CONSERVATION INNOVATION GRANT
Final Project Report

Project Title: Next Steps in Pollinator Conservation: Operations and Maintenance, Organic Habitat Restoration, Expanding Seed Mix Choices, and Assessing Conservation Effectiveness

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Timeframe Covered by Report: 9/1/12–8/31/16

Agreement Number: 69-3A75-12-253

Date Report Submitted: 11/18/16

Project-Specific Deliverables Identified in Grant Agreement:

- Long-term Operations and Maintenance Technical Guides for pollinator habitat (including case studies) for New England, the Mid-Atlantic, the Pacific Northwest, California, and Florida
- An Organic Habitat Restoration Technical Guide and demonstration sites at organic farms
- Production guidelines for previously unavailable pollen and nectar resource plants. New commercial sources for 6 to 10 high value pollinator plants that are not currently available
- At least 3 in-field trainings on Operations and Maintenance in at least 3 states
- • At least 3 in-field trainings on Organic Habitat Restoration for NRCS and organic producers
- National webinars on the Next Steps in Pollinator Conservation objectives
- Documentation of native plant values to honey bees
- Efficacy documentation of Operations and Maintenance activities in New Jersey
- Development of scientific articles and case studies on the effectiveness of NRCS efforts for pollinator conservation

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Executive Summary

Next Steps in Pollinator Conservation created field-tested guidance previously lacking for operations and maintenance of on-farm pollinator habitat plantings and habitat establishment using organic methods to strengthen existing NRCS pollinator conservation practices. In addition, this project bolstered supplies of native seeds that were previously unavailable for pollinator plantings and developed resources to help seed producers and conservation practitioners increase the seed supplies of high-value plants for pollinator conservation. In collaboration with academic partners, we assessed conservation effectiveness of existing pollinator conservation practices to help determine which NRCS efforts have been most successful and what additional technology is needed.

Over the four-year project period, we conducted field trials in eight states that evaluated management methods influencing the longevity of pollinator habitat, tested organic site preparation methods for establishing pollinator habitat, and investigated germination, propagation, and harvesting methods for high-value wildflower species that benefit pollinators. Multi-year assessments of native bees, honey bees, and other beneficial insects were conducted in California and New Jersey that documented the effectiveness of NRCS practices for supporting pollinators. In Minnesota, data was collected on the floral preferences of honey bees.

This project culminated in a series of publications that describe methods and costs associated with establishing wildflower meadows and hedgerows, methods for maintaining pollinator habitat, and strategies for increasing seed of wildflowers valuable to pollinators. In addition, our results were shared during farm field days, conferences, and other events where we reached over 5,000 farmers, NRCS staff, and other participants.

Through this project, we developed new organic site preparation guidance that includes practices, such as sheet mulching, that had not been addressed in other NRCS materials. In our organic habitat establishment trials, we found that solarization consistently outperformed other methods. Cost estimates for establishing wildflower plantings using solarization were developed and incorporated into a fact sheet. Guidance on solarization and smother cropping is significantly updated from other materials developed by the NRCS in the past.

We also identified recommended management techniques for either maintaining existing diversity or controlling weeds in habitat plantings. We found that using an active, adaptive management approach and scheduling management actions for highest impact maximized management effectiveness. Our operations and maintenance guidance offers innovative new components including flow charts and a decision matrix to help landowners and conservation planners best assess current site conditions and make decisions about O & M strategies.

By focusing on overcoming the production challenges for wildflower species, we have helped boost yields and make unique, highly valuable plants to pollinators widely available in the seed market. We brought 10 pollinator plant species to market that had been completely absent from the market or in limited supply, producing nearly 250 pounds of seed during the grant period. Four additional species are currently in the early stages of production and will be harvested in the coming years.

Native thistles are one group of plants that is gaining popularity for their recognized value to pollinators. In light of the challenges faced by native seed producers trying to grow native thistle species for prairie and pollinator conservation projects, we developed new guidance for conservation practitioners that will help native seed industry make a major step forward in making this seed more available.

Hedgerows are an increasingly valued tool for pollinator conservation, as they are relatively easy to establish and maintain, and they provide many other benefits for landowners in terms of wildlife habitat, farm beautification, wind and water erosion reduction, and beneficial insects that attack crop pests. New data from this project in California show that the inclusion of forb plantings in pollinator hedgerows is worthwhile in terms of the abundance and diversity of wild bees supported, and that forbs increase in their ability to support bees even while planted shrubs decline during drought.

Our results demonstrate that NRCS practices for installing pollinator habitat enhancements successfully attract native pollinators when they are implemented well. As successful habitat enhancements aged, plant communities within habitat enhancements varied with time, but contrary to our earlier prediction, they continued to attract a diverse assemblage of native bees. Data from New Jersey also showed that honey bees use, but do not prefer, native habitat enhancements, which suggests that there may be trade-offs in creating habitat enhancements for honey bees and native bees. Research conducted by the University of Minnesota identified native wildflower species used by honey bees including spiderwort, Culver's root, sumac, basswood, goldenrod, and aster, as well non-native legumes.

Introduction

Next Steps in Pollinator Conservation was a four-part project that supported NRCS clients by (1) developing long-term operations and maintenance guidance for established habitat; (2) testing habitat restoration practices for organic producers; (3) increasing the availability of critical plant materials; and (4) documenting the effectiveness of NRCS practices for supporting pollinators.

The goals and tasks for each objective are summarized below. All project activities were conducted from 2012 to 2016. See map (Figure 1) for locations of all project sites.

Objective 1: Developing long-term operations and maintenance guidance for established habitat

Goals: Evaluate management factors that influence the longevity of pollinator habitat; Test management treatments; Document costs; Develop long-term habitat management guidelines

Working with local partners, we tested and documented ongoing weed management strategies for wildflower meadows, techniques for regaining wildflower diversity when it declines, and methods for expanding habitat size/structure with additional plant materials—including plant materials propagated from already restored habitat. The selected weed management strategies minimize harm to pollinators, through techniques such as spot herbicide applications, localized mowing, burning, grazing, and other techniques.

Our findings were incorporated into a technical guide that will help growers perform maintenance and operations on existing pollinator plantings. *Maintaining Diverse Stands of*

Wildflowers Planted for Pollinators: Ongoing Management of Pollinator Habitat (see Appendix C) outlines management techniques that sustain and increase diversity of wildflowers in existing stands of vegetation. This publication includes case studies from across the country.

Objective 2: Testing habitat restoration practices for organic producers

Goals: Establish test plots where organic site preparation treatments will be tested; Develop seeding rates and species selection to maximize competitive advantage over weeds.

The Xerces Society conducted organic wildflower establishment field trials with EQIP-eligible producers in the eastern, midwestern, and western United States. Our objective was to gather information about the effectiveness of each method, and to compile this guidance as a resource for organic producers. We tested seven organic site preparation approaches: solarizing, smother cropping, sheet mulching, repeated shallow cultivating, soil inversion, organic herbicides, and sod removal. In each case, we documented cost and effectiveness. At the conclusion of these trials, we developed the guide *Wildflower Establishment: Organic Site Preparation Methods* (see Appendix C), summarizing the primary organic site preparation techniques we used to establish pollinator habitat. An additional fact sheet (see Appendix C) outlines an estimate of the materials and labor associated with establishing wildflower plantings using solarization, one of the most effective organic site preparation methods across regions that we tested.

