

Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States

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Abstract. Global trends in pollinator-dependent crops have raised awareness of the need to support managed and wild bee populations to ensure sustainable crop production. Provision of sufficient forage resources is a key element for promoting bee populations within human impacted landscapes, particularly those in agricultural lands where demand for pollination service is high and land use and management practices have reduced available flowering resources. Recent government incentives in North America and Europe support the planting of wildflowers to benefit pollinators; surprisingly, in North America there has been almost no rigorous testing of the performance of wildflower mixes, or their ability to support wild bee abundance and diversity. We tested different wildflower mixes in a spatially replicated, multiyear study in three regions of North America where production of pollinator-dependent crops is high: Florida, Michigan, and California. In each region, we quantified flowering among wildflower mixes composed of annual and perennial species, and with high and low relative diversity. We measured the abundance and species richness of wild bees, honey bees, and syrphid flies at each mix over two seasons. In each region, some but not all wildflower mixes provided significantly greater floral display area than unmanaged weedy control plots. Mixes also attracted greater abundance and richness of wild bees, although the identity of best mixes varied among regions. By partitioning floral display size from mix identity we show the importance of display size for attracting abundant and diverse wild bees. Season-long monitoring also revealed that designing mixes to provide continuous bloom throughout the growing season is critical to supporting the greatest pollinator species richness. Contrary to expectation, perennials bloomed in their first season, and complementarity in attraction of pollinators among annuals and perennials suggests that inclusion of functionally diverse species may provide the greatest benefit. Wildflower mixes may be particularly important for providing resources for some taxa, such as bumble bees, which are known to be in decline in several regions of North America. No mix consistently attained the full diversity that was planted. Further study is needed on how to achieve the desired floral display and diversity from seed mixes.

Key words: *agricultural landscapes; attractiveness; bees; biodiversity; floral resources; habitat enhancement; native plants; pollinator diversity; syrphids; wildflowers.*

INTRODUCTION

Agricultural intensification has increased food production over the past 60 years (Jorgenson and Gollop 1992) to feed a growing human population. Intensification has in many cases also reduced the availability of habitat to support wild bees and provide forage resources for honey bees on which crop pollination depends (Kremen et al. 2002, Carvell et al. 2006a, Klein

et al. 2007). In some landscapes, mass-flowering crops provide transient forage for certain bee species (Westphal et al. 2003, Jauker et al. 2012). However, because these are monocultures, they may support only a limited portion of the pollinator community, provide resources for bees only over a limited portion of the season, and lack nutritional diversity important for bee health (Diekötter et al. 2010, Di Pasquale et al. 2013). The lack of sufficient flowering plants that provide forage for bees throughout the season is a major driver of pollinator decline in agricultural landscapes (Kremen et al. 2007, Roulston and Goodell 2011, Winfree et al. 2011, Williams et al. 2012), and there has been a recent

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surge of interest in enhancing habitat to support diverse wild and managed bees within these areas.

In Europe, government funding is available to farmers through agri-environment schemes to mitigate the loss of pollinators and other beneficial insects (Batáry et al. 2011, Haaland et al. 2011, Kleijn et al. 2011, Pywell et al. 2012). When these programs have included pollinator-specific seed mixes, they have shown clear benefits to bumble bees (Carvell et al. 2006b, Redpath-Downing et al. 2013). Efforts to enhance farmland habitat to promote biodiversity and ecosystem services in the United States have lagged behind those in Europe (but see Morandin et al. 2011, Morandin and Kremen 2013). However, recent support for pollinators through U.S. Farm Bill programs such as the Conservation Reserve Program (Vaughan and Skinner 2008) has led to the planting of 120 000 acres of habitat focused on bee conservation (Mace Vaughan, Xerces Society, Portland, Oregon, USA, *personal communication*). Despite this significant public investment in pollinator conservation, to date very few quantitative studies exist documenting the potential value of wildflower plantings to pollinator biodiversity within agricultural lands in North America (Morandin and Kremen 2013). Additionally, managers and landowners lack research-based guidance for selecting seed mixes they can plant to best support pollinators.

Understanding the characteristics that make flower mixes attractive is particularly useful. As Carvell and colleagues revealed (Carvell et al. 2006b), bumble bee visitation to different enhancement schemes strongly reflected seasonal differences in floral abundance, whereas mix composition was less important. Few studies have partitioned composition vs. display size effects on mix attractiveness. The distinction is important because if the primary mechanism by which different wildflower mixes attract greater bee richness and abundance is simply floral display (Tuell et al. 2008), then perhaps plant species identity is less critical. This would allow greater flexibility in choosing plant species and potentially reduce the cost of mixes.

The design of habitat plantings for pollinators must recognize the importance of practical implementation. Recent results from woody hedgerows highlight the great potential that long-term set-aside can have for bees in farm landscapes (Morandin and Kremen 2013), but this approach requires significant investment to establish. Annual and perennial wildflowers may better match farm management in certain contexts, and can be fitted into land that is not used for production, such as between fields, on ditch banks, and along temporary field margins. Differences in plant life history may also provide flexibility in certain contexts; for example, annual plants are expected to provide large floral displays in the first season, whereas perennials might take several seasons to develop strong bloom, but may be managed easily during establishment to promote long-term performance (Packard and Mutel 2005).

We report on a multiregion study to test the effectiveness of different types of wildflower plantings to support unmanaged bees (hereafter wild bees), honey bees, and syrphid flies. Specifically we ask: (1) Do wildflower plantings provide large floral displays among years and throughout the season? (2) Do wildflower plantings attract greater abundance and diversity of wild bees, honey bees, and syrphid flies than unenhanced areas that represent the current practice most likely to support bees in agricultural landscapes? (3) Do wildflower mixtures containing annual species differ from mixes containing perennial species in attraction of wild bees, honey bees, and syrphids? (4) Does adding greater flower diversity support greater abundance and diversity of wild bees, honey bees, and syrphids? We considered bumble bees, honey bees, and syrphid flies separately from other wild pollinators because bumble bees are a conservation concern, honey bees are key crop pollinators, and syrphid fly larvae provide pest control services.

METHODS

Study sites

The study was carried out in three regions representing major production areas of pollinator-dependent crops in the United States: the northern Central Valley of California, north-central Florida, and western Michigan (Appendix A). Within each study region, we identified three field sites located in agricultural landscapes to provide representative growing conditions and bee communities. Sites were separated within each region to ensure spatial independence of the pollinator communities responding to seed mixtures (minimum distances between sites: California 9.4 km, Florida 0.9 km, Michigan 96.5 km). Although the 0.9-km separation in Florida is within the flight distance of bumble bees, their typical foraging distances and those of other species in our study are often much shorter than 900 m (Osborne et al. 1999, Knight et al. 2005, Greenleaf et al. 2007). At each site, we established six 3×15 m plots, five of which were planted with different seed mixtures and the sixth (control) which was left to naturally regenerate with local vegetation. Specific plot preparation varied by region according to locally appropriate management practices, but at each site the plots were prepared for seeding either by tillage followed by application of glyphosate or with solarization to control weeds. At least two weeks after weed control, plots were broadcast-seeded using a handheld or walk-behind drop seeder (Appendix A). The exact timing of seeding varied by region (Appendix A). In each region, we compared annual and perennial mixes at two levels of diversity: annual diverse (8–10 species), annual basic (subset of diverse mix, 4–5 species), perennial diverse (9–11 species), perennial basic (subset of diverse mix, 5 species), and combined annual–perennial basic mixes (9–10 species) (Table 1). Seed mixtures were composed of regionally relevant native or naturalized plant species reported to be attractive to diverse wild pollinator

TABLE 1. Native and naturalized seed mixtures tested in each region; full lists represent the “diverse mix” for annual and perennial species, with basic mixes and annual–perennial combinations drawn from these as indicated.

