Visitation by Wild and Managed Bees (Hymenoptera: Apoidea) to Eastern U.S. Native Plants for Use in Conservation Programs

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ABSTRACT Addition of floral resources to agricultural field margins has been shown to increase abundance of beneficial insects in crop fields, but most plants recommended for this use are non-native annuals. Native perennial plants with different bloom periods can provide floral resources for bees throughout the growing season for use in pollinator conservation projects. To identify the most suitable plants for this use, we examined the relative attractiveness to wild and managed bees of 43 eastern U.S. native perennial plants, grown in a common garden setting. Floral characteristics were evaluated for their ability to predict bee abundance and taxa richness. Of the wild bees collected, the most common species (62%) was *Bombus impatiens* Cresson. Five other wild bee species were present between 3 and 6% of the total: *Lasioglossum admirandum* (Sandhouse), *Hylaeus affinis* (Smith), *Agapostemon virescens* (F.), *Halictus ligatus* Say, and *Ceratina calcarata/dupla* Robertson/Say. The remaining wild bee species were present at <2% of the total. Abundance of honey bees (*Apis mellifera* L.) was nearly identical to that of *B. impatiens*. All plant species were visited at least once by wild bees; 9 were highly attractive, and 20 were moderately attractive. Honey bees visited 24 of the 43 plant species at least once. Floral area was the only measured factor accounting for variation in abundance and richness of wild bees but did not explain variation in honey bee abundance. Results of this study can be used to guide selection of flowering plants to provide season-long forage for conservation of wild bees.

KEY WORDS bumble bee, habitat management, prairie plants, pollination, restoration

Pollination by bees is essential for the productivity of many agricultural crops (Free 1993, Delaplane and Mayer 2000). A recent review found that of 115 cultivated plants grown for fruit, vegetable, or seed production, 87 depend on animal-mediated pollination, comprising 35% of global yields (Klein et al. 2007). Although honey bees (*Apis mellifera* L.) are the main crop pollinator in the United States, contributing $14.6 billion in pollination services annually (Morse and Calderone 2000), nonmanaged wild bees are estimated to be responsible for $3.07 billion in pollination to agricultural crops each year (Losey and Vaughan 2006). Wild bees are especially important for cropping systems in which honey bees are inefficient pollinators (e.g., alfalfa, blueberry, squash). Plant productivity in both natural and agricultural ecosystems has been linked to pollinator abundance and diversity, and this has resulted in greater attention to strategies that can support wild bee populations (Allen-Wardell et al. 1998, Kevan and Phillips 2001, Javorek et al. 2002, Kremen et al. 2002, Klein et al. 2003, Potts et al. 2003, Biesmeijer et al. 2006, Fontaine et al. 2006). In the midst of an apparent global decline of wild pollinators thought to be caused in part by habitat loss and fragmentation because of anthropogenic land use changes (Westrich 1996, Kremen et al. 2002, Tscharntke et al. 2005, Biesmeijer et al. 2006), and with increasing threats to managed honey bees caused by diseases and parasites (Watanabe 1994, Cox-Foster et al. 2007), the evaluation of strategies to improve pollinator habitat on farms is an important component of efforts to achieve long-term, sustainable crop pollination (Southwick and Southwick 1992, Kevan and Phillips 2001, Klein et al. 2007).

Bees derive almost all of their energy and nutrition from flowering plants (Michener 2007). Most wild bee species providing crop pollination services are active beyond the bloom period of crop fields near which they may be nesting, and those that are multivoltine (e.g., many halictine bees) or social (e.g., bumble bees) require flowering plants that are distributed throughout the growing season. Smaller bees have been shown to forage closer to their nests than larger bees, indicating a need for flowering plants near sites where wild bees nest (Gathmann and Tscharntke 2002, Greenleaf et al. 2007). Additionally, conservation of plant–pollinator interactions requires a community rather than an individual species approach (Kearns 1998), in which appropriate plant species are

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selected to provide resources for bees with diverse ecological attributes (Potts et al. 2003).

Because the active period for most flower-using insects endemic to agricultural landscapes extends beyond the time when a particular crop is in bloom, noncrop flowering plants have been evaluated previously for supporting beneficial insects in these landscapes, including pollinators (Patten et al. 1993, Kearns and Inouye 1997, Carreck and Williams 1997) and insects providing biological control (Bugg et al. 1989, Maingay et al. 1991, Bugg and Waddington 1994, Landis et al. 2000, Gurr et al. 2003, Pontin et al. 2006, Fiedler and Landis 2007a). Typically, non-native annual flowering plants have been recommended for these uses (Baggen and Gurr 1998, Baggen et al. 1999, Begum et al. 2006). However, these often require yearly sowing and would not be suitable for projects that also aim to conserve or restore native plant communities and the beneficial insects associated with them. A set of perennial plants that bloom throughout the growing season offers the potential of creating a more stable habitat within and around farmland and is expected to support beneficial insect communities more effectively than would a single sowing of an annual plant species. Plant species that are used by both pollinators and insects that provide biological control should provide greater economic benefit to growers and should also increase the likelihood that they are included in conservation programs designed to enhance arthropod-mediated ecosystem services (Olsen and Wäckers 2007).

A few studies in North America have evaluated native plants for their attraction to bees (Patten et al. 1993, Frankie et al. 2005), and some studies in the United Kingdom have evaluated pollinator attraction to cultivated and to native or naturalized flowering plants (Comba et al. 1999a, b, Carvell et al. 2006). However, selection of plants from these studies as part of a conservation or restoration project aiming to enhance pollinator populations is challenging because different plant species were tested in different years and at different sites. Given the variability in weather, soils, and climate found between study sites, direct comparison of plant species at the same site is expected to provide a more robust comparison of the potential suitability of plants for attracting beneficial insects (Patten et al. 1993, Carreck and Williams 2002, Gustafson et al. 2005). As part of a project designed to evaluate native eastern U.S. prairie and savanna plants for their attraction to natural enemies (Fiedler and Landis 2007a, b), we compared 43 native flowering plants for their attraction to bees. The goal of the combined projects was to identify plants that could be used in agricultural enhancement programs for beneficial insects. Here we report on which plants were visited most frequently by bees and whether simple floral characteristics can be used to predict a plant's degree of attraction to bees.