Objective 3: Increasing the availability of critical plant materials

Goals: Identify currently unavailable, high- value wildflower species (based upon previously documented bee and beneficial insect visitation rates); Investigate germination, propagation, and harvesting methodologies; Bring these additional species to market to expand restoration options.

Beginning with plants where high rates of visitation by bees, butterflies (especially monarch butterflies), and beneficial insects have been documented, we screened candidate species for commercial potential. These screening requirements included ease of germination, propagation, and harvesting, as well as the elimination of species that are weedy or alternate hosts for crop pests and disease. Information was gathered in consultation with a variety of sources, including native seed producers and NRCS Plant Materials Specialists.

We surpassed our initial goal, which was to identify local ecotype seed sources for six to ten candidate species, working with 14 native species over the course of the project. We partnered with private native plant nurseries in five states (California, Indiana, Minnesota, Oregon, and Texas) to conduct propagation field trials, identify production challenges, and establish solid stands up to 1 acre in size for mass seed production.

Project results were summarized in our publication *Increasing Seed of Wildflowers Valuable to Pollinators: Xerces Society and Seed Producer Partnerships* (see Appendix C), which describes the establishment of native plants for commercial seed production. A new guide for farmers, *Expanding Pollinator Habitat on Farms: Collecting and Using Your Own Wildflower Seed* (see Appendix C), outlines the basic steps of collecting native plant seed using readily available, non-specialized equipment. In addition, we developed a new publication called *Native Thistles: A Conservation Practitioner's Guide. Plant Ecology, Seed Production Methods, and Habitat Restoration Opportunities* (see Appendix C) to support native seed producers and conservation practitioners in the conservation of these important plants.

Objective 4: Documenting the effectiveness of NRCS practices for supporting pollinators

Working with four academic partners, University of California Berkeley, University of California Davis, Rutgers University, and University of Minnesota, our objective was to provide feedback on the long-term effectiveness of NRCS practices for pollinator conservation by testing the response of bee communities to these practices. The effectiveness metrics used include: 1) the role of habitat management in maintaining pollinator populations, 2) honey bee use of native plants within plantings, 3) pollinator use of restored hedgerow plantings, and 4) the role of plant diversity and structure in attracting pollinators.

Goal 1: Develop seeding and maintenance plans; conduct site preparation; document costs (UCD, collaborator).

This project formed part of the foundation for the bee monitoring work conducted under Goal 2, and contributed information regarding establishment and maintenance of wildflower installations in hedgerows, as well as information regarding germination and persistence, floral provisioning and bee use of individual forb species, including species that had not been previously tested, to inform plant recommendations for the region. We found that future wildflower augmentation of existing mature hedgerows should consider the potential for herbivory, and preventative measures should be taken to protect habitat.

During the course of the project labor, equipment, and material inputs for wildflower habitat establishment and maintenance were documented at each site, and culminated in an economic analysis of the costs of pollinator habitat establishment (see Tables 1–5).

Goal 2: Monitor bee communities and floral and nesting resources at 25 hedgerow and 20 control sites (UCB, collaborator).

This project documented how interplanting forb species in hedgerows impacts native bee and honey bee abundance and diversity. Forb interplantings were implemented at five young hedgerow sites. The bee communities associated with these sites were compared with control sites and mature hedgerows without forb plantings, and assessed for long-term pollinator persistence.

The goal of this research was to understand how NRCS and landowner conservation practices might improve pollinator conservation where it is needed most—in monoculture agricultural landscapes. To accomplish the goal the project investigated the following questions: 1) Do hedgerows influence the persistence of pollinator populations? 2) How do hedgerows influence the occurrence of pollinator species with different functional traits? 3) How do hedgerows influence regional richness and spatial turnover (β-diversity) and functional diversity of pollinator communities? 4) Do hedgerows influence nesting resources and nesting rates for pollinators as well as floral resources? 5) Do hedgerows improve pollination of adjacent crops? 6) Does the addition of forbs to existing hedgerows promote native bee abundance and diversity? and 7) Are neonicotinoid residues taken up by hedgerows and/or forb strips and inadvertently delivered to bees?

Findings demonstrated that hedgerows are an effective tool to support bee diversity in agricultural areas, and that the addition of forbs can help boost pollinator abundance, diversity, and richness above the levels of hedgerows without forbs, even in the face of drought.

Goal 3: Monitor mature habitat (and control sites) to record bee species, bee abundance, floral hosts, and wildflower abundance; Conduct ongoing landowner surveys to document operations and management practices (RU, collaborator).

We monitored nine NRCS-funded pollinator plantings while concurrently interviewing landowners about their management practices to determine the operations and maintenance practices associated with site failure versus success. Because plant community composition and thus the attractiveness of habitat plantings for bees may change through time, plantings were sampled across multiple years. Data collection included measures of abundance and species composition for both bees and flowering plants.

Results demonstrate that NRCS practices for installing pollinator habitat enhancements successfully attract native pollinators. Contrary to our earlier prediction, as habitat enhancements aged, they continued to attract a diverse assemblage of native bees.

Goal 4: Monitor honey bee and native bee visitation to highly diverse and less diverse seed mixes; Quantify how much of the total honey bee diet is composed of the native wildflower plots relative to the surrounding area; Quantify the pollen sources collected by honey bees before adjacent wildflower plots mature (UMN, collaborator)

The University of Minnesota evaluated the value of native plant seed mixes to honey bees. Honey bee and native bee visitation to wildflowers were compared across two different seed mixes at multiple sites. In addition, researchers quantified the pollen sources collected by honey bees before adjacent wildflower plots matured and monitored pollen diversity after the wildflower plots began to bloom. These data were then compared to determine the proportion of adjacent wildflowers the honey bees use.

Results of this project seem to indicate that even in the presence of diverse and abundant native wildflower species, honey bees find abundant, non-native legumes upon which they preferentially forage. These typically weedy species in the Upper Midwest and northern Great Plains are known to be preferred by honey bees because of the combination of their abundance and prolific nectar production.

Project support and leadership

Next Steps in Pollinator Conservation leveraged a total of $1,233,783 in cash and in-kind match. Of that total, university partners, native seed companies, and participating farmers provided $667,516 in in-kind support. In addition, the following foundations and businesses provided a total of $566,267 in cash matching funds:

Alice C. Tyler Perpetual Trust
Audrey & J.J. Martindale Foundation
Aveda
Ceres Trust
Cinco
Clif Bar Family Foundation
CS Fund
Deschutes Brewery
Disney Conservation Fund
Gaia Fund
Metabolic Studio
National Co+op Grocers
Organic Farming Research Foundation
Organic Valley
Sarah K. de Coizart Article TENTH Perpetual Charitable Trust
Swimmer Family Foundation
The Dudley Foundation
The Edward Gorey Charitable Trust
The Elizabeth Ordway Dunn Foundation

General Mills
Greater Milwaukie Foundation
Irwin Andrew Porter Foundation
Madhava Natural Sweeteners
Turner Foundation, Inc.
University of Minnesota
Whole Foods Market

This project was led by the Xerces Society's **Executive Director Scott Hoffman Black**, **Pollinator Program Co-Directors Mace Vaughan** and **Eric Lee-Mäder**, and **Senior Pollinator Conservation Specialist Jennifer Hopwood**. **Scott Hoffman Black** has more than 20 years of experience managing complex projects that meld conservation science and policy, including extensive experience in endangered species conservation, pollinator conservation, and sustainable agriculture. **Mace Vaughan** holds master's degrees in Entomology and Education from Cornell University, has years of experience in conservation, environmental education and entomology, and has conducted formal presentations to thousands of people around the country about pollinator conservation. **Eric Lee-Mäder's** professional background includes commercial beekeeping, native seed production, and consulting for various specialty crop industries. Eric is also Assistant Professor of Extension at the University of Minnesota's Department of Entomology. **Jennifer Hopwood** holds a master's degree in Entomology from the University of Kansas, where her research focused on bee communities in roadside prairie plantings and prairie remnants.