Mixture	California diverse	Florida diverse	Michigan diverse
Annual	<i>Clarkia unguiculata</i>	<i>Chamaecrista fasciculata</i> †	<i>Agalinis tenuifolia</i>
	<i>Helianthus bolanderi</i> ‡	<i>Coreopsis basalis</i> †	<i>Chamaecrista fasciculata</i> †
	<i>Lupinus succulentus</i> †	<i>Coreopsis leavenworthii</i> †	<i>Cleome serrulata</i>
	<i>Lupinus densiflorus</i>	<i>Coreopsis tinctoria</i> ‡	<i>Coreopsis tinctoria</i> †,‡
	<i>Nemophila menziesii</i>	<i>Gaillardia pulchella</i> †,‡	<i>Froelichia floridana</i>
	<i>Phacelia tanacetifolia</i> †	<i>Ipomopsis rubra</i> ‡	<i>Linum sulcatum</i> †
	<i>Trichostema lanceolatum</i> †	<i>Phlox drummondii</i>	<i>Lobelia inflata</i> †
	<i>Trifolium fucatum</i> †	<i>Salvia coccinea</i> ‡	<i>Triodanis perfoliata</i> †
	<i>Trifolium obtusiflorum</i>	<i>Trifolium incarnatum</i> †,¶	
	<i>Trifolium willdenovii</i> †		
Perennial	<i>Achillea millefolium</i>	<i>Asclepias tuberosa</i>	<i>Asclepias syriaca</i>
	<i>Eschscholzia californica</i> †,‡	<i>Baptisia alba</i> †	<i>Dalea purpurea</i> †,§
	<i>Grindelia camporum</i> †	<i>Coreopsis lanceolata</i>	<i>Lupinus perennis</i> †
	<i>Helianthus bolanderi</i> ‡	<i>Eryngium yuccifolium</i>	<i>Monarda fistulosa</i> †
	<i>Lotus scoparius</i> †,¶	<i>Helianthus angustifolius</i>	<i>Ratibida pinnata</i>
	<i>Lupinus formosus</i> †	<i>Liatris spicata</i> †	<i>Rudbeckia hirta</i> †
	<i>Phacelia californica</i> †	<i>Monarda punctata</i> ‡	<i>Silphium perfoliatum</i>
	<i>Rudbeckia hirta</i>	<i>Rudbeckia hirta</i> †	<i>Solidago speciosa</i> †
		<i>Solidago fistulosa</i> †	<i>Symphotrichum laeve</i>
		<i>Trifolium repens</i> †,¶	<i>Symphotrichum novae-angliae</i>
	<i>Vernonia gigantea</i> †		

† Species in basic as well as diverse mixes.

‡ Species that can be annual or perennial.

§ Note that Michigan perennial mixes were designed to have a 20% representation of prairie clover (*Dalea purpurea*).

¶ *Trifolium* species in Florida are naturalized in the region, but nonnative.

Lotus scoparius = *Acmispon glaber*.

species, provide continuous sequential bloom from spring through fall, and offer a variety of floral morphologies to support a diversity of bees. Our basic mixes were selected from what we believed to be the best-performing plant species that met these criteria; thus, diverse mixes compare potential gains from adding to a nonrandom set of flowering plants. Additional selection criteria included seed availability, seed costs, and drought tolerance. We chose to work with native or naturalized plants because their presumed adaptation to environmental conditions in each region would make them less likely to require inputs such as fertilizer and irrigation (Isaacs et al. 2009). The relative treatment locations were randomized within each site to avoid neighbor bias, and plots were separated from each other by 10 m.

Sampling flowers and flower-visiting insects

To assess the functioning of each seed mixture throughout the pollinator flight season, we sampled all plots at 3–4 week intervals (hereafter sample rounds) from spring through fall of 2010 and 2011 in California (six sample rounds) and Florida (eight sample rounds). In Michigan, plots were surveyed in 2011 and 2012 (three sample rounds each year) because the short season necessitated an additional year to get mixes established. We quantified floral display based on flower area rather than flower number. We first counted the number of fresh open flowers per blooming species using 10 0.5-m² (FL, MI), or 20 0.25-m² (CA) quadrats placed randomly within five equally spaced strata along the plot. We then averaged the area of five individual

flowers per species, and these values were multiplied by flower counts to estimate total floral area per species per plot. Appendix A contains detailed methods of measuring floral areas.

We assessed attractiveness of wildflower mixes to bees and syrphid flies using timed observations and aerial netting during favorable weather conditions (clear skies, temperature >16°C, and average wind speed <3.5 m/s) within one day of floral measurements at each site. Timed observations were conducted between 07:00 and 17:00 hours for 10 minutes in the morning and 10 minutes in the afternoon on each plot. For each 10-minute observation sample, observers walked the perimeter of the plot and counted the number of individuals of each floral visitor morphotype (*A. mellifera*, *Bombus* spp., other bees, syrphids, other Diptera, Lepidoptera, other insects) that were actively visiting flowers (contacting reproductive structures of the plant). Aerial net samples of floral visitors were collected within one day of observations during two additional 10-minute periods (morning and afternoon) per plot. All netted bees were segregated according to the plant species they were visiting. Collectors attempted to observe all open flowers within each plot, so sampling effort from each plant species within a plot was in proportion to its relative floral area. During each sample round, all sites within a region were sampled in as quick succession as possible, weather permitting. All collected wild bee specimens were identified to species and accessioned in the Bohart Museum of Entomology at University of California Davis, the Albert J. Cook Arthropod Research Collection at Michigan State

University, or the PI's laboratory reference collection at University of Florida.

Analysis

For each plot we calculated the total floral area, floral species richness, total number of wild bee species, and total abundance of wild bees over the entire year. The same was done with abundance of honey bees, bumble bees, and syrphid flies. Bumble bees were also included in our main analyses of wild bees. These totals are hereafter referred to as "year-long" values to distinguish them from seasonal values (i.e., the values from pooled morning and afternoon samples during a particular sample round). Analyses of wild bee species richness are based on netted specimens. Analyses of bee and syrphid abundance are based on observations.

All analyses of flowering plants and the visitors to them were carried out separately for each region using the same modeling framework. Models were fit to the data using packages *nlme* and *lme4* in the R statistical language (Pinheiro and Bates 2000). We modeled year-long floral area as a function of year and mix identity. We modeled bee abundance and richness as a function of mix identity, log-transformed floral area, and year. We included a year \times mix interaction, if a marginal *F* test or likelihood ratio test supported its inclusion (interaction term significant at $\alpha = 0.05$). Models included random intercepts for plot and site to account for the dependence of the response variable on the same plot in different years, and for multiple planted plots at the same site. For models of wild bee abundance, species richness, and floral area, we use Gaussian errors. We modeled the abundance of honey bees, bumble bees, and syrphid flies (where data contained many zeros) as overdispersed Poisson random variables with an offset term to account for differences in sampling effort between years.

The models allow us to examine different ways that wildflower mixes can influence insect visitor abundance and wild bee species richness: (A) an identity effect of each mix, which is the change in the response variable attributable to each mix once floral area has been accounted for; (B) an independent effect of the floral area of each mix, which is the change in the response attributable to the floral area that any mix possesses on average and is calculated using the fitted relationship between floral area and the response variable; and (C) an overall effect that is the sum of the mix and floral-area effects. To evaluate the attractiveness of different wildflower mixes to wild bees and specific groups of pollinators, we focus on the overall effect.

Using the year-long models, we first tested differences in floral area between wildflower mixes and controls and among mixes themselves (Question 1) using Tukey-style pairwise comparisons (R package *multcomp* version 1.3-6; Hothorn et al. 2014). To test differences in overall effect of wildflower mixes and unenhanced controls on wild bee abundance and species richness we used the

general linear hypothesis testing framework as a way to make multiple comparisons (R package *multcomp*; Hothorn et al. 2008). We created a linear combination of the estimated coefficients for the direct effect of mix (i.e., separate intercepts for each type of mix) and the effect of mix via floral area (i.e., the coefficient for floral area multiplied by the mean floral area observed for a given mix). We then performed simultaneous multiple comparisons among treatments with this linear combination to assess whether wildflower mixes in general performed better than unenhanced controls (Question 2); whether annual mixes differed from perennial mixes (Question 3); and whether basic mixes differed from diverse mixes (Question 4). For models with a significant year \times mix interaction, we performed multiple comparisons within years.