Materials and Methods

Study Site and Plants. The study site was established on a former agricultural field with Marlette fine sandy loam, previously managed in a corn and soybean rotation, at the Michigan State University Entomology Research Farm in Ingham County, MI. Forty-three native plant species were established in 1-m^2 blocks spaced 6 m apart with a background planting of orchard grass (*Dactylis glomerata* L.). The plots were established using a randomized complete block design with five replicates of each plant species. These plants were evaluated for their relative attractiveness to bees. Plant nomenclature follows Voss (1996) and plant taxonomy follows Judd (2002). Native plant species were selected for study using the following criteria: (1) native perennial plant, (2) adapted to agricultural field conditions (e.g., full sun, moderate drought tolerance), (3) species representing a diversity of bloom periods, (4) species from a variety of plant families, with varied flower color and morphology easily accessible by natural enemies, (5) forb or shrub species formerly found in eastern oak savanna and prairie, and (6) local genotypic plants commercially available in Michigan.

Three, five, or eight plugs of each plant species were planted per plot, depending on the growth habit of each species, to maximize plant density within the plot. Planting occurred during the fall of 2003, and all plots were maintained as described in Fiedler and Landis (2007a).

Plant Measurements. Floral area per meter square, corolla width, and corolla depth during peak bloom were recorded from each plant species evaluated. To estimate floral area per meter square of each plot, the number of open flowers per plot was counted weekly and multiplied by the average area of 10 representative flowers or clusters based on digital images taken at the site (Coolpix 4800; Nikon, Melville, NY), with a ruler in each image for reference. Digital images were prepared for analysis by converting flower images into white space (Knoll 2000) using Adobe Photoshop 6.0 software. ScionImage freeware (Alpha 4.0.3.2, www.scioncorp.com) was used to calculate individual floral area based on the converted images.

Floral morphology was measured on young, open flowers with intact stamens using a Spot Imaging System (v.3.5.9; Diagnostic Instruments, Sterling Heights, MI) in combination with an Olympus SZX12 stereoscope (Center Valley, PA). Corolla width and depth were measured on five flowers per species to the nearest 0.01 cm. For plants in the Asteraceae, one young open disc flower was measured per flower head, and for species with florets, one floret was measured. Width was measured at the point where the corolla fused, and depth was measured from the point of corolla fusion to nectaries (exceptions are described in Fiedler and Landis 2007b). Corolla depth was recorded as zero in species with nectaries located at the point where petals attach to the gynoecium.

Vacuum Sampling for Bees. Flower visitors were sampled weekly from 4 May to 27 September 2005 between 0930 and 1330 hours EST on calm, sunny days. Plants were sampled during bloom, and those samples collected before, during, and after the week of peak bloom (hereafter called full bloom period), based on the weekly counts of the number of open flowers on each plant species, were used in the analyses. A fine white mesh bag (Kaplan Simon Co., Braintree, MA) was placed over the intake on a leaf blower (Stihl BG55, Norfolk, VA) modified into a vacuum, and plots were vacuumed until all flowers were sampled, up to 30 s per plot. Each sample was frozen, and bees were subsequently sorted and identified to the lowest taxonomic level using the key of Michener et al. (1994) and the online key to eastern North American bee species at www.discoverlife.org. The number of bees per sample was recorded and averaged over the number of collections made during peak bloom per plot for analyses. For eight plant species, one or more of the plots were not in bloom during one of the three sampling visits and so the average was taken across the total number of plots sampled.

Bee Observations. Timed observations of bees visiting each plot in bloom were conducted from 1 June to 17 August 2005 between 1000 and 1700 hours EST on sunny, calm days when vacuum sampling was not taking place. Each plot was observed once during peak bloom for 5 min, for a total of five replicate observations per plant species. Bees visiting the plants during this time were either recorded and identified to the lowest taxonomic level (usually genus) in situ or collected with a modified Dustbuster insect vacuum (BioQuip Products, Rancho Dominguez, CA) for subsequent identification using the keys described above. No observations were made at the earliest blooming species (*Sambucus racemosa* L.) or from the last four blooming species (*Solidago riddellii* Frank ex Riddell, *S. speciosa* Nutt., *Aster novae-angliae* L., and *A. laevis* L.); however, vacuum sample data for these plants are presented in Table 1.

Plant species that were visited by five or more bees on average during either sampling method were considered highly attractive species, those that were visited between one and five times on average were considered moderately attractive, and those with an average visitation rate of less than one time were considered least attractive (modified after Frankie et al. 2005).

Statistical Analysis. Analysis of variance (ANOVA) with Tukey-Kramer adjusted means separation (PROC MIXED, SAS v 9.1) was used to determine differences among plant species in the number of non-*Apis* bees that visited plants within early (May to June), middle (July to mid-August), and late (late August to September) blooming periods for both the vacuum samples and timed observations. Simple linear regression analyses were conducted with each pair of floral characters to check for autocorrelation, and a multiple linear regression analysis was conducted on the bees obtained during vacuum sampling to determine whether bee abundance (honey bees, bumble bees, wild bees other than bumble bees, and all wild bees) and richness (number of different bee taxa represented in the samples collected from each plant species) varied with any of the three floral characteristics (average floral area during full bloom, corolla width, and corolla depth; PROC REG, SAS v 9.1). Finally, linear regression on the arsine square root transformed proportion of bees caught at each flower species using each method was used to compare the two sampling methods (PROC REG, SAS v 9.1).

Results

Summary of Bees Recorded. Over the period of vacuum sampling, 875 honey bees and 1,393 wild bees were collected. Honey bees recorded during the study were assumed to be from seven managed hives that were within 200 m of the study site. The most abundant wild bee in vacuum samples was *Bombus impatiens*, comprising 62% of the wild bees collected. In contrast, four other *Bombus* spp. found at the site, *B. bimaculatus* Cresson, *B. (Psithyrus) citrinus* (Smith), *B. fervidus* (Fabricius), and *B. griseocollis* (DeGeer), were collected at a rate of <1% of the wild bee total. *Lasioglossum admirandum* (93, 6%), *Hylaeus affinis* (71, 5%), *Agapostemon virescens* (66, 5%), *Halictus ligatus* (50, 4%), *Ceratina calcarata/dupla* females (38, 3%), and *Xylocopa virginica virginica* (34, 3%) were the next most abundant wild bee species (Table 1).