Background

The ecosystem services provided by pollinators are essential to human well-being, agricultural production, and ecosystem health. An estimated 85 percent of the world's flowering plants depend on animals—mostly insects—for pollination. More than two-thirds of crop species are dependent upon pollinators, including crops that produce fruits, vegetables, spices, nuts, seeds, oils, and livestock forage. The value of insect crop pollination in the U.S. is estimated to be up to $27 billion.

Unfortunately, pollinator declines put agricultural productivity and the health of natural ecosystems at risk. Habitat loss, alteration, and fragmentation, as well as pesticide use, are all contributing to pollinator declines.

For the domestic honey bee—the most familiar pollinator—the number of managed honey bee hives has declined by 50% since 1950 in the U.S. On top of this long-term trend, in recent years beekeepers have to make up for the loss of 29% to 42% of their hives each year. Numerous wild, unmanaged pollinator species native to North America are also experiencing declines. For example, at least 25% of North America's bumble bee species have undergone significant and swift declines, including species that were formerly common and widespread.

Today, many agricultural landscapes lack sufficient habitat to support pollinators. Fortunately, farmers are increasingly integrating pollinator habitat into farms to support pollinators and the crop pollination services they provide.

Next Steps in Pollinator Conservation built off previous work conducted by the Xerces Society and the NRCS to establish habitat plantings for pollinators, and provided the technology and innovation necessary to ensure that bee and beneficial insect habitat is successful in the long term, maximizing value for the NRCS and NRCS clients.

For the average producer who is already enrolled in a pollinator conservation contract, this real-world testing of operations and maintenance practices ensures the longevity of that restored habitat by helping producers select optimal maintenance methods depending on site and habitat conditions.

This project was also designed to provide new program accessibility to organic producers. Since pollinator conservation emerged as a priority resource concern under the Farm Bill, organic producers have been among the largest client groups to sign up for pollinator enhancement practices. However, we found that technical guidance for establishing diverse wildflower plantings using organic methods had been either lacking, untested, or even nonexistent. This project addressed this need by providing the first-ever nationwide field trials of organic habitat restoration, and creating habitat establishment guidance materials specifically for organic producers.

Seed producers, restoration practitioners, landowners, and wildlife will all benefit from the new native seed sources brought to market through this project. One observation from our previous work conducting restoration efforts across the country is that more diverse seed mixes tend to produce more resilient, weed-resistant, and successful habitats. The increased availability of less common species will assist landowners in planting diverse wildflowers that also have those qualities. This project also benefitted the seed industry by diversifying inventories and expanding knowledge of how to grow new species.

Before this project, the Xerces Society worked with academic partners to understand how habitat enhancements increase pollinator diversity and abundance in adjacent cropland. While these partners documented initial changes in communities of bees and other beneficial insects, key questions remained about how habitat enhancements can continue to provide benefits in the long term, and how operations and maintenance activities may optimize this effect. Similarly, assessing the value of native plants for honey bees is an important goal for supporting the beekeeping community.

Review of Methods

Next Steps in Pollinator Conservation provides the technology and innovation necessary to ensure that bee and beneficial insect habitat is successful in the long term, maximizing value for the NRCS and NRCS clients. This project strengthens existing NRCS pollinator conservation practices by creating field-tested guidance previously lacking for operations and maintenance of on-farm habitat plantings and habitat establishment using organic methods. In addition, this project bolstered supplies of native seeds that were previously unavailable for pollinator plantings and provides resources to help seed producers and conservation practitioners increase the seed supplies of high-value plants for pollinator conservation. In collaboration with academic partners, this project assessed conservation effectiveness of existing pollinator conservation practices to help determine which NRCS efforts have been most successful, the potential regional or national impact of those successes, and what additional technology is needed. This information will allow NRCS and other decision-makers to more effectively prioritize resources for maximum conservation impact.

To complete our operations and management field trials, we partnered with EQIP-eligible producers to plan, coordinate and implement project activities. Producers helped to monitor site conditions and provided feedback. Participating producers also agreed to alter their pesticide-use practices in order to protect pollinator habitat areas by selecting products that minimize risk to pollinators, and in some cases, increasing set-backs surrounding habitat areas.

In order to accommodate projects at their farm sites, producers worked with us to monitor the floral composition of habitat plantings and discuss multiple treatment methods to either move habitat from grass-dominated systems or to restore wildflower abundance. Unlike past management that might have included mowing with inconsistent timing or spot treatment of weeds to address woody plant encroachment or invasive species, we worked with land owners to document efficacy of carefully timed mowing, light disking, grass-selective herbicides, or interseeding. For many regions, such as California and Massachusetts, these are seldom used techniques.

For our organic habitat establishment field trials, producers worked with the Xerces Society to determine which conservation practices were most compatible with their farms and resources, and then helped implement these practices. Producers not only contributed land for each of the projects, but also contributed a significant amount of labor, equipment, and materials to help with site preparation, seeding, and maintenance of project sites.

To date, there is still a growing need for demonstrations of alternative/innovative site preparation techniques that are compatible with organic farming systems. Solarization continues to hold the most promise across much of the U.S., and was a new and innovative practice unfamiliar to most farmers.

In California, we trialed solarization side-by-side with conventional herbicide treatments, and found solarization to be significantly more effective. The solarized areas had significantly less weed-pressure for the first two years post-establishment than the areas that had been prepared using conventional herbicides. We took temperature readings under the plastic at several locations and had readings that ranged from 125° to 145° F. Over time, we found various tools and technologies to make the installation of solarization plastic, easier, faster, and less labor-intensive.

We also trialed several other methods of organic site preparation that were less effective than solarization, including the use of organic herbicides and smother cropping. The organic herbicides we used did burn down some of the weeds, but not all of them. Many of the weeds that were burned down recovered very quickly, necessitating multiple applications in a short period of time. This resulted in a very high cost for materials due to the high cost of organic herbicides and a high cost for labor of repeated applications. Our smother cropping trials also were not very effective at eradicating weeds in areas with high to moderate weed pressure. In areas with low weed pressure, this method was fairly effective.

In the Pacific Northwest, we found that solarization plastic needs to be laid in the early spring (ideally in May) in order to capitalize on the best insolation angle of the sun around the summer solstice. Our temperature readings from buried soil temperature loggers indicate that even with higher ambient temperatures in July and August, soil temperatures are higher in May and June.

