.g., Winfree et al. 2007a). Little information exists, however, on whether bees shift over space and time to track resources among habitats within the agro-natural landscape mosaic (Klein et al. 2007).

We explore seasonal and spatial patterns in habitat and resource use of wild bee communities to test whether complementary habitat use, defined here as the use of different habitats at different times by the same group of species during the course of their activity season, may be a mechanism facilitating bees' occurrence in agricultural landscapes. Specifically, we test whether complementarity in floral resource availability among habitats may be contributing to bees' occurrence. Additionally, we test how spatiotemporal resolution of habitat use data, i.e., data accumulated across the season vs. divided among spatiotemporal replicates, influences the conclusions drawn on relative importance of habitats for species occurrence in agricultural landscapes. Finally, we explore the conservation implications of our results for bee communities as a whole and for crop-visiting species in particular.

MATERIALS AND METHODS

Study system and design

The study was conducted in an approximately 53×73 km area of central New Jersey and eastern Pennsylvania, USA, where previous studies have shown that wild bees may have considerable economic value by pollinating a variety of crops and in some cases exceed the contribution of managed honey bees to crop pollination (Winfree et al. 2007b, 2008, 2011). This region is highly modified and fragmented, comprising a mosaic of native habitat (temperate deciduous forest), active agricultural fields, abandoned agricultural fields (old fields), and built-up areas (mainly suburban). We used a block design consisting of 18 plots total arranged into 6 blocks, each of which contained three habitat types: natural woodland habitat, active agricultural field, and old field. These are dominant land use types expected to be important bee habitats in the area (Winfree et al. 2007a). Plots (1 ha in size) of each habitat type within a block were 80–1500 m apart (mean 1 km distance). This is within foraging distance of many wild bee species in the region (Greenleaf et al. 2007; Fig. 1) and was expected to permit bees to track resources present in different habitat types across their activity season. Replicate block distances were 15–72 km (mean 40 km) apart, beyond foraging distance of these wild bees. The block design allowed us to compare bee diversity patterns among the three habitat types while controlling for landscape context (see Appendix A for description of landscape characteristics). To choose habitat plots within a block, we first chose an agriculture field sufficiently large to contain our 1-ha plot, and next located the closest forest (temperate deciduous forest) and old field that were also at least 1 ha in size. Within each of these habitats we positioned our sampling plot at

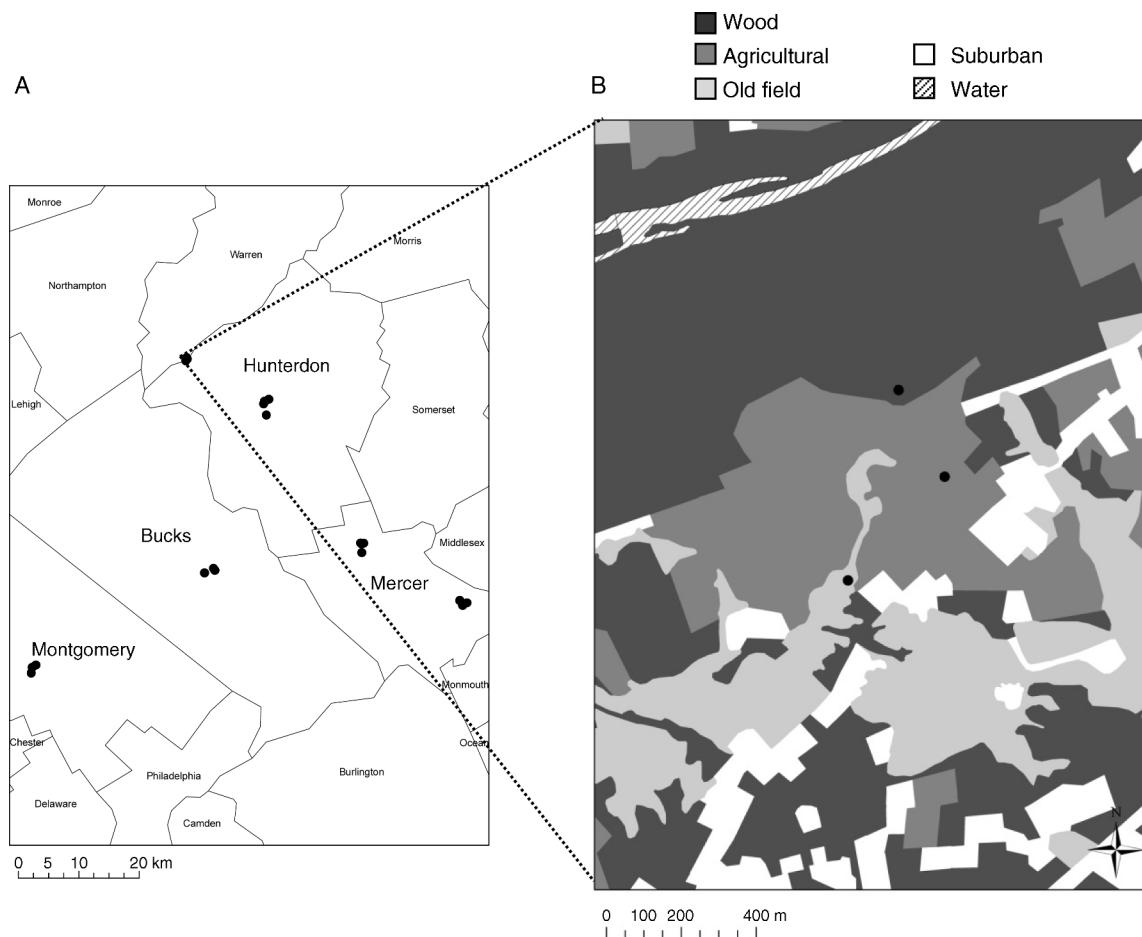


FIG. 1. Study region showing (A) six blocks, three plots in each, in four counties in eastern New Jersey (Mercer, Hunterdon) and western Pennsylvania (Bucks, Montgomery), USA, and (B) a close-up on one of the blocks, showing the three study plots (black dots) and the surrounding landscape.