The number of bees collected during vacuum sampling increased over the course of the 2005 growing season. Across all the plants in each of the three seasonal groupings, there was an average of 3.5 ± 0.1, 22.6 ± 5.7, and 69.8 ± 20.2 bees per plant species in the early, mid, and late season samples, respectively (Fig. 1). There was an associated increase in the richness of bees collected, with average number of bee taxa collected of 2.3 ± 0.5, 4.8 ± 0.8, and 7.1 ± 1.2 per plant species in the early, mid, and late season groups, respectively (Fig. 1).

During timed observations, 510 visits by honey bees and 920 visits by wild bees were recorded. Bees in the genus *Bombus* were also the most abundant wild bee

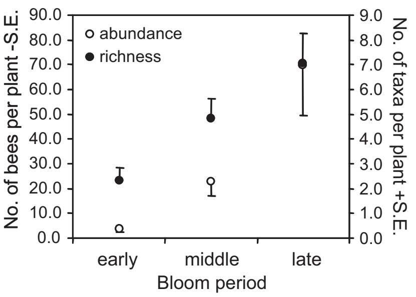

Fig. 1. Average abundance (number of bees per plant species) and richness (number of bee taxa per plant species) of all wild (non-*Apis*) bees collected at native plants in 2005 in Ingham Co., MI, by vacuum sampling during peak bloom. Samples are grouped by peak bloom periods: early (mid-May to June), middle (July to mid-August), and late (mid-August to September).

Table 1. Bees species collected by three vacuum samples during peak bloom at a common garden plot of 43 native perennial prairie plant species in Ingham County, MI

	Plant family[a]																													
	A										B	C	D	E	F		G		H	I			J	K	L			M	
Bee species	*Aster laevis* L. (9/27)	*Aster novae-angliae* L. (9/20)	*Cacalia atriplicifolia* L. (8/23)	*Eupatorium perfoliatum* L. (8/23)	*Helianthus strumosis* L. (8/30)	*Liatris aspera* Michx. (8/30)	*Ratibida pinnata* (Vent.) Barnh. (8/2)	*Silphium perfoliatum* L. (8/23)	*Solidago riddellii* Frank (9/13)	*Solidago speciosa* Nutt. (9/20)	*Vernonia missurica* Raf. (8/23)	*Zizia aurea* L. Koch (6/6)	*Apocynum cannabinum* L. (7/12)	*Asclepias incarnata* L. (8/2)	*Lobelia siphilitica* L. (8/23)	*Amorpha canescens* Pursh (8/2)	*Lespedeza hirta* L. (8/30)	*Agastache nepetoides* (L.) (8/16)	*Monarda punctata* L. (8/16)	*Allium cernuum* Roth (8/9)	*Potentilla fruticosa* auct. non L. (7/12)	*Rosa setigera* Michx. (7/12)	*Spiraea alba* Duroi (8/9)	*Cephalanthus occidentalis* L. (7/19)	*Heuchera americana* L. (6/21)	*Penstemon hirsutus* L. (6/14)	*Scrophularia marilandica* L. (7/27)	*Veronicastrum virginicum* L. (8/2)	*Verbena stricta* Vent. (8/2)	Total for all plants
Andrenidae																														
Andrena helianthiformis Viereck and Cockerell	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Andrena spp.	—	3	—	—	—	—	—	—	7	1	—	1	1	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	15
Apidee																														
Bombus bimaculatus Cresson	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	3
B. citrinus (Smith)	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
B. fervidus (F.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
B. griseocollis (Degeer)	—	—	—	—	—	—	3	4	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11
B. impatiens Cresson	13	12	37	6	8	57	7	233	19	69	20	—	—	—	136	2	7	91	5	13	—	4	22	3	—	—	21	66	5	856
Ceratina calcarata/dupla[b]	—	1	—	1	—	—	1	1	2	—	2	—	—	—	21	1	—	—	—	—	—	—	—	—	—	4	—	1	2	37
Melissodes bimaculata (Lepeletier)	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	3
Melissodes spp.	—	—	1	6	6	—	3	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	21
Nomada spp.	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Triepeolus concavus (Cresson)	—	1	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
T. lunatus (Say)	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
T. pectoralis (Robertson)	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
T. remigatus (F.)	—	—	—	—	—	—	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7
Xylocopa virginica L.	—	—	—	—	—	—	1	—	1	2	—	—	—	23	—	—	—	—	6	—	—	—	—	—	—	1	—	—	—	34
Colletidae																														
Hylaeus affinis (Smith)	—	—	—	2	—	—	—	—	13	—	—	2	4	1	3	—	—	—	—	—	21	—	24	—	—	—	—	—	—	70
H. annulatus L.	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	3
H. mesillae (Cockerell)	—	—	—	—	—	—	—	—	—	—	—	5	1	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	8
H. modestus Say	—	—	—	—	—	—	—	—	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Hylaeus sp.	—	—	—	2	—	—	—	—	9	—	—	—	2	—	—	—	—	—	—	—	1	—	2	—	—	—	—	—	—	16
Halictidae																														
Agapostemon splendens (Lepeletier)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Ag. virescens (F.)	3	4	—	3	2	1	—	23	19	—	6	—	—	—	2	—	—	1	—	—	—	1	—	1	—	—	—	—	—	66
Augochlorella aurata (Smith)	—	—	—	2	—	—	1	—	1	—	—	1	—	—	5	—	—	—	—	—	—	—	—	—	3	—	—	—	—	13
Halicrus confusus Smith	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	4
H. ligotus Say	—	—	5	5	1	—	33	1	2	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	50
H. parallelus Say	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	3
H. rubicundus (Christ)	—	—	—	2	—	—	—	—	1	—	—	—	—	—	3	—	—	—	—	—	1	—	—	—	—	—	1	1	—	9
Lasioglossum acuminatum McGinley	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	1	—	—	3
L. admirandum (Sandhouse)	—	1	1	3	—	—	1	—	10	8	—	2	1	3	14	8	—	2	—	7	3	—	1	1	3	1	8	4	—	82
L. coriaceum (Smith)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
L. cressonii (Robertson)	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
L. leucozanlum (Schrank)	—	1	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
L. nymphaearum (Robertson)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
L. pilosum (Smith)	—	—	1	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	3	3	—	—	—	—	—	—	—	—	9