In the Upper Midwest, we found mixed success with solarization at our trial sites. Solarization was most successful on sites with dry sandy soils in full sun. On these sites, solarization did not completely remove the existing weed community, but did dramatically change the weed composition (e.g., from dense smooth brome to rather benign purslane) such that natives were more easily established. Solarization was least successful at sites with high soil moisture, part shade, and/or high deer pressure (i.e., the plastic was heavily punctured, even with regular patching). Solarization was also unsuccessful against Canada thistle and yellow nutsedge, especially when the soil was cultivated prior to solarization. Cultivation is frequently recommended prior to laying the plastic, to ensure good seed-to-soil contact at planting. We learned, however, that this can be highly problematic if the existing weed community responds favorably to cultivation and is not strongly impacted by solarization.

With regard to solarization techniques, we discovered several approaches that expedited and/or improved the solarization process. In the Northeast and Midwest, we found that laying plastic as early as possible in the spring to be an effective strategy, because the plastic creates hospitable conditions for weed seed germination, thus flushing weed seed and subsequently killing the young seedlings. We also discovered that using a variety of trenching equipment to trench the perimeter of the plastic can improve the process for easier burying, and threading a pipe and chain through the plastic rolls can help in moving heavy rolls of plastic by hand or with ATVs. Repairing and repurposing used high tunnel plastic for successful solarization addressed concerns about the plastic waste generated by solarization.

In California, we also discovered that the soil temperatures were higher under thinner plastic, but that thinner plastic had a tendency to rip more easily. This suggests that medium-grade plastic may be optimal in most situations. However, we were not able to trial the different grades of plastic side-by-side in more than one location, and we believe that there is a need to examine the different grades more closely.

In our field trials, we learned that poor site preparation before the site is first planted can lead to high levels of weed encroachment and a need for aggressive management for weed control in the years following. We also learned the importance of managing the edges of our planted habitat area. Some of our plantings bordered fence lines or ditches with high weed pressure, and significant weed encroachment occurred from these areas. One technique we developed was the use of vegetative (e.g. dense native grass plantings) or mulched buffers around wildflower meadows to help repel weed invasion and allow for easier management of edges.

At some hedgerow field sites, herbivory from wildlife that shelter in the mature hedgerows impacted forb establishment. This was the case at sites where both of the following conditions were true: (1) shrubs had dense branches that came to the ground and (2) the forbs plot was less than ten feet from dense shrubs. In response we overseeded plots to ensure forb diversity was available for bee quantification of wildflower species in future years. After over-sowing, plots impacted by herbivory in the first year were immediately covered with floating row cover (reemay). Subsequent forbs establishment was greatly improved.

In the Northeast, we found that the combination of mowing and interseeding was successful in increasing wildflower diversity, and in general, was much more effective than grass-selective herbicides. However, certain weeds required different management strategies; for example, because mowing stimulated the growth of bindweed, we used spot-treatments with herbicides for large patches, and continuously cut plants to ground level where they were found in small patches.

Our project on native seed farms aimed to identify production and harvest challenges (e.g. plot die off) yet the cause of some of these problems was often unclear. Insect and disease pests are among the most significant challenges for producing many high-value pollinator plant species, and an emphasis on integrated pest management is becoming increasingly important for sustainably increasing yield. Future work could better address these issues with the use of a control or check plot to test alternative approaches for producing and harvesting seed or controlling pests. Because many wildflowers attract wildlife such as monarchs, we are also developing preventative control measures that emphasize strategies such as intercropping systems to improve conservation biological control.

Schedule of Events

A schedule of fieldwork and other activities conducted at project sites is outlined below by project objective. In addition to the work described below, over the four-year project period, we organized and participated in outreach events for farmers, NRCS staff, and others, including farm field days, workshops and conference presentations, where we shared information on operations and management methods, organic methods for habitat restoration, high-value pollinator plants, and new research from our university partners. At these events we reached over 5,500 people in 15 states.

1. Developing long-term operations and maintenance guidance for established habitat

In 2012 and 2013, initial sites were selected in California, Florida, Massachusetts, New Hampshire, Oregon, and Pennsylvania. We then developed operations and maintenance strategies during the fall of 2013 and winter/spring of 2014. In 2014, we decided to discontinue work at the Florida sites, and we began investigating options for organic farms where our field staff could work closely with local partners to implement field trials in the summer of 2015, ultimately deciding on the addition of several sites in Minnesota and New Hampshire, as well as an expansion of some projects in California. From 2014 to 2016, we implemented strategies at each of the sites. In 2016, we began synthesizing data from all operations and maintenance sites, and developed technical guidance for farmers and agricultural professionals on management techniques that sustain and increase diversity of wildflowers.

2. Testing habitat restoration practices for organic producers

During the fall of 2012 and winter of 2013, the Xerces Society identified and recruited farms to participate in field trials using organic methods for habitat establishment. We then established a core list of site preparation and weed abatement practices, selected based upon site-specific conditions. Initial trials included the following methods: solarization, smother cropping, and organic-approved herbicides. Because of the initial success of the solarization method, we decided to initiate additional solarization trials, testing different aspects of this method. In later trials, we also decided to expand our testing to include a variety of other methods such as sheet mulching, sod removal, soil inversion, and repeat shallow cultivation. Testing of site preparation methods continued from 2013 to 2015. Prepared sites were seeded and then monitored throughout the establishment phase for establishment success and ongoing weed pressure.

Project costs were tracked on a site-by-site basis, recording both time and materials for all phases of the projects. In the winter of 2016, we began to analyze these data, and based on this information, produced cost estimates for the site preparation, installation, and ongoing management of pollinator habitat projects. We also analyzed data for each organic habitat establishment method, and developed a guidance document describing best management practices for establishing pollinator habitat projects using organic methods. Project results for organic site restoration methods were presented during an NRCS webinar in February 2016, *Conservation Buffers to Support Beneficial Insects on Organic Farms,* which reached over 500 participants including over 150 NRCS staff.

3. Increasing the availability of critical plant materials

During the fall of 2012, we established partnerships with key native seed producers to launch this effort to increase seed supplies of high-value pollinator plants. All of these producers had previously collaborated with the Xerces Society on pollinator conservation initiatives and had proven to be valuable partners.

During April 2013, Xerces Society staff organized a meeting of native seed producers from across the country, which took place in Santa Fe, New Mexico, as part of the national Native Seed Conference. At this event, we met with our seed producer partners to finalize species selection and plans for the upcoming year of seed collection and stand establishment. We selected species that are highly attractive to pollinators, fit unique ecological niches such as tolerance to extreme drought, and support a wide diversity of pollinators.

During 2013, we coordinated with our partners to acquire the foundation seed needed to launch production of our target species. We initiated plug production of many species over the winter, so that transplanting could be done during spring 2014. By spring 2015, we had established production stands of eight species in cooperation with our project partners. We also collected seed from five additional species for establishment of production plots in 2016.