the side closest to the agriculture field, 30–40 m from the edge to minimize edge effects on microclimatic conditions and vegetation, after visually surveying a larger area to make sure our sampling point was representative of the patch.

A standard set of criteria was established to select plots of a particular habitat type (agriculture, forest, or old fields) so that they were as similar to one another as possible and yet representative of the larger landscape. For the agricultural plots our criteria were that they include a variety of insect-pollinated vegetable crops typical of the region including Cucurbitaceae and Solanaceae. Accordingly, we subdivided the agricultural plots into three subplots: Cucurbitaceae (watermelon and pumpkin; ~45% of total plot area), Solanaceae (cherry tomatoes; ~45% of total plot area), and fallow containing a variety of weedy flowers (patches of land rested from crop production for 1–2 years, narrow strips of weedy vegetation between crops, and hedges around the farm; ~10% of total plot area). Within each farm the

three subplots were in close proximity to each other (up to ~30 m apart). All farms studied were conventionally managed.

Old fields in the study region varied in their land-use history (mainly former crop or hay fields), age (years since last cultivated), and management (frequency of mowing, mainly 1–2 times/year). To be chosen as old-fields habitats, plots needed to be formerly crop (two plots) or hay (four plots) fields, mowed 1–2 times a year, and >2 ha and at least 75 m wide, to reduce edge effects. Selected old-fields plots had not been cultivated for 2–16 years (mean 6.6 years).

The natural habitats in the region were second growth deciduous forests with well-developed closed canopies and understory at variable heights and densities. We selected natural habitat plots that were >2 ha and at least 75 m wide. Selected forest plots were of variable understory cover and diversity (understory perennial cover, 6–30% of total plot area, 2–11 species; understory annual cover, 1–18% of total plot area, 2–8 species).

Data collection

We sampled bees and floral resources from mid-May until mid-September in 2005, in four sampling rounds, about 4–5 weeks apart (spring, mid-May; early summer, late June–early July; late summer, mid-August; autumn, mid-September). Because woods are the main habitat known to provide early spring bloom in our region (Westwood 2006), in early spring of 2006 (mid-April, beginning of the bloom in woods that year) we resampled bees and floral resources in the natural habitat plots only to better assess early spring bee species and floral availability. Compared with the 2006 data, we found the 2005 sampling to be representative of the bee fauna and of the floral resources available in the natural habitat plots (using measures of abundance and species richness; see details in Appendix B) and therefore utilize only the 2005 data in this study.

Bee sampling.—Bees were sampled using standardized netting and observations. Because netting and observational abundance data were highly correlated ($r^2 = 0.9$, $n = 18$, $P = 0.01$), we report here only the netting data and analyses because they provide greater precision regarding taxonomic identity (see details on bee observations in Appendix C). All three habitat types in each block were sampled by netting during a single day. The order of plot sampling in each day was randomly set. Bee sampling took place only during sunny, partially cloudy, or bright overcast days (ranging between 0 for completely clear skies, up to 10 for complete bright overcast), with wind velocity of < 2.5 m/s, and air temperature $> 15^\circ\text{C}$ in the beginning of the season (May) and between 18° and 34°C for the rest of the study. In each sampling round, bees were netted for a total of 1 h in each plot, 30 min in the morning and 30 min in the early afternoon, to account for variation in bee activity through the day. Netting was done while systematically surveying the entire plot area. The clock was stopped while bees were being transferred from the net to a kill jar. We define “wild bees” as unmanaged (non-*Apis*) bees and excluded honey bees from our analysis because when found, they are generally from managed hives.

Plant sampling.—We recorded species richness and relative abundance of blooming plants along transects using the line intercept method (Bullock 1996); the identity and number of all flowers intersecting the transects were recorded. In the old-field and natural plots we used three 50-m transects. The starting point of the first transect was randomized along the plot perimeter and two additional transects were evenly spaced. All transects started at least 5 m from the edge of the habitat patch, in order to standardize with respect to edge effects. In the agriculture plots, a 68-m transect was set in each of the Cucurbitaceae and the Solanaceae subplots, and a 15-m transect was set in the uncultivated subplot, following the ratio between the area of these three subplots. Floral sampling effort was determined in a preliminary study at the beginning of the season using asymptotic species richness and total abundance. For

analyses, floral richness and abundance were totaled across the three transects in each plot.

Statistical analysis

Bee richness and abundance.—We first applied the commonly used cross-season approach (cumulating data obtained in each habitat across the season) to evaluate the overall importance of the different habitats to wild bees and to compare it to the results we obtain when examining each spatiotemporal replicate separately to assess complementary habitat use across time. We used ANOVA and LSD tests to compare overall bee abundance and species richness between habitats.