To assess the independent contributions of floral area and mix identity to pollinator abundance and diversity, we calculated marginal (Type III) *F* tests and likelihood ratio tests (for non-Gaussian models) for the main effects of mix and floral area in the year-long models. Bumble bees can be highly specific to certain plant species; therefore, we performed an additional analysis in which we recalculated floral area using only those species that were visited by bumble bees. We then redid the year-long analysis for *Bombus* abundance using this modified floral covariate.

We used a separate set of models to evaluate seasonal performance of wildflower mixes. Linear mixed-effects models were used to fit repeated measures of floral area, wild bee abundance, and wild bee species richness across the sample rounds, separately for each year. Within each sample round, we modeled these responses as a function of mix identity by fitting intercepts for each sample round and a sample round \times mix interaction. For wild bee abundance and species richness, we also included floral area as a predictor and fitted a slope for floral area, and a floral area \times sample round interaction. These models allow differences in the response among mixes and the strength of the relationship between floral area and the response variable to vary across seasons. For these seasonal models, wild bee abundance and floral area variables were transformed as $\log(x + 1)$ prior to analysis to meet modeling assumptions. These models also included random intercepts for each site. To test if the response variables changed across season, across floral area, and among wildflower mixes (after accounting for floral area), we included the main effects of sample round, floral area, sample round \times mix interaction, and sample round \times floral area interaction using marginal (Type III) *F* tests. Results from seasonal evaluations are presented along with the year-long results for each main question.

Because plant establishment and weed encroachment varied among mixes and regions, we calculated a weighted diversity measure to assess how realized plant richness in the mixes corresponded to the plant richness intended by the experimental design. We multiplied the

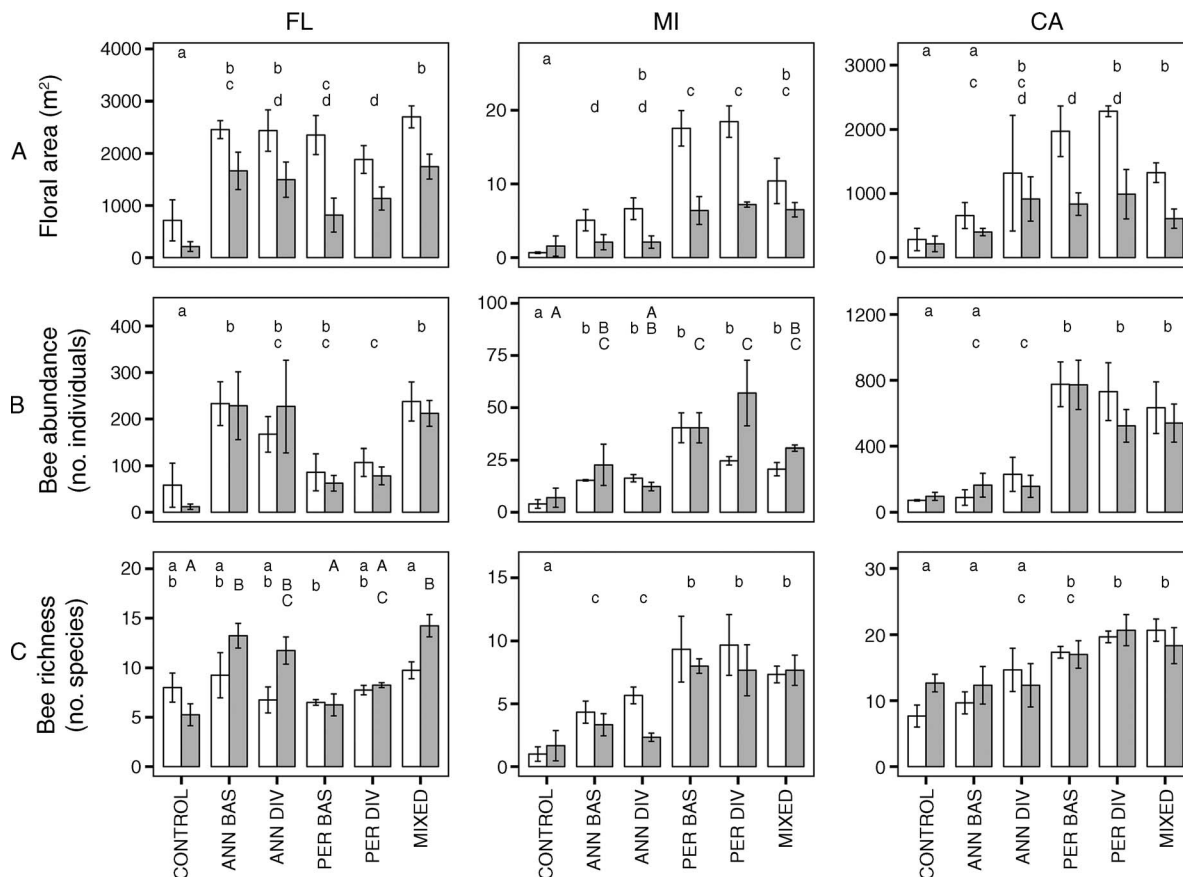


FIG. 1. Year-long totals (mean \pm SE) of (A) floral display area, (B) wild bee abundance, and (C) bee species richness for the three regions of the United States: Florida (FL), Michigan (MI), and California (CA) for Year 1 (open bars) and Year 2 (shaded bars) for various plant mixes. Each site had five plant mixture plots and a control plot of the same size. Mixes were ANN BAS, annual basic; ANN DIV, annual diverse; PER BAS, perennial basic; PER DIV, perennial diverse; MIXED, annual–perennial mix; CONTROL, no planted wildflower species. Basic mixes were a subset of the diverse mixes with half the species richness of the diverse mixes. Letters over the bars indicate significant differences based on pairwise comparisons of overall effects for floral area, bee abundance, and species richness ($\alpha = 0.05$, P values corrected for multiple comparisons). Comparisons were performed within each year, where lowercase letters indicate significant differences for both Years 1 and 2 where there was no support for a year \times mix interaction (determined by model comparison with F tests). Uppercase letters are for Year 2 where the best model included a year \times mix interaction. Note the differences in scaling of the y -axis among regions.

year-long richness of target and weed species in a plot by their respective proportional floral area. This measure effectively down-weights plants that contributed relatively little to total floral area. For the perennial and annual mixes of each region, we fit linear mixed-effects models to this weighted diversity measure. Each model had a three-way interaction that nested plant species richness (basic or diverse) within plant life-form (perennial or annual) within year. Thus we were able to independently compare annual and diverse plots within perennial and annual mixes, in each year and region.

For all models (year-long and seasonal), we graphically assessed whether the assumptions of homoscedasticity among groups and temporal independence of observations were violated. We included additional terms to account for these issues where necessary (Zuur et al. 2009).