Table 1. Continued

Bee species	Plant family[a]																													
	A											B	C	D	E	F		G		H	I			J	K	L			M	
	Aster laevis L. (9/27)	*Aster novae-angliae* L. (9/20)	*Cacalia atriplicifolia* L. (8/23)	*Eupatorium perfoliatum* L. (8/23)	*Helianthus strumosis* L. (8/30)	*Liatris aspera* Michx. (8/30)	*Ratibida pinnata* (Vent.) Barnh. (8/2)	*Silphium perfoliatum* L. (8/23)	*Solidago riddellii* Frank (9/13)	*Solidago speciosa* Nutt. (9/20)	*Vernonia missurica* Raf. (8/23)	*Zizia aurea* L. Koch (6/6)	*Apocynum cannabinum* L. (7/12)	*Asclepias incarnata* L. (8/2)	*Lobelia siphilitica* L. (8/23)	*Amorpha canescens* Pursh (8/2)	*Lespedeza hirta* L. (8/30)	*Agastache nepetoides* (L.) (8/16)	*Monarda punctata* L. (8/16)	*Allium cernuum* Roth (8/9)	*Potentilla fruticosa* auct. non L. (7/12)	*Rosa setigera* Michx. (7/12)	*Spiraea alba* Duroi (8/9)	*Cephalanthus occidentalis* L. (7/19)	*Heuchera americana* L. (6/21)	*Penstemon hirsutus* L. (6/14)	*Scrophularia marilandica* L. (7/27)	*Veronicastrum virginicum* L. (8/2)	*Verbena stricta* Vent. (8/2)	Total for all plants
L. rohweri (Ellis)	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	1	—	5
Lasioglossum sp. 1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Lasioglossum sp. 2	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
L. tegulare (Robertson)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
Megachilidae																														
Anthidium manicatum L.	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Megachile pugnata Say	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Megachile sp.	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
No. of non-*Apis* bees	16	23	48	33	19	58	58	272	90	84	32	13	10	34	186	13	7	97	12	24	41	6	50	6	6	7	32	72	8	1357
No. of non-*Apis* bee species	2	7	8	11	5	2	12	13	16	7	7	7	6	7	10	5	1	6	3	4	12	3	5	4	2	4	5	4	3	42
No. of *Apis mellifera*	2	12	2	22	—	—	2	10	178	89	9	1	10	197	1	—	—	8	23	106	1	6	19	—	—	5	3	140	18	864

Shown here are plants in families (A) Asteraceae, (B) Apiaceae, (C) Apocynaceae, (D) Asclepiadaceae, (E) Campanulaceae, (F) Fabaceae, (G) Laminaceae, (H) Liliaceae, (I) Rosaceae, (J) Rubiaceae, (K) Saxifragaceae, (L) Scrophulariaceae, and (M) Verbenaceae from which at least 5 non-*Apis* bees were collected. The date in parentheses after each plant name indicates its peak bloom date (month/day) during 2005.

[a] Not shown are the following plants from which fewer than five wild bees and no *A. mellifera* were collected: *Coreopsis lanceolata* L. (two bees; two species) (Asteraceae); *Angelica atropurpurea* L. (one bee) and *Heracleum maximum* Bartr. (three bees; three species) (Apiaceae); *Asclepias tuberosa* L. (four bees; three species) (Asclepiadaceae); *Sambucus racemosa* L. (one bee) (Caprifolaceae); *Desmodium canadense* (L.) DC. (two bees; two species) (Fabaceae); *Geranium maculatum* L. (one bee) (Geraniaceae); *Anemone canadensis* L. (three bees; two species) and *Aquilegia canadensis* L. (two bees; one species) (Ranunculaceae); *Ceanothus americanus* L. (two bees; two species) (Rhamnaceae); *Fragaria virginiana* Duchesne (three bees; two species) (Rosaceae); and *Senecio obovatus* Muhl. ex Willd (Asteraceae) and *Oenothera biennis* L. (Onagraceae), from which no bees were collected.

[b] The females of these two species, *C. calcarata* Robertson 1900 and *C. dupla* Say 1837, are morphologically indistinct. Only one male was captured, and it was *C. dupla*.