Next, we conducted detailed spatiotemporal analyses of species richness and abundance of wild bees and floral resources across the landscape. We analyzed bee richness and abundance patterns using linear mixed-model analysis (SPSS statistics version 17.0; IBM, Somers, New York, USA) in which habitat type and sampling date were used as main factors, block as a random factor, species richness and abundance of blooming plants and daily weather conditions in each sampling plot (air temperature, wind velocity, and cloud cover) as covariates, and species richness and abundance of wild bees as dependent factors. Individual subjects of the repeated measurements were the plots within each of the six blocks (18 plots in total). In all analyses bee abundance and species richness were square-root transformed to achieve normality and homogeneity of variances. The goal of this analysis is to explore how bees' species richness and abundance change in space and time across the landscape and whether these patterns are significantly related to floral availability; a significant interaction between habitats and sampling dates coupled with a significant effect of the floral covariates would suggest that bees are tracking resources that vary in space and time, i.e., exhibiting a complementary habitat use.

Bee assemblages.—Complementary habitat use means that the same assemblage of species changes its distribution of habitat use over the course of the season. Hence, showing complementarity in bee species composition requires demonstrating that the same bee assemblage is using the different habitats (habitats share a common pool of bee species), and that bee species change their habitat use, i.e., change their abundances in different habitats, along the activity season. We thus conducted multiple regression analyses on bee distance (dissimilarity) matrices (MRM; Lichstein 2007) to statistically test the factors that might affect wild bee community composition. MRM is analogous to a Mantel test in which a response matrix (here, differences in bee species composition) is regressed on explanatory matrices; however with MRM, unlike the Mantel test, the significance of each explanatory variable as well as their interactions can be assessed. We used the ecodist package (Goslee and Urban 2007) for R (R Develop-

ment Core Team 2005) and calculated significance values by permutation (Lichstein 2007).

We conducted two MRM analyses. In the first, we were interested in identifying the extent of overlap in bee assemblages in the three habitats accumulated across the activity season. Because we expected bee abundances to vary considerably between habitats and sampling dates and we wanted to focus first on the identities of bee species, we conducted the first MRM using the Jaccard measure for presence-absence data (Magurran 2004), combining all samples from each plot over all sampling dates. We regressed the bee composition matrix with a habitat matrix in which pairs of samples of the same habitat were coded as 0, pairs of samples of agriculture and old field were coded as 1, and pairs of samples of wood and agriculture or old field were coded as 2, based on our empirical impression of the differences between these vegetation types.

Next, we wanted to test how bee assemblages change between habitats over the season. We thus conducted a second MRM analysis incorporating both species identities and their abundances using the Bray-Curtis (Sorensen) distance measure (Faith et al. 1987, Magurran 2004), considering each plot in each sampling round as a sample. We hypothesize that if complementary habitat use was taking place, different habitats should largely overlap in bee composition when compiling occurrence (presence-absence) data accumulated over the whole season (the first MRM). However, differences between habitats would appear when considering abundances of bee species in each plot in each sampling round, because the bee assemblage is shifting its habitat use along the season (the second MRM). Accordingly, there should be a habitat-season interaction in bee composition. In the second MRM we related the bee dissimilarity matrix (Bray-Curtis measure) to matrices containing the absolute values of inter-sample differences of the following variables: habitat type (using the same coding as in the first MRM), the time along the season (represented by days elapsed from the start of the first sampling), blooming plant species richness, overall abundance of bee-visited flowers, and blooming plant species composition (using the Bray-Curtis measure) in each plot and sampling date. We added a habitat-season interaction term. We selected variables for inclusion in the final model on the basis of forward and backward stepwise variable selection using the stepAIC function in R; because the procedure tends to be overly permissive (inclusion of nonsignificant variables in the model; Venables and Ripley 2002), we manually removed nonsignificant variables from the final model. Significance values were calculated from 10 000 permutations.

To visualize the results of the MRM analyses we used nonmetric multidimensional scaling (NMDS; PC-ORD version 5; MjM Software, Gleneden Beach, Oregon, USA). NMDS is used to find and graphically display the configuration of an ordination space in which distances between samples best represent pairwise dissimilarities in

species composition in a reduced number of dimensions (Clarke 1993, Leps and Smilauer 2003). We used the Bray-Curtis measure, considering each plot in each sampling round as a sample. We hypothesize that if complementary habitat use was taking place, the different habitats should exhibit differential separation along the bee activity season and show a habitat-season interaction when considering abundances.

Floral richness, abundance, and composition.—Blooming plants' species richness and abundance were analyzed using ANOVA with repeated measures (SPSS statistics version 17.0; IBM, Somers, New York, USA) in which habitat type and sampling date were used as main factors, block as a random factor, and species richness and abundance of blooming plants as dependent factors. In addition we explored how the availability of floral resources was distributed between crop and uncultivated area within the agricultural field along bees' activity season. We conducted an MRM analysis to relate vegetation composition to habitat, season (using the same coding as used for the bee analyses), and their interaction. As before, significance values were calculated from 10 000 permutations. The goal of these analyses is to explore how the amount, richness, and composition of foraging resources change in space and time across the landscape; a significant interaction between habitats and sampling dates would point to complementary resource availability along bees' activity season.