RESULTS

Comparison among mixes for flower display

Flower mixes produced substantial floral displays in both sample years in all three regions, and, with the exception of the annual basic mix in California, year-long total display areas of mixes were consistently greater than those of control plots (Fig. 1A). The mixes that produced the most bloom differed among regions, but within each region, differences were relatively consistent between years, even though bloom area was lower in Year 2 (Fig. 1A; see Appendix B: Table B1). In Florida and California, there were no consistent differences in bloom between basic and diverse mixes or annual and perennial mixes in either year, although the perennial mixes tended to produce larger displays in California in Year 1. In Michigan, perennial mixes produced significantly larger displays than did annual

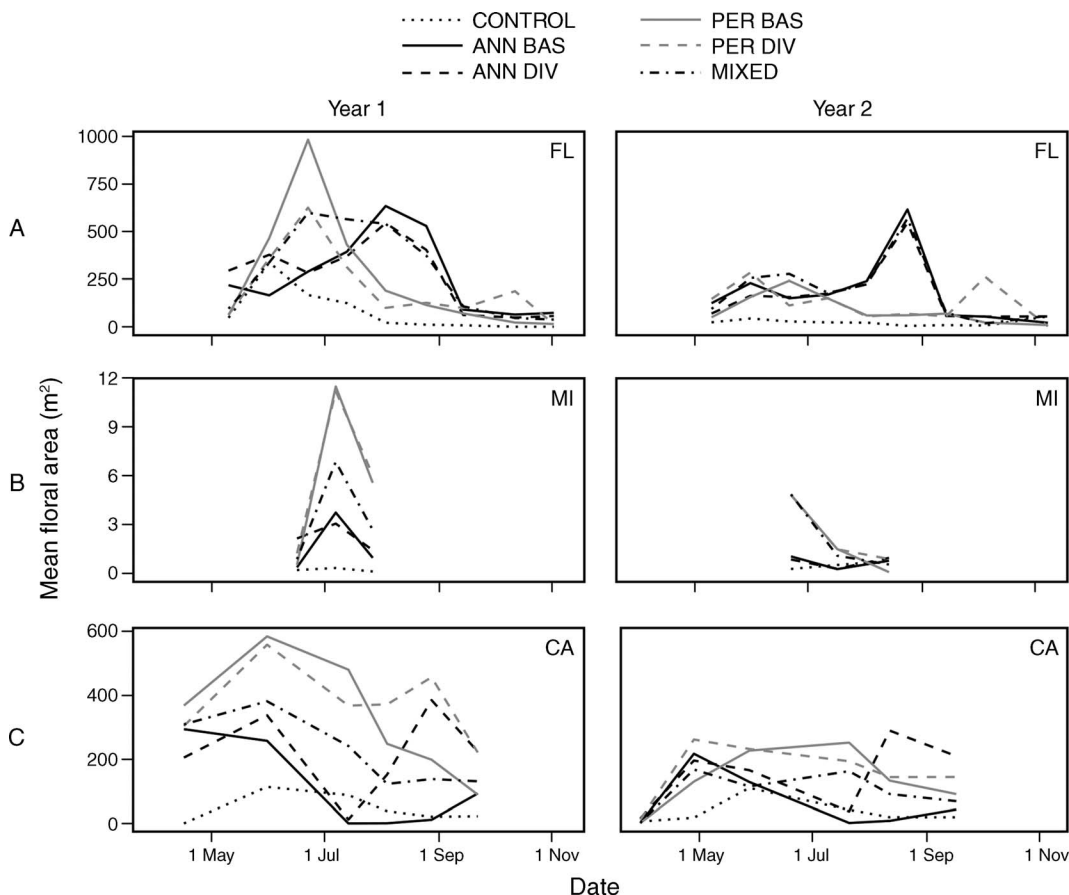


FIG. 2. Seasonal bloom patterns for Year 1 and Year 2. Data are means among three independent sites within each region in (A) Florida, (B) Michigan, and (C) California. The dotted line indicates control, black lines indicate annual mixes, gray lines indicate perennial mixes, and the dot-dash line indicates annual-perennial mix. Note differences in scaling of the y-axis among regions. Abbreviations of states and mixes are as in Fig. 1.

mixes, and the annual-perennial mix was intermediate (Fig. 1A).

Floral displays differed significantly among mixes over the season (sample round \times mix interaction, $P < 0.01$ all regions; Appendix B: Table B2); however, there were few consistent patterns or seasonal trends (Fig. 2). In Florida, the annual and perennial mixes showed somewhat complementary seasonal bloom patterns. Perennial mixes had slightly larger displays in spring, or they were equivalent to annual mixes (Fig. 2A). Annual mixes increased through the summer, peaking in August (sample rounds 5–6; Fig. 2A; Appendix B: Table B3), with the result that annual mixes had a longer bloom duration overall. In California, the annual basic mix senesced by midsummer (sample rounds 4–5), such that its bloom duration was much shorter than the other planted mixes (Fig. 2C). In the diverse annual mix, some species flowered late in the summer, adding to the bloom duration.

Although testing the impact of additional plant species richness was part of our study design, the diverse mixes did not consistently reach double the richness of

basic mixes as intended (Fig. 3; Year 1). In some cases, weedy species also contributed substantially to the display; as a result, differences in flowering plant richness between basic and diverse mixes were sometimes modest. This effect was especially evident in Michigan annual plots, where *Trifolium pratense*, *Daucus carota*, and *Erigeron* sp. were dominant weeds. In California and in the perennial plots in Michigan, the order of plant richness among the plots matched what we planted, for both years. In Florida, the order of plant richness matched what we planted in the first year but, by the second year, differences between the basic and diverse mixes were minimal (Fig. 3; Year 2).

Comparison of mixes for wild bee abundance and diversity

Wildflower mixes attracted diverse communities of wild bee species in each region: 60 species in Florida (FL), 52 in Michigan (MI), and 80 in California (CA); see Appendix C. Over 20 000 specimens were collected: 7752 in FL, 874 in MI, and 14 750 in CA. On average (all values expressed as mean \pm SE), 14.3 ± 0.2 (FL), 28.0 ± 3.5 (MI), and 48.3 ± 1.2 (CA) bee species were

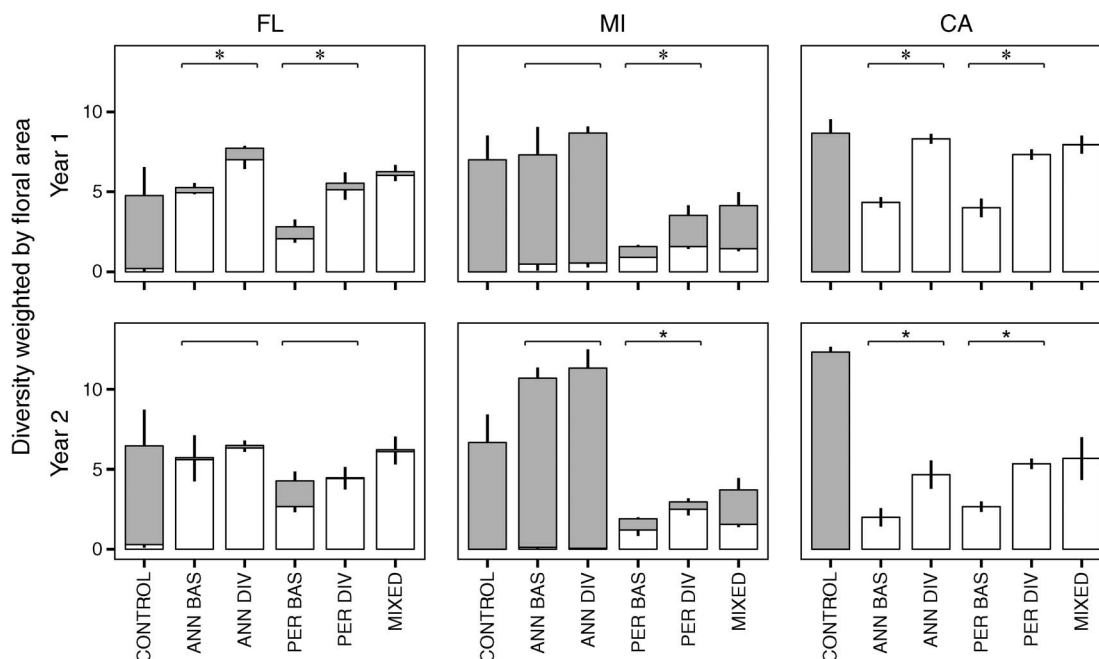


FIG. 3. Weighted flowering plant diversity (mean with SE) in each region (Florida, Michigan, and California) for Year 1 and Year 2. In each stacked bar, open bars indicate sown plant species and gray bars “weedy species.” Upward error bars are SE for total diversity and downward error bars are for sown species. An asterisk indicates significant differences between basic and diverse mixes ($\alpha = 0.05$). Comparisons were tested separately for annual and perennial mixes. Abbreviations are as in Fig. 1.

identified per wildflower mix, which exceeded that at control plots in all regions: 10.0 ± 0.4 (FL), 2.7 ± 0.4 (MI), and 14.3 ± 0.2 (CA) bee species per mix. Abundance and species richness remained high from Year 1 to Year 2 in all regions.