For all target species, we worked with our partners to document propagation practices used, and incorporated this information into our publication, *Increasing Seed of Wildflowers Valuable to Pollinators: Xerces Society and Seed Producer Partnerships* (See Appendix C). This year, we completed a technical guide to collecting and using your own wildflower seed to expand on-farm pollinator plantings, and developed a draft of a guide to conserving and growing native thistles. *Native Thistles: A Conservation Practitioner's Guide. Plant Ecology, Seed Production Methods, and Habitat Restoration Opportunities* is now undergoing final review from seed industry experts including Plant Materials Center representatives, with publication design and distribution planned for 2017. The draft document and sample publication layout is included in Appendix C.

4. Documenting the effectiveness of NRCS practices for supporting pollinators

Goal 1 (California): Develop seeding and maintenance plans; conduct site preparation; document costs (UCD, collaborator).

In fall 2012 we selected ten hedgerows for monitoring in Yolo County, CA (Figure 2). At each site a 0.2-acre planting area was established either directly adjacent to mature shrubs or interplanted between patches of shrubs. Plots were disked or roto-tilled to prepare seed beds in the spring of 2013. Sites were drip or micro-sprinkler irrigated one or two times between early

June and early July, and solarization plastic was laid over moist beds within three days of irrigation at each site. All sites were visited weekly to check for holes in the solarization plastic; any holes were repaired with UV-resistant tape.

Solarization plastic was removed from all five sites in October and November of 2013. Several days before plastic removal any broadleaf weeds with the potential to drop seed on the plot were cut with a string trimmer and removed. Two wildflower mixtures were then seeded with a three-foot Truax WF-32 pull-type broadcast seeder and ring-rolled with a cultipacker to ensure good seed-soil contact. The fall of 2013 was characterized by extreme drought conditions.

Site maintenance activities were performed on an ongoing basis from the spring of 2014 through 2016. Maintenance included weed control by hand-pulling, trimming, spraying of grass-specific herbicide, and spot-spraying of broadleaf weeds within and surrounding the plots with glyphosate. In the fall of 2014 and 2015, forbs were overseeded to increase diversity, and reemay was added to plots closest to shrubs. Establishment and persistence of the seeded wildflowers was monitored over the duration of the grant, and quantified establishment and persistence of wildflower species in the forbs plots.

UC Davis also assisted the UC Berkeley team in monitoring bee use of hedgerows. Hedgerows were sampled three to five times from April through July each year from 2013 through 2015. The UC Davis team continued sampling the forbs plots in 2016 to strengthen data on wild bee use of individual wildflower species.

Goal 2 (California): Monitor bee communities and floral and nesting resources at 25 hedgerow and 20 control sites (UCB, collaborator).

A number of the hedgerow and control sites used in this project were established prior to the project period. In 2006, in part with funding from a previous California NRCS CIG grant and a national NRCS Fish and Wildlife grant, the UC Berkeley hedgerow project began a before-after control-impact study and monitored field edges along large farms in the Yolo County area. After a year or two of monitoring pre-restoration, in 2007 and 2008 five hedgerows were installed with native perennial trees and shrubs. Ten sites within 1 to 3 km of hedgerows, with similar crop systems and landscape contexts, were left as controls.

In 2012, with the beginning of this grant, the site monitoring increased to 20 hedgerows and 20 paired control sites, including the sites that had been monitored in the original study. In 2013, we began monitoring on an additional five mature hedgerows to which forb strips were planted in the fall; each forb hedgerow was paired with a non-forb hedgerow control. Monitoring of these forb sites continued in 2014 and 2015, post-seeding of forbs. In 2014, an additional five natural habitat sites were monitored as well. Additional studies on hedgerows included the monitoring of hedgerows and controls adjacent to sunflower fields as well as testing for residue analysis of neonicotinoid pesticides in hedgerow shrub and forb flowers, soil, and bees.

California experienced a severe drought from 2012 through 2015. It is possible that our results from those years are skewed because of changes in floral resource phenology, altered agricultural plantings, or other effects of the drought. We attempt to distinguish the effects of drought from the effects of hedgerow restoration through our analyses. Because of the dry August months in

2014 and 2015, sampling was stopped after three or four rounds rather than the five sampling rounds conducted in 2013.

Goal 3 (New Jersey): Monitor mature habitat (and control sites) to record bee species, bee abundance, floral hosts, and wildflower abundance; Conduct ongoing landowner surveys to document operations and management practices (RU, collaborator).

In 2013, we worked with NRCS staff to choose sites where habitat enhancement plantings were recently installed, and a suitable old-field control site was available within 100 to 300 m. We reviewed nearly 50 enhancement sites and avoided sites that were destroyed by mowing, or where establishment of seeded plants was unsuccessful in the first two years. We sampled each of the 18 sites continuously for three to four years beginning the year after establishment.

Sampling took place four times each season starting in June 2014. From these sites, we collected nearly 7,000 native bee specimens. From 2014 to 2016, we curated specimens (pinned, labeled, and bar coded) and identified them to the species level. We also collected over 300 voucher plant specimens of 150 plant species, which are now curated in the Rutgers herbarium. Our observational data was fully databased, including data on honey bee flower visits, and flower species and abundances of each in our study transects.

In 2015, we surveyed landowners to link performance of pollinator enhancements with the establishment and management practices the landowner used. We were only able to contact landowners with whom we worked, as per NRCS privacy policy. Thus we were not able to conduct a large, randomized survey of all landowners that attempted to install pollinator enhancements. We asked 21 questions (see Appendix B) of seven landowners for the nine enhancements sites we studied. These questions were written to determine the goals, establishment and maintenance history, and concerns of landowners.

Goal 4 (Minnesota): Monitor honey bee and native bee visitation to highly diverse and less diverse seed mixes; Quantify how much of the total honey bee diet is composed of the native wildflower plots relative to the surrounding area; Quantify the pollen sources collected by honey bees before adjacent wildflower plots mature (UMN, collaborator).

In 2012, we identified and secured multiple field research locations at both native wildflower seed producers and a private research and development vegetable breeding farm in central and south-central Minnesota. Wildflower plots were established on the private vegetable breeding farm and were managed to reduce weed growth. Honey bee hives were moved to the field sites, and a monitoring protocol was designed to collect and identify plant sources of pollen and nectar collected by honey bees. Many of these preliminary activities took place prior to the CIG project start date.

Beginning in 2012, pollen was collected from three honey bee colonies at Werth Farm, the vegetable breeding farm in Le Sueur County, Minnesota. Samples were processed, divided by color, and mounted on slides for pollen identification to species or to feasible taxonomic level.

In 2013, pollen samples were taken from three colonies at Werth Farm and two additional sites biweekly from early spring to late fall. Nectar samples were also taken from the outer edge of the brood nest. Anthers containing pollen were collected from both target native prairie plants and non-target plants to generate a pollen reference collection essential to ensuring proper, species level identification of pollen and honey samples from each colony.

In 2013, we found that the native plantings at Werth Farm had not been maintained and were becoming overcome with non-native weeds. In 2014, we identified two new sites, Belwin Nature Conservancy and Carleton College, to locate honey bee colonies where at least 50 to 150 acres of native forbs were present. We decided to continue to collect pollen from Werth Farm because the data collected would still inform us more about the non-native plants honey bees use as food/pollen sources.

Honey bee colonies were weighed at Werth Farm in 2013 and at Belwin Nature Conservancy and Carleton College in 2014.