RESULTS

In total we netted 1999 wild bees of 93 species/morpho-species (84 identified to species; see Appendix D for complete species list).

Bee richness and abundance

Overall wild bee abundance and species richness was highest in old fields and lowest in woods. Abundance values (number of bees, mean \pm SE) were as follows: agriculture 30.62 ± 3.72 , old field 47.71 ± 9.01 , wood 4.5 ± 1.22 ($F_{2,15} = 11.3$, $P = 0.001$; agriculture-old-field, $P = 0.08$; agriculture-wood, $P = 0.01$; old-field-wood, $P < 0.001$). Species richness values (number of species, mean \pm SE) were as follows: agriculture 7.37 ± 0.62 , old-field 10.92 ± 1.4 , wood 2.25 ± 0.62 ($F_{2,15} = 50.8$, $P < 0.001$; agriculture-old-field, $P = 0.01$; agriculture-wood and old-field-wood, $P < 0.001$).

Wild bee abundance was significantly affected by season, habitat type, and the interaction between the two factors, as well as by the abundance of blooming plants (Table 1). Wild bee species richness was significantly affected by season, habitat type, and the interaction between the two factors as well as by cloud cover, but not by abundance or species richness of blooming plants (Table 1). Wild bee species richness and abundance in the woods were low throughout the season and decreased gradually during the activity season (Fig. 2A, B, respectively), similar to the patterns observed in species richness and abundance of floral resources (Fig.

TABLE 1. Results of the linear mixed model for the effect of season, habitat type, abundance, and richness of blooming plants and weather conditions (air temperature, wind velocity, and cloud cover) on wild bee abundance and species richness in four counties in eastern New Jersey and western Pennsylvania, USA.

Model parameters	Wild bee abundance			Wild bee species richness		
	df	F	P	df	F	P
Season	3	6.01	0.002	3	10.91	<0.001
Habitat	2	6.03	0.006	2	7.07	0.003
Season × habitat	6	4.89	0.001	6	6.16	<0.001
Blooming plant abundance	1	10.7	0.002	1	2.72	0.11
Blooming plant richness	1	2.13	0.15	1	1.12	0.3
Air temperature	1	2.89	0.1	1	2.21	0.14
Wind velocity	1	0.59	0.45	1	0.51	0.48
Cloud cover	1	1	0.32	1	4.7	0.036

2C, D respectively). The agriculture habitat maintained a similar level of species richness throughout the season, but abundances peaked in late summer (August) and decreased sharply in autumn. In the agricultural habitat all wild bees sampled in the spring were in the uncultivated area. In early and late summer wild bees were found mostly on crops (90–95%), while in the autumn 78% of wild bees were sampled off crops and the rest were sampled in the uncultivated area (a much greater amount relative to the sampling effort of 10% invested in the uncultivated subplots compared to the total sampling effort in the agricultural plots). In all samples wild bee species richness was higher in the uncultivated area compared to crops. In old-fields, both

wild bee richness and abundance increased from spring to early summer (June–July) followed by a decrease in autumn. The majority of wild bee species were sampled in more than one habitat; 75%, 63%, and 66% of species sampled in agriculture, old fields, and woods respectively, were also sampled in other habitats.

We found 48 wild bee species visiting crop flowers and potentially contributing to their pollination (see Appendix D). Of the nine most abundant crop visiting bee species (≥ 15 individuals), eight were found in other habitats in addition to agriculture, mainly in old fields, and foraged on numerous plant species in addition to crop flowers (20 ± 3.5 wild flower species per bee species on average, based on netting data). *Peponapis pruinosa*,