In all study regions, certain wildflower mixes attracted significantly more wild bees and bee species than did control plots (Fig. 1B, C). As was the case with floral area, the most attractive type of mix varied among regions. In Florida, the annual mixes tended to attract greater total abundance of wild bees (and in Year 2 more bee species) than controls or the perennial mixes, although the differences between annual and perennial mixes were not always significant. The combined annual–perennial mix performed similarly to the annual mixes. In Michigan, perennial mixes attracted a significantly greater abundance of wild bees than did controls and more species than control plots or annual mixes (Fig. 1B, C). In California, the perennial mixes attracted significantly greater abundance and more species of wild bees than did controls or annual mixes, although the difference between annual diverse and perennial basic was not significant for wild bee richness (Fig. 1C). The combined annual–perennial mixes performed similarly to the perennial mixes in both Michigan and California. The response of bees to increased floral diversity of the mixes was variable and differences were never significant for any region (Fig. 1).

In all regions, the mixes showed seasonal shifts in the abundance of wild bees visiting them (significant sample

round \times mix interaction; $P < 0.01$, except for Michigan in Year 2; Appendix B: Table B2, Appendix D). Seasonal shifts were less dramatic for wild bee diversity (Appendix B: Table B2). These shifts probably contributed to the differences in total wild bee abundance for California. There, all mixes attracted similar numbers of bees and bee species in spring. Mixes containing perennials attracted a greater abundance of wild bees in summer through fall than did annual mixes (sample rounds 4–6, annual–perennial contrast; Appendix B: Table B3). The seasonal pattern of wild bee richness was broadly similar to that for abundance, but the differences among mixes were less dramatic and not consistently significant. New bee species continued to arrive late in the season at plots containing perennial mixes and the annual–diverse mix in which two new flower species bloomed (Appendix B: Table B3, Appendix D).

The role of floral display in attracting pollinators

Floral area was an important predictor of the abundance and often also the species richness of wild bees collected on the different wildflower plots. Residual year-long floral area strongly predicted the total abundance of wild bees per plot in all regions independent of mix identity and, in California and Michigan, it also strongly predicted total species richness of bees per plot (Fig. 4). Floral area was less predictive for individual pollinator groups; only honey bee visitation in California was significantly associated

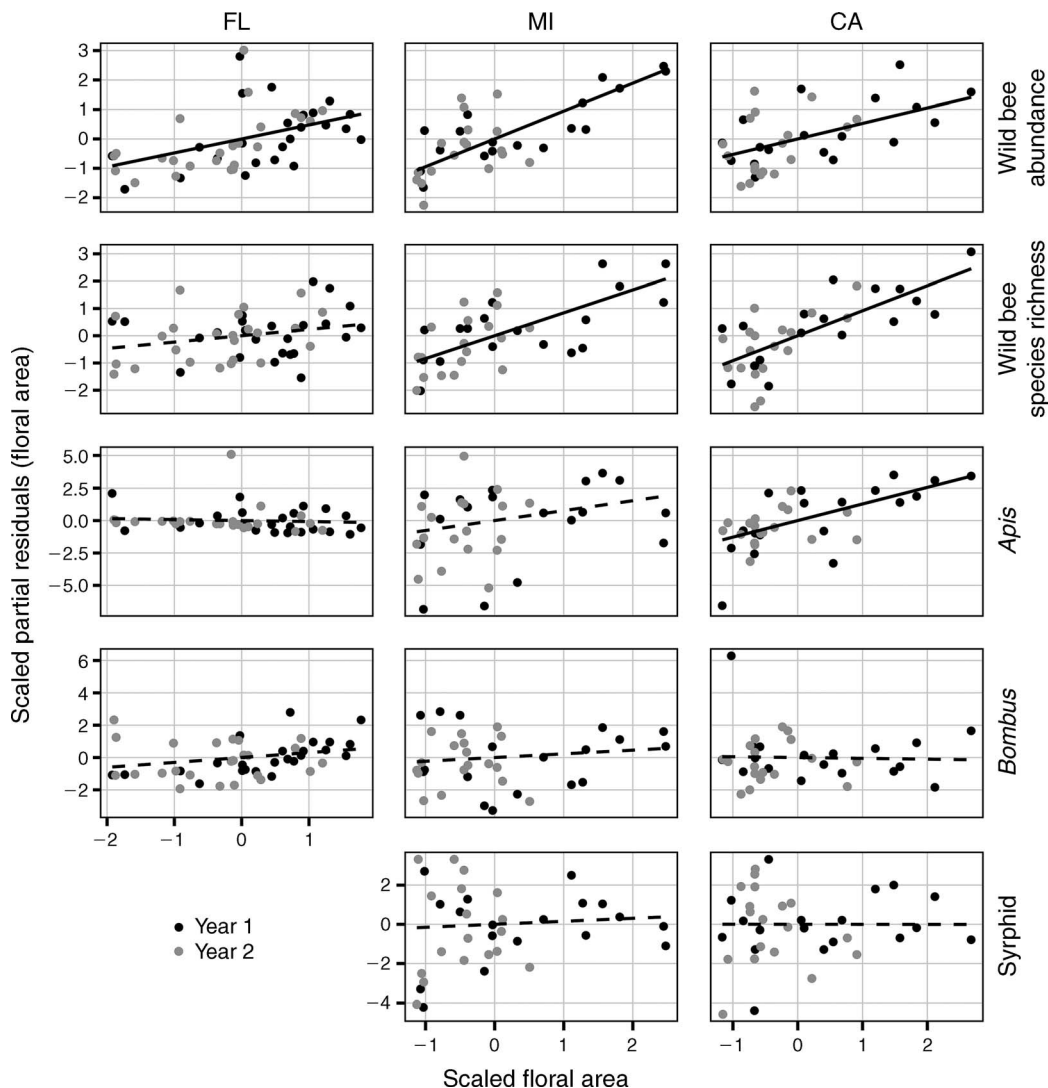


FIG. 4. Partial residual plots illustrating the effect of floral area on year-long totals per plot for different response variables in each region (Florida, Michigan, and California) for Years 1 (black circles) and 2 (gray circles): wild bee abundance, wild bee species richness, honey bee abundance, bumble bee abundance, and syrphid abundance. In each case, the use of partial residuals controlled for effects of floral mix and year, as well as their interaction where an F test (or likelihood ratio test for non-Gaussian response variables) supported its inclusion. Solid lines indicate significant slopes and dashed lines indicate nonsignificant slopes ($\alpha = 0.05$).

with it. In California, bumble bee abundance was significantly associated with the floral area of the subset of plants visited by the control plots, which had substantially fewer flowers used by bumble bees than did wildflower mixes.

Responses of key pollinator groups

The attraction of the mixes to honey bees differed somewhat from the patterns for wild bees, depending on the region (Fig. 5A; Appendix B: Table B1). In Florida, there were too few honey bee data to accurately test differences among the mixes, although there were notably no honey bee visits to either perennial mix. In

Michigan, the numbers of honey bees per plot did not differ significantly between wildflower mixes and weedy control plots, nor among the mixes themselves (Fig. 5A). In California, honey bees responded strongly to wildflower plantings compared to control plots. In Year 1, annual wildflower mixes attracted significantly more honey bees than did the control plots (Fig. 5A). In Year 2, all mixes attracted more honey bees than the control plots.