From September 2013 to January 2014, the creation of a pollen reference library was compiled from the floral (anther) pollen samples, and bee collected pollen and nectar identification to floral species was conducted based on the reference library.

In 2014, pollen and nectar samples were collected from honey bee colonies at all four sites. Pollen analysis from Werth Farm began in 2014, while analysis from the other three sites began in early 2015.

Discussion of Quality Assurance

Farm sites were distributed in different regions of the country to ensure our results have nationwide relevance. Project activities took place in California, Indiana, Massachusetts, Minnesota, Montana, New Hampshire, New Jersey, Oregon, Pennsylvania, Texas, and Wisconsin. See map (Figure 1) for locations of all project sites.

Throughout the duration of the project, field site conditions were monitored and costs were tracked, in order to document conservation- and cost-effectiveness of methods tested. These results were reported in a series of publications (see Appendix C) including guidelines and fact sheets.

Objective 1: Developing long-term Operations and Maintenance guidance for established habitat

In order to understand the regional differences in pollinator habitat weed management and methods for maintaining floral diversity, we selected a variety of project sites in different regions of the country. Sites were located in California, Massachusetts, Minnesota, New Hampshire, Oregon, and Pennsylvania, at almond, peach, and apple orchards; berry farms; cranberry bogs; and organic vegetable farms. Chosen sites had wildflower meadows and field border habitat enhancements that had been established for one to three years. To help facilitate information transfer to NRCS conservation planners and farmer-clients, one habitat site was located at a University of California Davis academic research station and another at a NRCS Plant Materials Center.

Several sites were selected to address problematic regional weeds or to monitor and test the performance of pollinator habitat seed mixes over time. At each farm site, we partnered with an

EQIP-eligible producer to plan, coordinate and/or implement operations and maintenance activities. Producers helped to monitor site conditions and provided feedback.

Objective 2: Testing habitat restoration practices for organic producers

To identify farms for conducting field trials of organic habitat establishment techniques, we consulted with university partners, project partners at conservation nonprofits, native seed companies, NRCS and conservation district staff, and grower-collaborators from previous partnerships. Organic farm sites were selected in California, Minnesota, Montana and New Hampshire, and Oregon representing a range of farm sizes, cropping systems, and site conditions. A sample of project farm sites is described below:

- A 1,000-acre farm in Montana with organic dryland crops, such as lentils, spelt, barley, ancient wheat varieties, flax, safflower, and sunflower. Growers were seeking to expand pollinator and beneficial insect habitat areas and expressed interested in trialing tillage (i.e., soil inversion) as a method of pollinator habitat site preparation.

- Three neighboring organic farms in Minnesota spanning a wide range of ecological conditions, including varying soil moisture, soil types, light levels, weed pressures, and weed types. Site histories were also highly varied, and habitat areas included those coming out of conventional row crops, organic crop production, and fallow/weedy areas. Because of their proximity to each other, these farm sites were ideal for hosting combined field days demonstrating pollinator habitat conservation practices in a variety of farming operations.

- An incubator farm in Oregon run by the local conservation district that provides leased land to beginning farmers along with training in sustainable farm practices and farm conservation. The pollinator habitat site was located immediately adjacent to the vegetable fields of a beginning row-crop farmer, and was installed with the assistance of the farmer and the farm manager as part of training on the incorporation of pollinator habitat into a farm system.

Throughout the duration of the grant, project costs were tracked on a site-by-site basis, recording both time and materials for all phases of the projects. During the last year of the project, we analyzed these data and used them to produce realistic, project-based cost estimates for the site preparation, installation, and ongoing management of pollinator habitat projects. Organic wildflower establishment data were also gathered at each farm site, which allowed us to compare efficacy of each technique across project sites. These results were used to produce technical guidelines describing best practices for establishing pollinator habitat projects using organic methods.

Objective 3: Increasing the availability of critical plant materials

For this initiative, we worked with native seed collectors and nurseries in California, Indiana, Minnesota, Oregon, and Texas, to conduct propagation field trials, identify production challenges, and to establish solid stands up to 1 acre in size for mass seed production.

For the purpose of this project, we limited our definition of local ecotype to the geographic service areas of the NRCS Plant Materials Centers. Among the sources we considered were conservation agency collections and natural plantings. Where wild seed collection was required, we acquired necessary permits and followed guidelines established by the Bureau of Land Management's Seeds of Success program to prevent depletion of wild populations and to maintain genetic integrity.

In the southern Great Lakes region, we partnered with Cardno Native Plant Nursery in Walkerton, Indiana, targeting native thistles (*Cirsium* spp.) and wingstem (*Verbesina alternifolia*) for seed production. With Minnesota Native Landscapes (Otsego, Minnesota), we brought meadow blazing star (*Liatris ligulistylis*) and field thistle (*Cirsium discolor*) into production. In addition, in summer 2015, the Xerces Society and Minnesota Native Landscapes collaborated on locating, identifying, and collecting three additional native thistle species including tall thistle (*Cirsium altissimum*), hill's thistle (*Cirsium hillii*), and flodman's thistle (*Cirsium flodmanii*).

We also partnered with Hedgerow Farms Inc., one of the largest native seed producers in California, to bring bladderpod (*Peritoma arborea*) and Pacific aster (*Symphyotrichum chilense*) into production. The foundation seed used to initiate production activities was wild-collected from local populations by Hedgerow Farms staff and Xerces Society volunteers.

In Junction, Texas, in collaboration with Native American Seed we targeted Leavenworth's eryngo (*Eryngium leavenworthii*) and white rosinweed (*Silphium albiflorum*) for seed production. Finally, in the Pacific Northwest, we worked with Humble Roots Farm & Nursery, LLC to bring yellow beeplant (*Cleome lutea*) into production, and to collect seed of plains coreopsis (*Coreopsis tinctoria 'atkinsonii'*) to support local habitat restoration projects.

Objective 4: Assessing Pollinator Conservation Effectiveness

Field studies were conducted in California, Minnesota, and New Jersey at more than 40 sites consisting of previously restored habitat, non-restored sites (study controls), and locations currently undergoing the restoration process. These sites included both field border as well as hedgerow plantings.

Goal 1(California): Develop seeding and maintenance plans; conduct site preparation; document costs (UCD, collaborator).

In fall 2012, we selected ten hedgerows for monitoring in Yolo County, California (Figure 2). Criteria for inclusion of forb-augmentation sites were: 1) proximity to unenhanced hedgerows being monitored as part of the ongoing long-term study; these forbs-free mature hedgerows were spatially independent controls, 2) similar size (~350 m long) and species composition as paired unenhanced control hedgerows, 3) area available for planting with forbs was at least 0.2 acre and existing weed pressure was manageable.

The planting design at all five sites included two wildflower mixtures surrounding a strip planting of *Asclepias eriocarpa*, which was sown in monoculture because it is easily shaded out by competitors. At each site, we planted 60% of the planting area with a "tried-and-true" seed mix (Old Mix) of seven native species that reliably provides season-long bloom and attracts abundant and diverse wild bees in the Central Valley of California (Ward and Williams, unpublished data). We planted 30% of each site with a novel mixture (New Mix) composed of the seven species in the Old Mix plus five new species that are likely to add value (Table 6). We planted the remaining 10% with a strip of the milkweed to determine if a monoculture planting could improve establishment of this species.