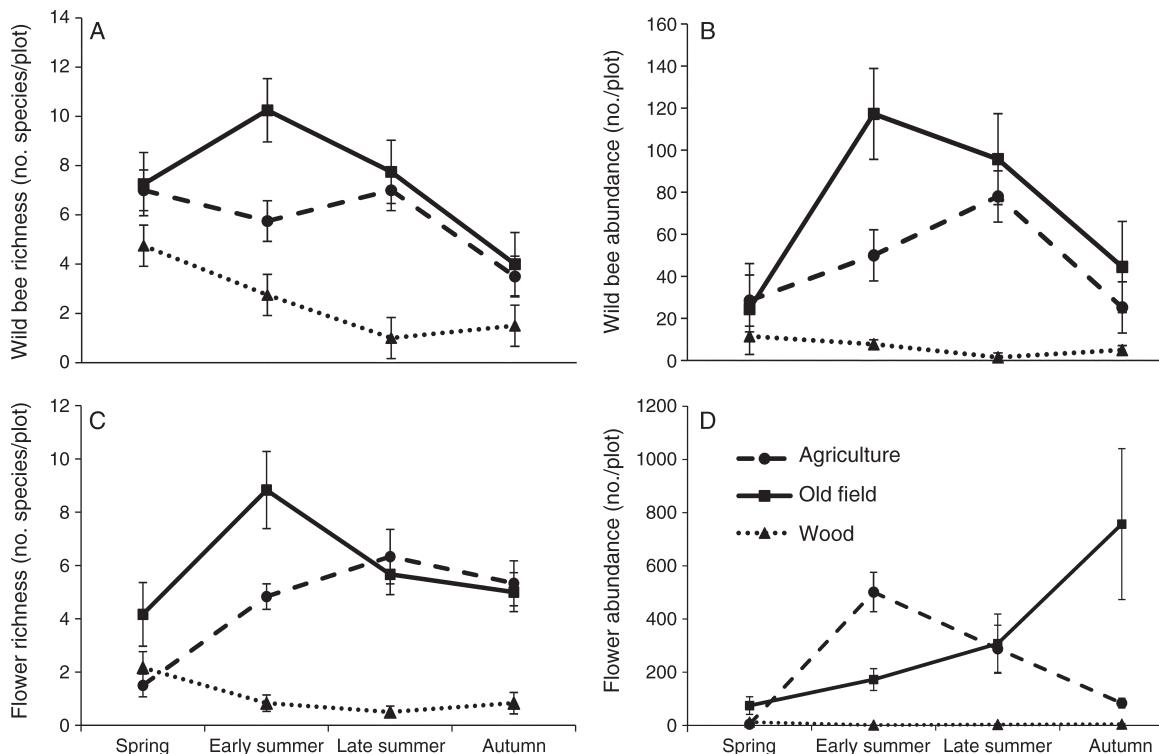


FIG. 2. Seasonal patterns in (A) wild bee species richness, (B) wild bee abundance, (C) blooming plants species richness, and (D) flower abundance. Data are means \pm SE.

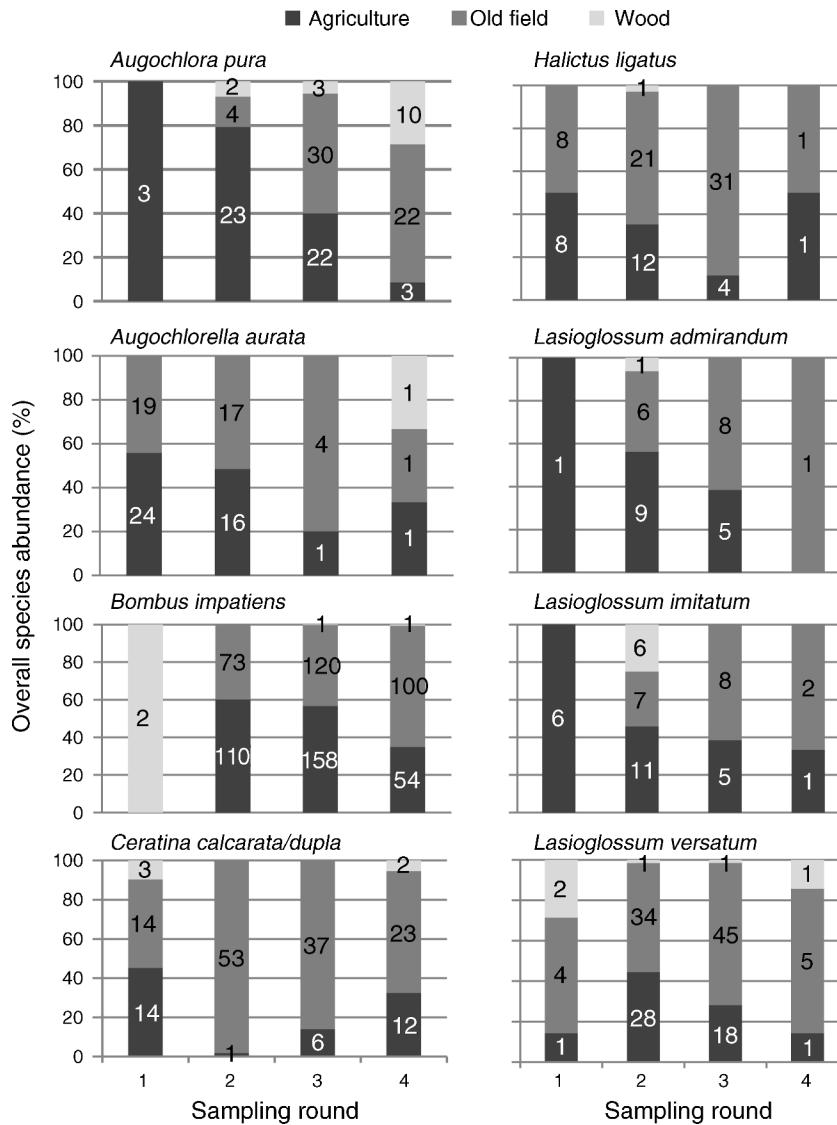


FIG. 3. Shifts in habitat use along the season of the eight most abundant crop visitors with at least 15 individuals visiting crop flowers (excluding *Peponapis pruinosa*, which was found exclusively on pumpkin flowers). Numbers in the bars represent the number of individuals sampled in each habitat along the season. Sampling rounds are as in Fig. 2 (spring, early summer, late summer, autumn).

a specialist on pumpkin, was the only species found exclusively on crop flowers (pumpkin). The eight most abundant crop visiting species (excluding *P. pruinosa*) were found in all four sampling rounds (i.e., May–September; Fig. 3), and when considered across their entire distribution range have a long flight season spanning on average 7.6 months from early spring to autumn (March–October; based on Discover Life database; *available online*).⁵ For all eight species, woods accounted for an average of only 4.8% of all individuals sampled and with no clear seasonal pattern across species, e.g., *Bombus impatiens* used woods mostly in the

beginning of the season while *Augochlora pura* used woods more toward the end of the season (Fig. 3). For all species except *Ceratina calcarata/dupla* there was a trend toward increased use of old fields and reduced use of agriculture as the season progressed, though this is qualified by the fact that abundances at the end of the season were often very low (Fig. 3). For *C. calcarata/dupla* old fields were almost exclusively used in the summer, while at the beginning and end of the season there was some use of the agriculture habitat as well.