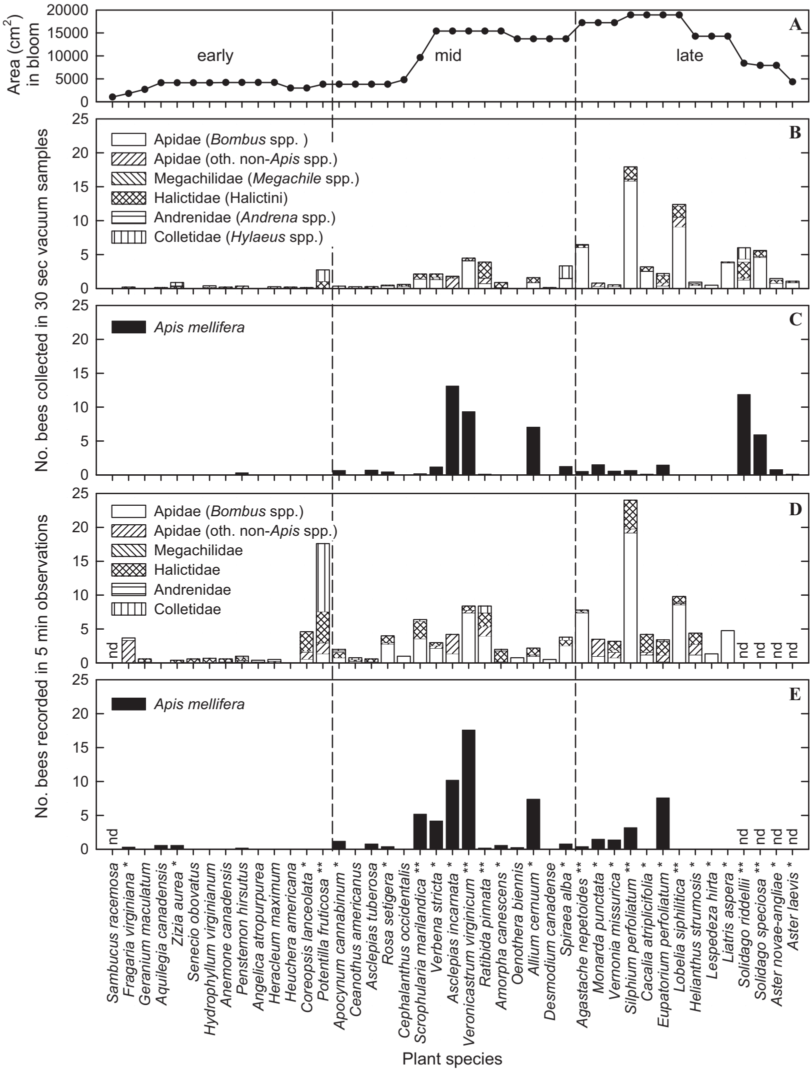

Fig. 2. (A) Floral abundance (cm^2) summed over all native plant plots in bloom during the peak bloom date of each plant species in the study indicated that floral abundance was greater in the mid to late season than earlier in the study. The average number of (B) wild bees and (C) honey bees collected during 30-s vacuum samples at 43 plant species and (D) wild bees and (E) honey bees recorded during 5-min observations at 38 plant species in Ingham Co., MI, in 2005 are shown here. Plants are organized from left to right by peak bloom phenology: early (mid-May to June), middle (July to mid-August), and late (mid-August to September) in 2005. Plants that were moderately attractive to wild bees are indicated by one asterisk; highly attractive plants are indicated by two asterisks. nd, no data.

taxa recorded during timed observations (57%) followed by bees in the tribe Halictini (26%), all other non-*Apis* Apidae (14%), and *Hylaeus* spp. (9%). Both andrenid and megachilid bees were recorded <1% of the time during observations.

Attractiveness of Plants. The total area of bloom provided by the evaluated plants increased through the summer, declining in September (Fig. 2A). All of the plant species evaluated in this study had at least one wild bee visitor collected from or observed on them. Most of the plants were visited with low frequency by bees, whereas a smaller subset was visited by relatively greater numbers of bees (Table 1). Bees were more often collected or observed on plants in the following families: Asteraceae, Asclepiadaceae, Campanulaceae, Laminaceae, Liliaceae, Rosaceae, and Scrophulariaceae (Table 1). Based on the criterion used, nine of the plant species were highly attractive to wild bees: *Potentilla fruticosa* auct. non L., *Scrophularia marilandica* L., *Veronicastrum virginicum* L. Farw., *Ratibida pinnata* (Vent.) Barnh., *Agastache nepetoides* L. Kuntze, *Silphium perfoliatum* L., *Lobelia siphilitica* L., *Solidago riddellii* Frank ex Riddell, and *Solidago speciosa* Nutt. (Fig. 2, B and D). Twenty of the other plant species were moderately attractive to wild bees (Fig. 2, B and D). Honey bees visited 26 of the 43 native plants and were highly

Table 2. Floral attributes, bloom period, and the average number of wild bees collected during vacuum sampling for floral visitors during peak bloom of each plant in 2005