In all three regions, some wildflower mixes generally attracted many more bumble bees than control plots, which received few if any visits (Fig. 5B; Appendix B: Table B1). The relative performance of mixes differed among regions. In Florida, wildflower mixes containing

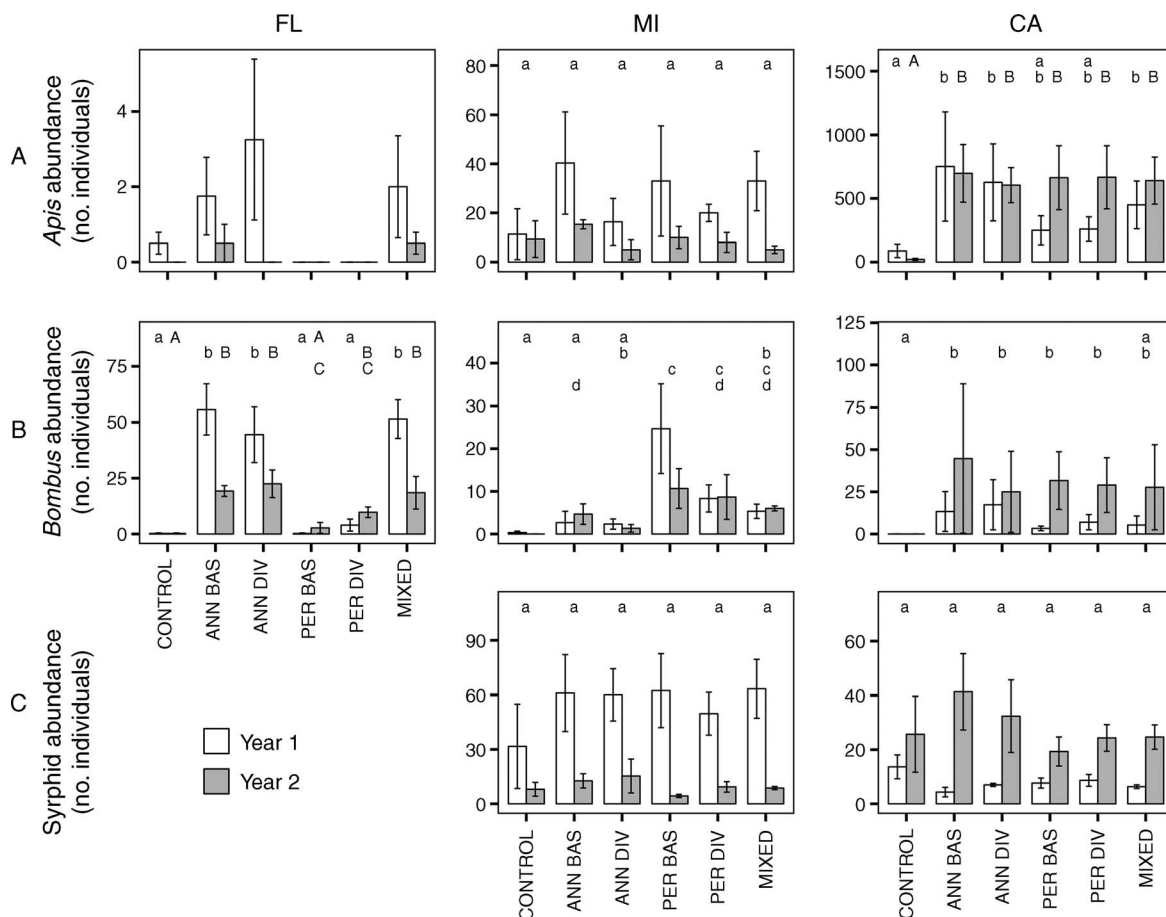


FIG. 5. Year-long totals of abundance for (A) *Apis mellifera*, (B) *Bombus* spp., and (C) syrphid flies for the three regions, Florida (FL), Michigan (MI), and California (CA) in Years 1 (open bars) and 2 (shaded bars). Letters over the bars indicate significant differences based on pairwise comparisons ($\alpha = 0.05$, P values corrected for multiple comparisons). Comparisons were performed within each year; lowercase letters indicate significant differences for both Years 1 and 2 where there was no support for a year \times mix interaction (determined by model comparison with likelihood ratio tests). Uppercase letters are for Year 2 where the best model included a year \times mix interaction. Mix abbreviations are as in Fig. 1. In Florida, there were no observations of syrphid flies, and insufficient data to test for differences among mixes in honey bee abundance, so significance testing was limited for that region. Note differences in scaling of the y-axis among regions.

annuals, including the annual–perennial mix, were most attractive to bumble bees. In Michigan, the perennial mixes attracted significantly more bumble bees than either the annual mixes or the annual–perennial mix. In California, mixes were all similarly attractive to bumble bees (Fig. 5B).

The response of syrphids to wildflower mixes could not be tested in Florida due to lack of data; however, in both Michigan and California, they were similarly abundant among all wildflower mixes and the controls (Fig. 5C; Appendix B: Table B1). The most striking effect was the contrast between years. In 2011 (Year 1 for MI and Year 2 for CA), syrphids were three times more abundant than they were in the other year.

DISCUSSION

Our study shows the great potential of wildflower mixes to attract wild pollinators and to support honey

bees in agricultural landscapes. Very few published studies exist that assess targeted plantings for pollinators, particularly in North America (Carvell et al. 2006b, Morandin and Kremen 2013), and none compare similar approaches among geographic regions. Our results highlight the importance of using mixes of flower species that provide abundant season-long bloom rather than those simply containing higher flower diversity. They highlight regional and seasonal variation in the amount of flower resources provided by plantings and in the response of bees. The mixtures of wildflowers supported at least 11% more species richness and over 60% more wild bee abundance than that found in unmanaged weedy control areas. In some cases, specific seed mixes contained over 10 times the number of bees found on the control plots.

The type of plant mix (annuals vs. perennials) that attracted the greatest bee abundance and/or diversity

differed among study regions; in Florida it was annual-containing mixes, whereas in Michigan and California, it was perennial mixes. We tested separate annual and perennial mixes because we expected plants with these life histories to offer complementary benefits. Annual species were expected to flower strongly in the first year and be ideal for applications where immediate bloom is desired, whereas perennial species might take an additional year or two to establish and produce strong bloom, but would then persist more reliably for multiple seasons. We found little evidence for such differences between plant types in California or in Florida. Perennial mixes produced large displays during Year 1 in these regions and the relative bloom area among mixes was consistent from Year 1 to Year 2. This result suggests that even where immediate bloom is desired, flower mixes need not target annuals, but instead should focus on plant species that support the most abundant and diverse pollinators and that, as a mixture, provide season-long bloom. Differences in phenology among some annuals and perennials further support the suggestion that wildflower mixes that include both plant types might better achieve season-long bloom. In Michigan, the superior performance of perennial species supports the use of mixes containing species with this life history to provide long-term resources for pollinators.