Bee assemblages

We found no significant effect of habitat on bee composition using presence–absence data accumulated

⁵ www.discoverlife.org

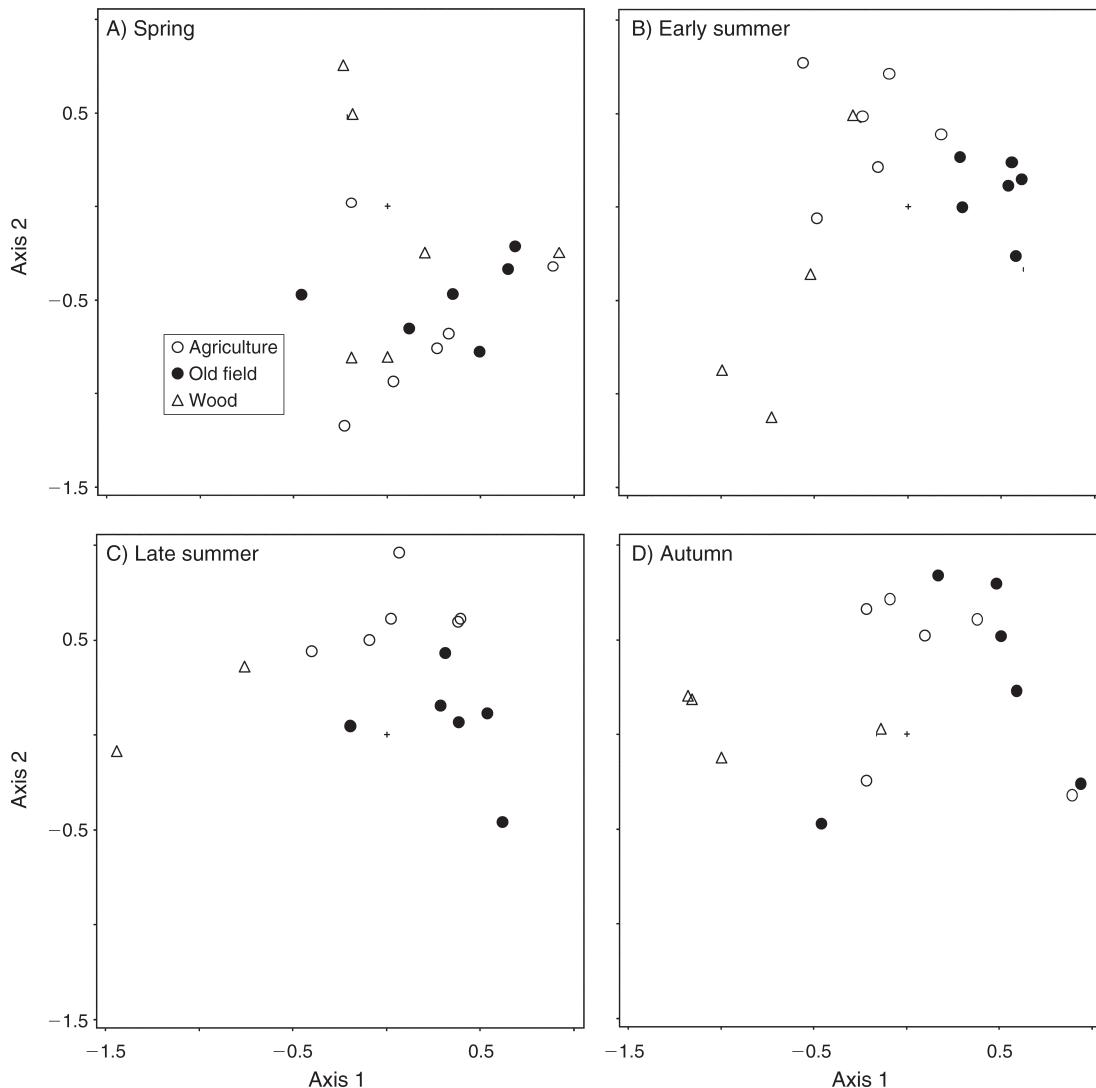


FIG. 4. Nonmetric multidimensional scaling ordination of wild bee species using the Bray-Curtis similarity measure on detailed spatiotemporal abundance data, separated by four seasons.

across the season (MRM; $P = 0.63$), i.e., the three habitats overlapped in their overall bee assemblage. In contrast, when using abundance data for each plot and sample replicate, there were highly significant ($P \leq 0.0001$) relationships between bee community composition and habitat type ($\beta = 0.084$; β is the rate of change of one matrix with respect to the other matrix), season ($\beta = 0.0013$), habitat–season interaction ($\beta = 0.00059$), floral abundance ($\beta = 0.00012$), and plant composition ($\beta = 0.17$). The MRM model explained 30% of the variation in bee community composition.