Species[a]	Family[b]	Floral area (cm^2)	Corolla width (mm)	Corolla depth (mm)	Bloom period[c] (May, June, July, Aug., Sept.)	Average no. wild bees[d]
Early season						
Sambucus racemosa	F	821.3	1.0	0.0	▫ □ ▫ —	0.07 b
Fragaria virginiana	O	730.6	3.7	0.0	— ▫ □ ▫ —	0.20 ab
Geranium maculatum	H	364.5	2.7	0.0	▫ □ ▫ — —	0.07 b
Aquilegia Canadensis	M	373.3	6.0	22.3	— ▫ □ ▫ — —	0.13 b
Zizia aurea	B	682.7	1.0	0.0	— — ▫ □ ▫ —	0.87 a
Senecio obovatus	A	667.4	5.2	0.7	— ▫ □ ▫ —	0 b
Hydrophyllum virginianum	I	868.1	4.1	5.5	▫ □ ▫	0.40 ab
Anemone Canadensis	M	556.3	2.3	0.0	— ▫ □ ▫ ▫ — —	0.20 ab
Penstemon hirsutus	R	610.4	2.2	18.2	▫ □ ▫	0.47 ab
Angelica atropurpurea	B	274.2	1.3	0.0	▫ □ ▫ —	0.07 b
Heracleum max	B	115.3	1.3	0.0	— □ ▫ ▫	0.25 ab
Heuchera Americana	Q	327.3	3.0	2.0	— ▫ □ ▫ — —	0.40 ab
Coreopsis lanceolata	A	494.3	0.9	5.1	▫ □ ▫ — — — — — — — — —	0.13 b
Mid Season						
Potentilla fruticosa	O	974.6	4.2	0.0	— — ▫ ▫ □ ▫ ▫ — — — — — — — —	2.73 bcd
Apocynum cannabinum	C	428.0	1.6	1.8	— ▫ ▫ □ ▫ — —	0.67 cd
Ceanothus americana	N	128.9	1.2	0.0	— ▫ □ — — —	0.25 cd
Asclepias tuberose	D	344.4	0.3	1.6	▫ □ ▫ — — — — — —	0.27 cd
Rosa setigera	O	725.7	3.9	0.0	▫ □ ▫	0.46 cd
Cephalanthus occidentalis	P	55.1	1.7	7.0	▫ □ ▫ — —	0.60 cd
Scrophularia marilandica	R	168.2	3.3	4.1	— — ▫ ▫ □ ▫ — — — —	2.13 bcd
Verbena stricta	S	492.7	0.9	5.1	— — ▫ ▫ □ ▫ — — —	0.53 cd
Asclepias incarnate	D	1408.0	0.2	0.8	— — ▫ ▫ □ ▫ —	2.27 bc
Veronicastrum virginicum	R	774.3	1.3	3.8	— ▫ □ ▫ —	4.80 ab
Ratibida pinnata	A	3865.6	0.7	2.3	— ▫ □ ▫ ▫ —	3.87 a
Amorpha canescens	G	18.2	0.5	0.0	▫ ▫ □ ▫ — — — —	0.87 cd
Oenethera biennis	L	123.9	3.1	28.9	— ▫ ▫ □ ▫ — —	0 d
Allium cernuum	K	910.9	1.8	0.0	— ▫ □ ▫ ▫ — —	1.60 bcd
Desmodium canadense	G	139.6	0.8	0.0	— ▫ □ ▫ —	0.13 d
Spiraea alba	O	213.3	2.0	0.0	▫ □ ▫ ▫ — —	3.33 bc
Late Season						
Agastache nepetoides	J	2766.4	1.4	6.3	— ▫ ▫ □ ▫ ▫ —	6.47 cd
Monarda punctata	J	473.0	13.1	2.4	— ▫ ▫ □ ▫ ▫ — — — —	0.80 cd
Vernonia missurica	A	586.6	0.9	7.0	— ▫ □ ▫ — —	2.13 cd
Silphium perfoliatum	A	3870.9	5.6	1.2	— — — ▫ □ ▫ —	18.13 a
Cacalia atriplicifolia	A	612.1	1.0	6.4	— ▫ ▫ □ ▫ — —	3.20 cd
Eupatorium perfoliatum	A	5878.2	0.5	2.1	— — ▫ □ ▫ — —	2.20 cd
Lobelia siphilitica	E	829.3	0.3	2.6	— — — ▫ □ ▫ — — —	12.40 ab
Helianthus strumosis	A	3132.5	5.4	1.2	— — — — ▫ □ ▫ — —	1.27 cd
Lespedeza hirta	G	96.3	0.7	0.0	— ▫ □ ▫	0.47 d
Liatris aspera	A	370.9	1.5	8.3	— ▫ □ ▫ — —	3.87 cd
Solidago riddellii	A	878.3	0.6	2.9	▫ □ ▫ —	6.00 bc
Solidago speciosa	A	3814.2	0.6	3.8	— ▫ □ ▫ —	5.60 cd
Aster novae-angliae	A	1232.5	0.7	4.7	— ▫ □ ▫ —	1.53 cd
Aster laevis	A	623.9	0.8	4.7	— ▫ □ ▫	1.07 cd

Plants are listed in order of bloom.

[a] All natives are perennials except for *O. biennis*, which is a biennial.

[b] Codes for plant families: A = Asteraceae, B = Apiaceae, C = Apocynaceae, D = Asclepiadaceae, E = Campanulaceae, F = Caprifolaceae, G = Fabaceae, H = Geraniaceae, I = Hydrophyllaceae, J = Laminaceae, K = Liliaceae, L = Onagraceae, M = Ranunculaceae, N = Rhamnaceae, O = Rosaceae, P = Rubiaceae, Q = Saxifragaceae, R = Scrophulariaceae, S = Verbenaceae.

[c] Key for bloom period: □ = peak bloom date, ▫ = full bloom, — = sparse bloom.

[d] Averages followed by different letters are significantly different (Tukey-Kramer means separation).

attracted to seven plant species: *S. marilandica, Asclepias incarnata* L., *V. virginicum, Allium cernuum* Roth, *Eupatorium perfoliatum* L., *S. riddellii,* and *S. speciosa* (Fig. 2, C and E, bars > 5).

When the three periods of the growing season were considered separately, the most attractive plants that bloomed early, middle, and late in the season were identified. Vacuum sampling of plants that bloomed during the early season showed that relatively few bees were collected, but that wild bees were most abundant at *Zizia aurea* L. Koch ($F_{12,48}$ = 3.46, P = 0.001; Table 2). The most attractive mid-season blooming plants using this method were *P. fruticosa, A. incarnata, V. virginicum, R. pinnata,* and *Spiraea alba* Duroi ($F_{18,71}$ = 9.93, $P < 0.0001$; Table 2). The most attractive late season plants were *A. nepetoides, S. perfoliatum, L. siphilitica,* and *S. riddellii,* and *S. speciosa* ($F_{15,57}$ = 16.83, $P < 0.0001$; Table 2).

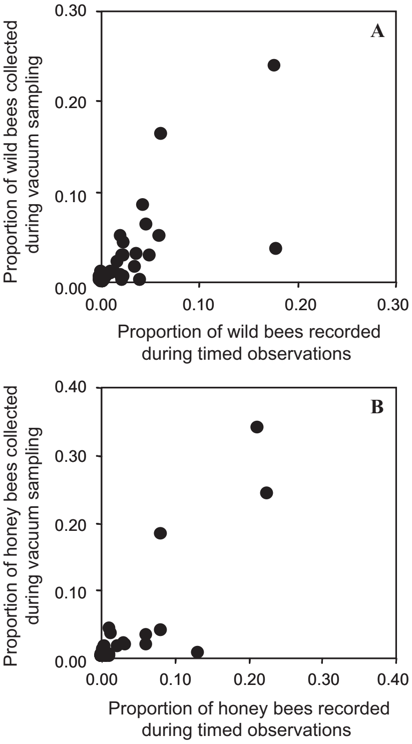

Fig. 3. Comparison of bee sampling methods using simple linear regression of (A) the proportion of wild bees and (B) the proportion of honey bees caught or recorded using each method at the 38 plant species on which both methods were used in Ingham County, MI, in 2005. Data were arcsine square root transformed before analysis.