Stability over time

Existing data on the performance of wildflower plantings over time are relatively uncommon, but they can show decreases in flower density over successive seasons (Pakeman et al. 2002, Wilkerson et al. 2014). In Europe where most comparisons of wildflower plantings for pollinators have been conducted, recommendations are that wildflower strips be plowed and restarted after a maximum of 7 years (but see Blake et al. 2011, Haaland et al. 2011). In our study, which included the first two years post-establishment, flowers were less abundant in all mixes in the second year compared to the first (reductions were 36% in Florida, 57% in Michigan, 40% in California). Floral resources might be better maintained beyond the year of establishment with modified region-specific management regimes. Studies in the UK have suggested that annual fall mowing with thatch removal can improve reseeded of sown species and reduce grass and broadleaf weed dominance (Carvell et al. 2007). Nonetheless, mixes in this study remained highly attractive to bees and other floral visitors in the second season. Neither the number of individuals collected nor bee species richness declined in a consistent way among the mixes for any region. Performance among mixes was also surprisingly consistent between the two years. Although there were significant mix \times year interactions for wild bee abundance and, in some regions, for wild bee richness, the order of performance among mixes remained consistent between Year 1 and Year 2 for both response variables. The one exception

was for Michigan, where the perennial diverse mix attracted the greatest number of bees in Year 2, perhaps in response to the increasing floral area from a plant species that took the additional year to establish. In that year (2012), Michigan also experienced a severe drought that limited bloom as well as bee populations (Karl et al. 2012), and this also may have resulted in native perennial plants outperforming the nonnative weeds in the landscape, leading to enhanced performance relative to the other mixes and control (Tilman and El Haddi 1992). We encourage future longer-term monitoring of plantings to quantify the dynamics of wildflower bloom and pollinator responses across variable interannual weather conditions.

The role of floral display and flower phenology

The simplest explanation for differences in best mixes among regions, and indeed for the success of pollinator mixes in general, would be that those attracting the greatest number of bees and bee species had larger flower displays and rewards through the season. Indeed, when we partitioned out the direct effects of seed mix to examine the effects of floral area, it was a strong predictor of abundance in all regions, and also was significantly correlated with wild bee richness in California and Michigan. Florida showed this same trend for richness, although it was not significant. Our results agree with those of Tuell et al. (2008), who compared individual wildflower species for their attractiveness to honey bees and wild bees. Such differences in the year-long floral display potentially result from differences in flower abundance at specific times, and/or differences in flowering duration. In Florida and California, mixes whose bloom persisted longer through the season attracted more individuals and species of wild bees; these were annual mixes for Florida and perennial mixes for California. A similar effect of longer bloom duration appears to be critical to the success of wildflower mixes for promoting bumble bee abundance and diversity in the UK (Redpath-Downing et al. 2013). This extended bloom, in part, is produced by complementarity in phenology among species within mixes.

The larger displays and greater attraction of perennial species in Michigan highlight the benefit of developing native perennial seed mixes for supporting pollinators in the Midwest region of the USA, where these plants can provide multiple seasons of bloom and may be better adapted to survive the fluctuating weather conditions predicted to become more common in this region (Tilman and El Haddi 1992, Wuebbles et al. 2014).

Mix diversity

A persistent question in restoration ecology is how many species are required to achieve successful functioning: in our case, support of diverse pollinator communities. Among all regions, high-diversity mixes failed to support higher abundance or higher species

richness of wild bees. Compared to differences among annuals and perennials or among seasons, differences between basic and diverse mixes were minor. Two aspects of the mixes are important to consider. First, we did not select the composition of the basic mix randomly from a more diverse pool, but instead chose the basic mixes to support the greatest number of pollinators and provide continuous bloom throughout the growing season. In each region, the basic mixes often contained the strongest performing plants and provided season-long bloom; thus, adding more plant species had limited impact. Second, realized diversity of mixes rarely reached what we seeded, in part because of flowering weeds (nontarget species); in some cases, there was little difference in realized richness between basic and diverse mixes.

These results have important practical implications when deciding where to invest limited funds for pollinator conservation. Plant identity and mix composition are critical. It is possible to achieve highly attractive mixes with a simpler species composition; however, because of inconsistencies in realized richness between our study regions, the question of whether greater flowering plant richness can enhance pollinator diversity requires further testing. Determining the identity and number of plant species that provide the greatest support for pollinator diversity and abundance for a given cost is a priority for future investigation, as are methods to achieve high diversity within planted wildflower mixes. It is important to recognize that, in some cases, plots might take multiple years to show their true diversity and adding additional plant diversity to increase resilience in the face of variable weather and changing climate will be important (Folke et al. 2004).

Key pollinator groups

Bumble bees are a wild bee group that provide significant pollination services to many crops (Greenleaf and Kremen 2006, Artz and Nault 2011) and are of particular conservation concern both in North America and Europe, where habitat loss has contributed to the decline of multiple species (Goulson et al. 2005, Williams and Osborne 2009). Wildflower mixes in all of our study regions provided resources for bumble bees, which were absent from control plots entirely. Similarly strong responses of bumble bees to wildflower mixes are reported from the UK (Pywell et al. 2005, Carvell et al. 2006b, Redpath-Downing et al. 2013). In these cases, the wildflower mixes provided higher quality pollen and nectar resources critical to bumble bees (Hanley et al. 2008) and plant diversity promoted flowering throughout the flight season (Redpath-Downing et al. 2013).

Our results suggest that managed honey bees also can benefit from the provision of floral resources such as those tested here. Similar investigation of wildflower mixes in the UK (Carvell et al. 2006b) showed contrasting patterns of visitation between honey bees and certain wild bee species, and earlier evaluations of

individual native plant species in Michigan revealed contrasting responses between wild bees and honey bees (Tuell et al. 2008). Loss of forage resources for honey bees within agricultural landscapes, in particular the lowered diversity of pollen and nectar sources, is identified by bee keepers as a primary threat affecting colony strength (National Honey Bee Health Stakeholder Conference Steering Committee 2012). Augmentation of floral resources by planting diverse, drought-tolerant native plant mixes thus offers considerable promise for honey bees in these landscapes. No strong differences among wildflower mixes were obvious in our study, except that the wildflower mixes tested in California were visited more by honey bees than were the weedy control plots. The relative unattractiveness of all plots in Florida may simply reflect low numbers of colonies kept in the study landscapes.

Such differences in attractiveness among bee groups highlight the need to carefully articulate the goals of a wildflower planting so that appropriate plant species are selected. Our primary goal was support of wild bee species, but where multiple goals can be met, these should be included in the plant selection process (N. M. Williams and E. Lonsdorf, *unpublished manuscript*).

All mixes supported syrphid flies in Michigan and in California, but no more so than did the control plots. Syrphid flies can be important pollinators in some agricultural systems and their larvae provide biological control of some pest insects (Fontaine et al. 2006, Jauker and Wolters 2008). These insects are also threatened by land use change and habitat loss (Biesmeijer et al. 2006, Jauker et al. 2009, Meyer et al. 2009) and are expected to be enhanced by the addition of wildflower habitats to farmland. As may be the case for honey bees in Florida, support of these species by wildflower plantings may require more targeted plant selection.

CONCLUSIONS

Our results are a first step toward assessing the role of native wildflower plantings for supporting pollinators across North America and suggest great promise as a means to promote pollinator biodiversity and also potentially their pollination services. We confirm the importance of sustained flowering over the season for supporting the greatest diversity of pollinators and suggest that regional assessment of pollinator-attractive mixes be expanded to learn more about how pollinator attraction varies with the seed diversity, seed source proximity, seed cost, seeding density, and soil type. These plantings were attracting bees from across the local landscape, but we do not yet know whether they increased bee populations or simply attracted them at the expense of other areas. In this regard, our investigation is similar to recent investigations in Europe that have demonstrated the value of crop border plantings to support bumble bees and other groups (Pywell et al. 2005, Carvell et al. 2006b). A next important step in our work and elsewhere must be to

separate out potential behavioral responses, or aggregative responses (Heard et al. 2007) from true population effects, either through coordinated assessments of individual bee fecundity (e.g., Williams and Kremen 2007) or robust population assessments, such as with occupancy analysis (MacKenzie et al. 2003). Although there is much yet to learn about how to optimize this practice for sustaining pollinators in the United States, our results provide support for this approach to pollinator conservation on farmland and demonstrate that significant enhancement can be realized within a few years.