Similarly, the NMDS demonstrated a habitat–season interaction in bee composition; in season 1 and to some extent season 4 there was no clear separation between the three habitats (Fig. 4A, D, respectively), while in season 2 and 3 the three habitats, and especially the old fields and agriculture, were separable (Fig. 4B, C,

respectively). The agriculture and old fields were more closely related in their bee composition compared to the woods, which exhibited higher beta diversity (turnover rates in species composition between sites) throughout. Two dimensions were selected, the stress (the overall fit of the ordination, which is inversely related to the match between the dissimilarity indices and the distance in the ordination between pairs of sites [McCune and Grace 2002]) was 18.05, and the instability was 0.0006 (instability is the variation in the stress measure between subsequent runs of the ordination algorithm; low instability values of around 10^{-4} indicate higher confidence in the stress measure).

Floral richness, abundance, and composition

Species richness and abundance of blooming plants were significantly affected by season, habitat type, and

TABLE 2. Results of the ANOVA with repeated measures for the effect of season, habitat type, block, and the interaction between them on blooming plants abundance and species richness.

Model parameters	Floral abundance			Floral species richness		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Season	3, 15	4.07	0.027	3, 15	5.65	0.009
Habitat	2, 10	6.13	0.018	2, 10	34.86	<0.001
Season × habitat	6	8.34	<0.001	6	6.43	<0.001
Block	5, 30	38.82	0.002	5, 30	107.59	<0.001

the interaction between the two factors, as well as the block (Table 2). The two main habitats offering floral resources were agriculture and old fields, while the native vegetation type, woods, provided a very limited amount and richness of blooming plants throughout the season (Fig. 2C, D). Agriculture and old fields had similar patterns of floral species richness through the season, with highest richness in the summer. However, the two habitats differed in the amount of foraging resources they provided through the season, with a continuous increase in floral abundance in old fields and a sharp increase in late season contributed mainly by *Solidago* spp. (accounting for 96% of overall floral resource in old fields in the autumn) compared to a peak in floral abundance in early summer and a sharp decrease afterwards in the agricultural fields (Fig. 2D). In early summer, agricultural fields provided the highest amount of floral resources while in the autumn old fields provided the highest amount.

We found a strong shift in the distribution of floral resources between the crop and the uncultivated area within agricultural fields along the season. The uncultivated area accounted for 100%, $3\% \pm 0.9\%$, $33\% \pm 6\%$, and $52\% \pm 10\%$ of overall floral resources in the agricultural fields in the spring, early summer, late summer, and autumn, respectively. Because only 10% of the total sampling effort in the agricultural plots was invested in the uncultivated subplot, these figures are considerably above expected, except in early summer. In all samples floral species richness was higher in the uncultivated area compared to crops.

The MRM model of vegetation composition included highly significant ($P \leq 0.0001$) relationships between vegetation composition and habitat ($\beta = 0.079$), season ($\beta = 0.0012$), and their interaction ($\beta = -0.00075$). The MRM model explained 15% of the variation in vegetation composition.

DISCUSSION

Each of the three habitats comprised by arable landscapes (agricultural fields, old fields, and woodlands) exhibited a unique seasonal dynamic in amount, diversity, and composition of floral resources, and together they created phenological complementarity in foraging resources available for bees across the agromat landscape. Bees responded to these seasonal patterns in floral resources and exhibited a parallel pattern of complementary habitat use evident at both

the species and the community level. In light of the high overlap between habitats in cross-season bee assemblages and the fact that plots representing different habitats were in close proximity to each other (1 km on average), the alternative hypothesis that bee communities in each of the three habitats within a block were independent of each other is unlikely. Instead, the highly similar set of bee species in the agriculture, old fields, and woods used the three habitats differently along the season. The anthropogenic habitats (agricultural fields and old fields) were used complementarily by the majority of wild bee species in the studied ecosystem, while the natural habitat supported a very limited number of bees, and these were mostly not pollinators of crops. Hence, for maintaining crop pollination, old fields are an important feature in arable landscapes.

When bee communities are summed over time, agriculture and old fields have highly similar sets of bee species. However, the extent of use of each of these habitats by specific bee species and by the bee community as a whole, changed through the season. In the beginning of the season bees were more closely associated with the agriculture habitat, and as the season progressed, there was a gradual shift in habitat use toward old fields, as evident from the species-specific patterns of crop visitors. These patterns were associated with concurrent changes in blooming plants' species richness, abundance, and composition in the two habitats along the season. Floral resource availability is considered a major driving force that directly regulates the abundance and diversity of wild bees' communities (Potts et al. 2003, Roulston and Goodell 2011). We found a significant correlation between bee composition and floral abundance and composition along the activity season. This suggests that wild bees may be moving among habitats in the agro-natural landscape to track resources that varied in space and time. Hence the complementary habitat use may serve as a mechanism of surviving in this highly dynamic environment. Without detailed analysis of spatiotemporal resource and habitat use patterns this complementarity would be overlooked.

Old fields were found to be an important bee habitat in our region, for the bee community as a whole and for crop visiting bee species in particular. The eastern United States and the study region in particular is experiencing significant rates of land abandonment for over a decade (Hobbs and Cramer 2006). While in our study region old fields constitute a small proportion of

the total landscape (see Table A1 in Appendix A), they are well-distributed across the area and various small patches of old fields can be found throughout the landscape surrounding our study sites. Our old-field sites differed in their land-use history (crops vs. hay fields) and age since abandonment, major factors in shaping floral composition and early successional dynamics (Myer and Pickett 1990, Meiners et al. 2006). Despite this variation, the old-field sites consistently had the highest cross-season bee abundance and species richness compared to the nearby natural habitat and agricultural fields, suggesting that land-use history and successional stage (in ca. the first 16 years) have only secondary effects on the relative importance of old fields as habitats supporting many individuals and species of bees.