From timed observations during the early season, wild bees were most attracted to *Fragaria virginiana* Duchesne and *Coreopsis lanceolata* L. ($F_{11,35} = 7.38, P < 0.0001$; Fig. 2D). Of the mid-season plants, wild bees were most frequently recorded at *P. fruticosa, S. marilandica V. virginicum,* and *R. pinnata* ($F_{18,62} = 10.65, P < 0.0001$; Fig. 2D). During the late season bloom period, wild bees were most attracted to *A. nepetoides, S. perfoliatum,* and *L. siphilitica* ($F_{11,37} = 16.07, P < 0.0001$; Fig. 2D). Honey bees were observed visiting *S. marilandica* at much higher rates than from samples taken with the vacuum (compare Fig. 2, C and E).

Regression analysis of the proportion of wild bees captured during vacuum sampling against the proportion of wild bees recorded during timed observations provided support for general similarity of the methods, with a slope of 0.84 and a regression coefficient of 0.60 ($P < 0.0001$; Fig. 3A). For honey bees, there was a stronger positive correlation between the two methods ($R^2 = 0.73, P < 0.0001$ and a slope of 0.93; Fig. 3B). These results suggest that direct observation is a slightly better method for recording bees at flowers than vacuum sampling, as indicated by the slopes being less than one.

Relationship Between Floral Characteristics and Bee Abundance. The native plants evaluated in this study ranged in their peak bloom period from the first week in May to the first week of October. The range of peak bloom covered by these plants indicates the temporal range of flowering resources achievable with a combination of mostly herbaceous native plants (Table 2). Early blooming plants typically had the smallest average floral area, with the overall abundance of flowers increasing toward the end of the season among species (Table 2; Fig. 2A). Average corolla width and depth of the flowers tested did not vary significantly among species throughout the season (Fiedler and Landis 2007b).

Floral characteristics explained only 14% of the variation in all wild bee abundance, 14% of the variation in bumble bee abundance, and 13% of the abundance of wild bees other than bumble bees. Of the three flower parameters measured, floral area was the only one that explained a significant amount (floral area parameter estimate $P < 0.03$) of the variation in wild bee abundance at flowers (Table 3). Almost none of the variation in honey bee abundance was predicted by the three floral characteristics measured (Table 3). Higher bee taxa richness was strongly correlated with greater floral area and was the most significant factor in the full model (28%, $P < 0.001$; Table 3).

Discussion

Agricultural habitats can be inhospitable to beneficial insects during much of the growing season because of intensive crop production practices, such as the use of agrochemicals for pest control and removal of vegetation in field margins and hedgerows resulting in a reduction in flower abundance and diversity in

Table 3. Results of multiple linear regressions of the abundance and diversity of bees collected at native flowering plants during peak bloom against three floral characters

Variable	Overall model			Parameter estimate probabilities		
	R^2	$F_{3,39}$	P	Floral area	Corolla width	Corolla depth
Bee abundance						
Honey bees (*A. mellifera*)	0.05	0.69	0.56	0.54	0.29	0.65
Bumble bees (*Bombus* spp.)	0.14	2.18	0.11	**0.02**	0.57	0.99
Wild bees other than bumble bees	0.13	2.01	0.13	**0.03**	0.86	0.44
All wild bees	0.14	2.08	0.12	**0.03**	0.69	0.61
Bee diversity						
No. of wild bee species	**0.28**	**5.09**	**0.005**	**0.001**	0.45	0.42

Significant regression coefficients and probability values ($P < 0.05$) are highlighted in bold.

farm landscapes (Buchmann and Nabhan 1996, Kearns 1998, Steffan-Dewenter and Tscharntke 1999). Agricultural intensification has been highlighted as an important factor in the putative decline in native bee populations (Osborne et al. 1991, Matheson et al. 1994, Allen-Wardell et al. 1998, Stubbs and Drummond 2001), and loss of plant diversity can translate into both spatial and temporal gaps in the availability of floral resources (Matheson et al. 1994, Banaszak 1996). If wild bee populations are supported throughout the season by the addition of flowering plants into farmland, growers of pollination-dependent crops may receive greater pollination services from wild bees when the crop is in bloom. Perennial flowering plants have the potential to be a relatively low maintenance way to incorporate additional floral resources into the landscape, as opposed to the multiple sowings per season necessary if one relies on annual plants for this purpose (Carreck and Williams 2002).

Native bees endemic to agricultural landscapes, which are active beyond the bloom period of pollinator-dependent crops, necessitate farm management practices that will provide or increase the abundance of flowering plants throughout the growing season. The investment required to create a managed area of flowering plants blooming throughout the season would suggest that optimizing the suitability of the plant species for local pollinators will give the greatest return on that investment in terms of pollinator conservation and benefit to the crop. Based on two sampling methods, this study has identified 29 native perennial plants to which wild bees in southern Michigan show affinity, from which a smaller selection of plants with overlapping bloom periods could be selected. These plants were originally selected to be suitable for use by natural enemies (Fiedler and Landis 2007a, b), so their use in agricultural settings could promote both pollination and biological control, the two main ecosystem services provided to agriculture by arthropods. With increasing concern about the suitability of agricultural landscapes for wild pollinators (NAS 2007) and other beneficial insects (Baggen and Gurr 1998, Landis et al. 2000, Begum et al. 2006), conservation activities on managed land are expected to increase. Plants reported here as being attractive to wild bees within their flowering season can help land managers select native perennial plants for use in these conservation programs.