We plug-planted starts of California sunflower (*Helianthus californicus*) within the portion of the plot seeded with the New Mix. California sunflower's ploidy level differs from cultivated sunflower, making it impossible to contaminate production fields by hybridization, so we tested its ability to establish and support bees as a possible replacement for *H. bolanderi* in areas of California where sunflower seed production is abundant. While *Helianthus bolanderi* has been shown to support diverse and abundant wild bees (Ward and Williams, unpublished data), this species is capable of crossing with the cultivated sunflower grown for hybrid seed production and therefore cannot be planted within a mile of a sunflower production field, making it impractical for use in the region.

Both wildflower mixtures were seeded with a three-foot Truax WF-32 pull-type broadcast seeder and ring-rolled with a cultipacker to ensure good seed-soil contact. Prior to seeding, most sites were lightly harrowed using a 3 foot × 5 foot–chain harrow to ensure loose enough soil for seed penetration. If the soil was loose, no harrowing was required. Polenta was used as a carrier to ensure even distribution of seed throughout the planting area. *A. eriocarpa* was hand-sown into ½- to 1-inch deep furrows, covered, and pressed into the soil.

Establishment of sown plants was assessed after planting, each spring and fall from spring 2014 through spring 2016. Density and percent cover of sown species was quantified in 40 quadrats (1 m^2 each) placed in a stratified random design to cover the two seed mixes and milkweed monoculture that were planted at each site.

All wild bees visiting floral resources in the hedgerows and surrounding forbs plots were net collected during a 60-minute sample period on each sample date. Bees were kept separated by the plant species they were collected from. Samples were conducted only when temperatures were over 60°F, winds were less than 2.5 m/s and skies were sunny or lightly overcast. On each sample date, floral resources were quantified in 50 quadrats (1 m^2 each), evenly spaced throughout the length of the hedgerow and on either side. Floral cover (the percent cover of floral material) was estimated for each species according to Braun-Blanquet cover scores. At forb-enhanced sites an additional 25 quadrats were quantified; in 2014 floral cover of each species was recorded while in 2015 flowers were counted and multiplied by the average corolla area of each species to calculate floral area in cm^2 per m^2 area sampled.

Sampled bees were curated and identified by Robbin Thorp. Bees collected by the UC Berkeley team are accessioned in the Kremen lab at UC Berkeley, those collected by the UC Davis team will be accessioned in the Bohart Museum of Entomology at UC Davis.

Goal 2 (California): Monitor bee communities and floral and nesting resources at 25 hedgerow and 20 control sites (UCB, collaborator).

Hedgerows were restored with native trees and shrubs, and were irrigated and weeded for three years post-restoration to help them establish. They range from 3 to 6 m wide, and we monitored a set length of 350 m. Hedgerows and their unrestored edge controls were located 1 to 3 km from each other and were selected to be in similar cropping systems (see Figures 3 and 4 for maps).

Each site was sampled at least three times between April and August, in a randomized order within each round. We sampled during allowable weather conditions: sky cover clear to bright overcast, wind speed < 2.5 m/s, temperature >21.0°C for net specimens and >18°C for pan traps. Seven sets of white, blue, and yellow pan traps were set out in the morning along the 350 m of hedgerow and collected five hours later into microcentrifuge tubes with 70% ethanol. During netting, we collected all flower visitors (except *Apis mellifera*) during a timed hour of searching with the timer stopped during handling of specimens and recording of flower species. Specimens were put into ethyl acetate–charged kill jars according to the species it was caught on, and after the netting period they were then transferred into plastic snap caps and stored in a cooler with ice packs; at the end of the day they were transferred to a freezer.

We collected data for 66 vegetation quadrats (1 m^2 each) at all sites. In each quadrat we recorded percent cover of bare ground, vegetation, and dead wood, as well as the percent flower cover by species. One sampling round per year contained additional cover score categories to determine various possible nesting habitats: percent cover of litter, rocks, and cracks; whether cracks were small, large or both; number of hollow stems; number of small and large cavities; level of shade (none, part, or full); slope measurements at three points across the quadrat; and three penetrometer readings up to 5 psi at the same points. For forb addition sites, we collected additional floral cover data within the forb strips at each sampling date, in addition to the standard hedgerow vegetation data. We estimated number of flowers per species at 25 equally spaced plots along the forb strip in order to provide additional data on floral abundance and seeding success.

Net specimens were stored in the freezer for at least two weeks prior to pinning while pan specimens were stored in alcohol for up to 24 months. All specimens are pinned and kept in drawers where they are subsequently numbered and assigned unique identifying codes, and then labeled with their full information (state, county, site name, coordinates, collection date, collector name or "Kremen," flower species or pan color and number, and the unique code). They were then sorted and sent to taxonomists for identification: Dr. Robbin Thorp, professor emeritus at UC Davis, identified our bee specimens and Dr. Martin Hauser at the California Department of Food and Agriculture identified our syrphid flies. Specimens will be given to the Essig Museum of Entomology at UC Berkeley. All data are recorded into a relational database: an R script combines separate weather, vegetation, specimen, and identifications while checking for errors.

Goal 3 (New Jersey): Monitor mature habitat (and control sites) to record bee species, bee abundance, floral hosts, and wildflower abundance; Conduct ongoing landowner surveys to document operations and management practices (RU, collaborator).

To evaluate the effectiveness of enhancements, we sampled bees and plants in nine high quality New Jersey habitat enhancements and at nine nearby old-field control sites (for a total of 18 sites surveyed). This allowed us to focus on the effects of planting and management of pollinator habitat enhancements.

In selecting sites, we reviewed nearly 50 enhancement sites and avoided sites that were destroyed by mowing, or where establishment of seeded plants was unsuccessful in the first two years. Further, sites that were shaded were not sampled as pollinator visitation in shaded areas is lower than in full sun. Therefore, our enhancement sites represent high-quality pollinator habitat.

We used old fields as control sites as this is the typical habitat that is converted to pollinator enhancements. These control sites thus represent a control of “no enhancement” to which each enhancement is compared. Further, previous work has demonstrated that old fields in New Jersey have some of the highest abundance and diversity of pollinators; thus old fields represent a rigorous control against which the added value of active pollinator restorations can be compared.

At each site, we established equal-area standardized data collection transects, within which we hand-netted wild bees, quantified floral abundance and diversity, and observed honey bees foraging. For the net-collected bees, each specimen represents a bee visiting a flower, and we refer to the number of specimens we collected at each site as “visitation.”

Avoiding data bias: We implemented several study design and data collection practices to avoid bias. First, we sampled each habitat enhancement and its paired, nearby old-field control in parallel and on the same day, avoiding effects of weather. Furthermore, we controlled sampling effort in each site by means of using both fixed distance transects and timed observations within those transects. Second, each observer alternated sampling between the enhancement planting and the old field, so that observer biases could not drive observed difference between the two habitat types. All observers were trained to accurately distinguish native pollinators and identify bees, and used identical equipment and protocols throughout the duration of the grant.