Old fields provided highest richness of floral resources in the spring and early summer, and highest amount of floral resources later on. The majority of bees in general, and of crop-visiting bee species in our study in particular, are polylectic and require a suite of pollen and nectar sources in order to survive (Westrich 1996, Cane 2001). Old fields may be crucial for the survival of these polylectic species in arable landscapes, as the agriculture fields and woods generally have low floral richness throughout much of bee activity season (at any given time). The abundant fall bloom in old fields (of mainly *Solidago* spp. typical in our study region; Ginsberg 1983, Meiners et al. 2006) provided the main foraging sources late in the season when other habitats are mostly devoid of blooming plants. This may be critical for the survival of multivoltine species and species with long flight seasons, such as the dominant crop visitors in our study. From a population point of view, fall resources will matter for *Bombus* queens and for solitary bees that are provisioning nests (collecting pollen), as found for most bees foraging on autumn bloom. In addition to providing foraging resources, old fields may also provide nesting sites and substrates, which may be limited in intensively managed farms (but see Klein et al. 2007, Kremen 2008 for instances where wild bees nest within agricultural fields). The highly similar bee assemblages found in the agricultural fields and the old fields suggest that the latter may be a main nesting source of crop-visiting bee species.

Crop plants provided ample foraging resources but only during the relatively short period of crop bloom in the summer. During the rest of the bee activity season, overall amounts of floral resources in the agricultural fields were limited but diverse, and found mostly in the uncultivated area within farms. Abundance of weedy flowers within farms was positively associated with abundance of solitary bees in the same study region and crops (Winfree et al. 2008). Bee activity within agriculture fields shifted from the uncultivated area in spring, to mostly crops in the summer, and to a combination of both crops and uncultivated area in autumn. Hence, the agriculture habitat is largely composed of two distinct and phenologically comple-

mentary microhabitats: crops and uncultivated land within a farm. The uncultivated land has an important role especially early in the season, by providing floral resources for bees before crops bloom, and also late in the season, when crop bloom decreases. Therefore the uncultivated area within farms should not be mowed until crop bloom starts and after crop bloom ends. Additional weedy habitats (early successional stage, defined as being weedy vegetation with <5% brush cover) and roadside area constitute only ~4% and 2% of the landscape in the study region, respectively (R. Winfree, unpublished data).

Woods may be an important source for early spring bloom in our region (Westwood 2006) utilized by some specialized bee species (Schemske et al. 1978, Ginsberg 1983). However, we found that woods were limited in their contribution to floral resources for crop-visiting bee species in the study region, similar to the limited importance of natural habitats to wild bees in late season in other studies (Heinrich 1976, Winfree et al. 2007a). Our study applies to woods in their current state, usually heavily browsed and degraded, in this region. Woods may have formerly been a better bee habitat here (Michener 1974) before many of the early spring wildflowers were extirpated, likely by deer (Balgooyen and Waller 1995). If protected and properly managed, woods may thus be an important bee habitat providing floral resources in early season. In addition, woods may provide substrates and favorable nesting conditions for a variety of bee nesting guilds, e.g., ground-, cavity-, and twig-nesting. Edge effects along woodland perimeter may increase light, temperature, and floral availability compared to woodland interior, and thus may create favorable conditions for some bee species (Vallet et al. 2010, Wright et al. 2010).

The agro-natural ecosystem we studied exhibits strong seasonal patterns in floral resources at both the local (within habitats) and landscape (between habitats and sites) scales, typical of human-dominated landscapes (Tscharrntke et al. 2005). Organisms need to shift their foraging patterns accordingly in order to persist in these highly dynamic systems. Our data suggest that the complementary habitat use exhibited by individual bee species and by the bee community as whole may be a mechanism that allows bees to persist in the highly dynamic agroecosystem. Landscape heterogeneity is considered important for biodiversity conservation in agricultural landscapes in general (Tscharrntke et al. 2005), and for wild bee conservation in particular (Kremen et al. 2007). The conservation of wild bees in agro-natural ecosystems and the insurance they may provide against pollination shortages (Kremen et al. 2002, Winfree et al. 2007b, Winfree and Kremen 2009, Garibaldi et al. 2011) require a broad cross-habitat perspective and the prevalence of both natural and anthropogenic habitats. Spatial planning and management of agricultural landscapes as well as habitat restoration in these landscapes should therefore promote

a mosaic of natural and anthropogenic habitats in a way that maintains the seasonal and temporal phenological complementarity in foraging resources for pollinators across the landscape. Monitoring agro-natural landscapes requires detailed spatiotemporal perspective in order to fully evaluate the role of different habitats during the course of the activity season.

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SUPPLEMENTAL MATERIAL

Appendix A

Landscape characteristics for the different study sites (*Ecological Archives* A022-080-A1).

Appendix B

A comparison of richness and abundance of floral resources and wild bees in the natural habitat in spring 2005 vs. spring 2006 (*Ecological Archives* A022-080-A2).

Appendix C

The protocol used for bee observations (*Ecological Archives* A022-080-A3).

Appendix D

The complete bee species list sampled in this study (*Ecological Archives* A022-080-A4).