Plants in this study were divided into early-, middle-, and late-blooming groups, and we found increasing bee abundance and diversity as the season progressed. This temporal pattern in bee abundance at flowers mirrors the availability of floral resources, variation in weather (Pywell et al. 2005), and population growth of multivoltine and social bees later in the season (Michener 2007). By taking this approach, plants that attracted relatively few bees in the spring (mid-May) were not directly compared with those in bloom during the warmer summer months when social bee colony size was greatest. The plants most attractive to wild bees using either sampling method and in their peak bloom order were as follows: *Fragaria virginiana, Zizia aurea, Penstemon hirsutus* L., *Coreopsis lanceolata, Potentilla fruticosa, Apocynum cannabinum* L., *Rosa setigera* Michx., *Scrophularia marilandica, Verbena stricta* Vent., *Asclepias incarnata, Veronicastrum virginicum, Ratibida pinnata, Amorpha canescens* Pursh, *Allium cernuum, Spiraea alba, Agastache nepetoides, Monarda punctata* L., *Vernonia missurica* Raf., *Silphium perfoliatum, Cacalia atriplicifolia* L., *Eupatorium perfoliatum, Lobelia siphilitica, Helianthus strumosis* L., *Lespedeza hirta* L., *Liatris aspera* Michx., *Solidago riddellii, Solidago speciosa, Aster novae-angliae* L., and *Aster laevis* L. (Fig. 2, B and D). These plants are representatives from 11 different plant families: 12 species of Asteraceae, 4 Rosaceae, 2 each of Fabaceae, Laminaceae, and Scrophulariaceae, and 1 each of Apiaceae, Apocynaceae, Asclepiadaceae, Campanulaceae, Liliaceae, and Verbenaceae. All of these families contain species of plants that have been shown to be attractive to bumble bees and other wild bees (Corbet et al. 1994, Frankie et al. 2005, Carvell et al. 2006).

Because this study was designed primarily to select plants attractive to natural enemies, a vacuum sampling method was used to collect insects. Although this is an unconventional method for monitoring bees, we found high correlation between bee abundance at plants during timed observations and in vacuum samples, and slopes were close to unity. The traditional method of sampling for bees is to hand net bees directly from flowers (Kearns and Inouye 1993), which was the method used in this study to verify the kinds of bees recorded during observations. A method becoming more common for sampling bees across multiple sites simultaneously is pan trapping, in which colored bowls are filled with a weak aqueous soap solution to attract and passively capture bees (LeBuhn et al. 2003). Floral records of bee visits are difficult to obtain using pan traps, so a combination of methods has been recommended (Cane et al. 2001, Roulston et al. 2007). Vacuum sampling could be considered for use across a large number of field sites as a rapid and reproducible method to obtain an estimate of the bee community visiting particular flowers, especially when used in combination with a more passive method.

To our knowledge, this study is the first to examine the response of endemic wild bees to replicated plantings of native northeastern U.S. flowering perennial plants. The plants indicated as being the most attractive could be used in future long-term studies to test whether the addition of floral resources causes positive changes in bee abundance and species richness over time in agricultural landscapes. This study was conducted at a site with relatively low landscape diversity in a field that was previously planted to various field crops in rotation. This may explain the low bee diversity at this site, as opposed to the much higher species richness found in natural habitats (Reed 1995), in larger sample areas (Marlin and LaBerge 2001), or in agricultural landscapes containing flowering crops (MacKenzie and Eickwort 1996). The necessity of obtaining an established planting in a relatively short period of time excluded most flowering woody plants; however, many early spring blooming woody plants are important forage plants for bees emerging in spring (e.g., many species of *Andrena, Colletes,* and *Osmia*). Future studies should include early blooming woody plants to support early-season pollinators (Stubbs et al. 1992). Finally, foraging resources (i.e., pollen, floral and extra-floral nectar) alone are not enough to sustain populations of bees; nesting resources are also needed. It may be that our research site is depauperate of the kind of nesting resources required by cavity nesting bees (Medler 1967, Michener 2007).

Of the three floral attributes measured in this study, floral area was the most explanatory factor for the abundance of bees other than honey bees found at the sampled flowering plants. This suggests that unlike honey bees, that receive information from hive mates about rewarding patches, wild bees maximize reward for their foraging efforts by seeking patches with greater floral abundance. This finding agrees with previous studies showing that pollinating insects concentrate their foraging in dense patches of flowers (Thomson 1981, Westphal et al. 2003, Hegland and Totland 2005, Hegland and Boeke 2006). Plants with greater average floral area were also more likely to have higher wild bee taxa richness (Table 3). Together, these results suggest that floral area might be a simple indicator of the potential for a particular plant species to attract bees and could be used in selection of plants within the same bloom period when designing wild bee conservation projects.

Recent studies have linked plant community diversity to pollinator community diversity in natural systems (Potts et al. 2003), and long-term declines in bee pollinated plants have been linked to declines in pollinators (Biesmeijer et al. 2006). Further evidence comes from experimental studies that have shown that pollinator diversity is linked to the persistence of plant communities (Fontaine et al. 2006). In agricultural systems, diverse pollinator communities can increase productivity in crops such as sunflowers (Greenleaf and Kremen 2006), watermelon (Kremen et al. 2002), and coffee (Klein et al. 2003), so enhancing pollinator diversity is a worthwhile goal for managers of landscapes in which pollinator-dependent crops are grown. In California, Frankie et al. (2005) found that native flowering plants in residential landscapes were more attractive to both honey bees and other bee taxa than non-native ornamentals. Although the conversion of agricultural land into suburban development is often viewed as being negative (Greene and Harlin 1995), native flowering perennials used in ornamental plantings may provide a corridor of forage plants in urban/rural landscape interfaces.

The link between plant and pollinator diversity supports the continued development of native perennial plants for use in beneficial insect conservation programs in agricultural settings. Perennial plants may have higher initial planting costs than annuals and take more time to mature and reach their potential floral area, but there are long-term benefits. In addition to providing resources for pollinators (Pywell et al. 2005, Carvell et al. 2006) and insect natural enemies (Landis et al. 2000, Colley and Luna 2000, Gurr et al. 2003, Fiedler and Landis 2007a), these plant species are adapted to the local environment (Gustafson et al. 2005) and can also provide esthetic value to the landscape (Goulder and Kennedy 1997, Fiedler et al. 2008).

A first step toward conservation of native bees on farmland is to determine which plants are most suitable for providing foraging resources at different times of the growing season. The results from this direct comparison of co-blooming plants can be combined with the findings of Fiedler and Landis (2007a, b) related to natural enemy attraction. Using these two studies, future research should evaluate combination plantings of highly suitable plants that provide overlapping bloom periods through the growing season. Such a combined floral planting can be tested for its use in conserving beneficial insects within agricultural settings, with the ultimate aim of improving sustainable pollination of crops that depend on bees for reaching their potential yield.

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