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LITERATURE CITED

- Artz, D. R., and B. A. Nault. 2011. Performance of *Apis mellifera*, *Bombus impatiens*, and *Peponapis pruinosa* (Hymenoptera: Apidae) as pollinators of pumpkin. *Journal of Economic Entomology* 104:1153–1161.
- Batáry, P., A. Báldi, D. Kleijn, and T. Tschardtke. 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society B* 278:1894–1902.
- Biesmeijer, J. C., et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313:351–354.
- Blake, R. J., B. A. Woodcock, D. B. Westbury, P. Sutton, and S. G. Potts. 2011. New tools to boost butterfly habitat quality in existing grass buffer strips. *Journal of Insect Conservation* 15:221–232.
- Carvell, C., W. R. Meek, R. F. Pywell, D. Goulson, and M. Nowakowski. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology* 44:29–40.
- Carvell, C., D. B. Roy, S. M. Smart, R. F. Pywell, C. D. Preston, and D. Goulson. 2006a. Declines in forage availability for bumblebees at a national scale. *Biological Conservation* 132:481–489.
- Carvell, C., P. Westrich, W. R. Meek, R. F. Pywell, and M. Nowakowski. 2006b. Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. *Apidologie* 37:326–340.
- Di Pasquale, G., M. Salignon, Y. Le Conte, L. P. Belzunces, A. Decourtye, A. Kretschmar, S. Suchail, J.-L. Brunet, and C. Alaux. 2013. Influence of pollen nutrition on honey bee health: do pollen quality and diversity matter? *PLoS ONE* 8:e72016.
- Diekötter, T., T. Kadoya, F. Peter, V. Wolters, and F. Jauker. 2010. Oilseed rape crops distort plant–pollinator interactions. *Journal of Applied Ecology* 47:209–214.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- Fontaine, C., I. Dajoz, J. Meriguet, and M. Loreau. 2006. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology* 4:129–135.
- Goulson, D., M. E. Hanley, B. Darvill, J. S. Ellis, and M. E. Knight. 2005. Causes of rarity in bumblebees. *Biological Conservation* 122:1–8.
- Greenleaf, S. S., and C. Kremen. 2006. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation* 133:81–87.
- Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153:589–596.
- Haaland, C., R. E. Naisbit, and L. F. Bersier. 2011. Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity* 4:60–80.
- Hanley, M. E., M. Franco, S. Pichon, B. Darvill, and D. Goulson. 2008. Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Functional Ecology* 22:592–598.
- Heard, M. S., C. Carvell, N. L. Carreck, P. Rothery, J. L. Osborne, and A. F. G. Bourke. 2007. Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. *Biology Letters* 3:638–641.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50:346–363.
- Hothorn, T., F. Bretz, P. Westfall, R. M. Heiberger, A. Schuetzenmeister, and S. Scheibe. 2014. Multcomp: simultaneous inference in general parametric models. Version 1.3-6. <https://cran.r-project.org/web/packages/multcomp/>
- Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment* 7:196–203.
- Jauker, F., T. Diekötter, F. Schwarzbach, and V. Wolters. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology* 24:547–555.
- Jauker, F., F. Peters, V. Wolters, and T. Diekötter. 2012. Early reproductive benefits of mass-flowering crops to the solitary bee *Osmia rufa* outbalance post-flowering disadvantages. *Basic and Applied Ecology* 13:268–276.
- Jauker, F., and V. Wolters. 2008. Hover flies are efficient pollinators of oilseed rape. *Oecologia* 156:819–823.
- Jorgenson, D. W., and F. M. Gollop. 1992. Productivity growth in U.S. agriculture: a postwar perspective. *American Journal of Agricultural Economics* 74:745–750.
- Karl, T. R., et al. 2012. U.S. temperature and drought: recent anomalies and trends. *Eos, Transactions of the American Geophysical Union* 93:473–474.
- Kleijn, D., M. Rundlöf, J. Scheper, H. G. Smith, and T. Tschardtke. 2011. Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology and Evolution* 26:474–481.
- Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tschardtke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B* 274:303–313.

- Knight, M. E., A. P. Martin, S. Bishop, J. L. Osborne, R. J. Hale, R. A. Sanderson, and D. Goulson. 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology* 14:1811–1820.
- Kremen, C., et al. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10:299–314.
- Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences USA* 99:16812–16816.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.
- Meyer, B., F. Jauker, and I. Steffan-Dewenter. 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic and Applied Ecology* 10:178–186.
- Morandin, L., R. F. Long, C. Pease, and C. Kremen. 2011. Hedgerows enhance beneficial insects on farms in California's Central Valley. *California Agriculture* 65:197–201.
- Morandin, L. A., and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications* 23:829–839.
- National Honey Bee Health Stakeholder Conference Steering Committee. 2012. Report on the National Stakeholders Conference on Honey Bee Health, 15–17 October 2012. USDA, Alexandria, Virginia, USA.
- Osborne, J. L., S. J. Clark, R. J. Morris, I. H. Williams, J. R. Riley, A. D. Smith, D. R. Reynolds, and A. S. Edwards. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* 36:519–533.
- Packard, S., and C. F. Mutel. 2005. *The tallgrass restoration handbook*. Island Press, Washington, D.C., USA.
- Pakeman, R. J., R. F. Pywell, and T. C. E. Wells. 2002. Species spread and persistence: implications for experimental design and habitat re-creation. *Applied Vegetation Science* 5:75–86.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-effects models in S and S-PLUS*. Springer, New York, New York, USA.
- Pywell, R. F., M. S. Heard, R. B. Bradbury, S. Hinsley, M. Nowakowski, K. J. Walker, and J. M. Bullock. 2012. Wildlife-friendly farming benefits rare birds, bees and plants. *Biology Letters* 8:772–775.
- Pywell, R. F., E. A. Warman, C. Carvell, T. H. Sparks, L. V. Dicks, D. Bennett, A. Wright, C. N. R. Critchley, and A. Sherwood. 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation* 121:479–494.
- Redpath-Downing, N. A., D. Beaumont, K. Park, and D. Goulson. 2013. Restoration and management of machair grassland for the conservation of bumblebees. *Journal of Insect Conservation* 17:491–502.
- Roulston, T. H., and K. Goodell. 2011. The role of resources and risks in regulating wild bee populations. *Annual Review of Ecology and Systematics* 56:293–312.
- Tilman, D., and A. El Haddi. 1992. Drought and biodiversity in grasslands. *Oecologia* 89:257–264.
- Tuell, J. K., A. K. Fiedler, D. Landis, and R. Isaacs. 2008. Visitation by wild and managed bees (Hymenoptera: Apoidea) to eastern U.S. native plants for use in conservation programs. *Environmental Entomology* 37:707–718.
- Vaughan, M., and M. Skinner. 2008. *Using Farm Bill programs for pollinator conservation*. USDA Natural Resources Conservation Service, Washington, D.C., USA.
- Westphal, C., I. Steffan-Dewenter, and T. Tschardt. 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters* 6:961–965.
- Wilkerson, M. L., K. L. Ward, N. M. Williams, K. S. Ullmann, and T. P. Young. 2014. Diminishing returns from higher density restoration seedings suggest tradeoffs in pollinator seed mixes. *Restoration Ecology* 22:782–789.
- Williams, N. M., and C. Kremen. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications* 17:910–921.
- Williams, N. M., J. Regetz, and C. Kremen. 2012. Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. *Ecology* 93:1049–1058.
- Williams, P. H., and J. L. Osborne. 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie* 40:367–387.
- Winfree, R., I. Bartomeus, and D. P. Cariveau. 2011. Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution, and Systematics* 42:1–22.
- Wuebbles, D. J., K. Kunkel, M. Wehner, and Z. Zobel. 2014. Severe weather in United States under a changing climate. *Eos, Transactions American Geophysical Union* 95:149–150.
- Zuur, A., E. N. Leno, N. Walker, and A. Saveliev. 2009. *Mixed effect models and extensions in ecology with R*. Springer, New York, New York, USA.

SUPPLEMENTAL MATERIAL

Ecological Archives

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