Ensuring data quality: We took a number of steps in ensure data quality. We net collected bee specimens in the field. All 6,919 of our wild bee specimens were identified to the species level by Dr. Jason Gibbs, a professional taxonomist based at Michigan State University, who visited our lab for one week each year to determine and confirm species identification. These specimens have been fully curated, labeled, bar coded, and properly stored in the Winfree Lab. Second, we recorded flower abundance and diversity at each site. Plant determination was accomplished on site through the use of keys. Two plant specimens were collected for each plant species observed. Collected plants were pressed, labeled, and stored in an herbarium in the Winfree lab. Occasionally, plant specimens could not be identified to species level in the field, and staff from the Chrysler Herbarium at Rutgers assisted Winfree Lab members in determining these plants based on pressed specimens. Finally, we recorded *Apis mellifera* visits to flowers based on visual observation, as this species is readily identifiable in the field. All observers were trained prior to data collection and passed tests on discriminating between wasps, several morphotypes of native bees, several families of flies, and could reliably detect and discriminate honey bees without collecting them.

Data storage: All data are stored in a MySQL database. Field data and specimen identifications were entered by technicians in the Winfree Lab, and the resulting data tables were checked to eliminate entry errors. The server is managed by Rutgers University, and the database is backed up in the cloud and on redundant hard drives. These data will be made available as peer-reviewed manuscripts are published.

Goal 4 (Minnesota): Monitor honey bee and native bee visitation to highly diverse and less diverse seed mixes; Quantify how much of the total honey bee diet is composed of the native wildflower plots relative to the surrounding area; Quantify the pollen sources collected by honey bees before adjacent wildflower plots mature (UMN, collaborator).

Pollen and nectar samples were collected from honey bee colonies in the following locations:

1. Werth Farm, a vegetable breeding farm owned by General Mills in Le Sueur County, MN where two 1-acre plots were planted in native wildflower mixes recommended by the Xerces Society in 2012. This site provided an excellent reference point for comparison with the larger prairie sites, given the relatively small size of the native prairie plot and the fact that 68% of the land within 2 miles of Werth Farm is covered with corn and soybeans (based on data from CropScape).

2. A native prairie restoration company, Prairie Restoration, Inc, located in Princeton, MN, that grows dense plots of native forbs for seed collection and has over 50 acres of restored prairie near the company headquarters.

3. A 100-acre restored prairie with a high density of forbs, at Belwin Nature Conservancy in Afton, MN.

4. A 150-acre restored prairie with a high density of forbs owned by Carleton College in Northfield, MN.

Three or four colonies of honey bees were located at the Werth Farm and Prairie Restoration, Inc. sites in 2013 and all four sites in 2014 (each fitted with a pollen trap). Pollen was collected over a two-day period every two weeks at each site, and stored at −20°C. Fresh nectar samples were also collected every two weeks from each colony.

For the pollen analysis, subsamples of pollen from each colony were mixed to produce a total of 8 grams of pollen from each site/collection date and dissolved in 30 ml of filtered water using a vortex mixer. Approximately 0.25 ml of the dissolved pollen was acetolyzed using standard procedures (Erdtman 1963; Jones & Bryant 2004). Five drops of glycerin and one drop of Calberla's stain was added to the pollen and then the pollen was mounted on slides. At least 300 pollen grains were counted per slide (Faegri et al. 1989) and the types of pollen present were identified as specifically as possible based on their structure.

Freshly stored unripe honey (12–50 grams) was collected from combs in each colony into centrifuge tubes and stored at −20°C. Almost all of the pollen from nectar samples has been concentrated and acetolyzed (Louveaux et al. 1978). A spike of microspheres (Faegri et al. 1989) prepared by the LacCore Laboratory at the University of Minnesota was added to check that pollen grains were not lost during acetolysis. The nectar was dissolved in filtered water and 95% ethanol before spinning it to concentrate the pollen grains (Jones & Bryant 2004).

Findings

Objective 1: Developing long-term operations and maintenance guidance for established habitats

To sustain wildflower diversity and abundance in pollinator plantings over the long term, we found that using a variety of management techniques tailored to site conditions and to specific weed types to be most effective. A description of each management technique tested, and our findings on the optimal circumstances and timing on when each method should be applied are detailed in our guide, *Maintaining Diverse Stands of Wildflowers Planted for Pollinators: Ongoing Management of Pollinator Habitat* (See Appendix C). In some cases when wildflower establishment is low and/or weeds dominate the planting, we found that a combination of weed control and interseeding may be needed to achieve the goal of restoring diversity and function. The guide also includes case studies from across the country.

Objective 2: Testing habitat restoration practices for organic producers

In our organic habitat establishment trials, we found that solarization consistently outperformed other methods. This technique was especially well suited to hot climates on small pollinator habitat sites up to ~0.5 acre. Organic herbicides were the least effective in our trials, requiring repeated applications for effective control of some plants (we found that many grasses were not effectively controlled by organic herbicides). Our findings are summarized in the guide, *Wildflower Establishment: Organic Site Preparation Methods* (See Appendix C). This guide summarizes the primary organic site preparation techniques, including timelines for completion, and highlights the situations in which each technique is most effective.

We documented the costs of establishing wildflower habitat for pollinators using the solarization method for relatively small-scale (< 1 acre) on-farm habitat plantings. While specific costs vary from project to project and region to region, we estimated material costs to be $46.50 to $122.60 per 1,000 square feet without irrigation, and an additional $100 in labor costs for this same unit area (assuming $20/hour labor rate). For further information on these costs please see *Estimated Costs to Establish Wildflower Plantings Using Solarization* in Appendix C.

In order to better understand cost differences between habitat establishment techniques, we also developed estimates for establishing wildflower plantings using a conventional site establishment method. These estimates help to inform NRCS cost payments/reimbursements to producers implementing conservation practices using these techniques. Per 1,000 square feet of wildflower meadow, we estimated materials costs to be $7.90 to $24.00. Interestingly, labor costs were significantly higher because of the need to visit the site on multiple occasions to treat weeds and conduct more follow up maintenance than was required at our solarization sites. We estimated labor costs (including all site preparation, planting and follow up maintenance) to be approximately $250 per 1,000 square feet. For further information on these costs please see *Estimated Costs to Establish Wildflower Plantings Using Chemical Fallow* in Appendix C.

Finally, we also estimated costs for establishing hedgerows. Estimates represent average costs of establishing hedgerows from transplants and are derived from a series of pollinator hedgerow habitat projects throughout the United States. We found that per 100 linear feet of hedgerow, material costs were an estimated $107.16 without irrigation and $218.06 with irrigation. Note that for hedgerow projects in arid states, irrigation for the first two years after planting is important for successful establishment. Labor costs for hedgerows without and with irrigation were estimated at $110.00 and $120.00, respectively. For further information on these costs please see *Estimated Costs to Establish Pollinator Hedgerows* in the Appendix.

Objective 3: Increasing the availability of critical plant materials

One of the critical challenges facing habitat restoration professionals today is finding native plants that are adaptable to climate change and climate variability. Responding to this need, we expanded our focus on species that offer robust drought or flood tolerance, as well as species that provide bloom at critical times of the year when few other native plants are still flowering.

In California, we found that bladderpod (*Isomeris arborea*) can play an important role in meeting this challenge. A small-statured desert shrub, it readily adapts to a wide range of conditions from roadsides to desert arroyos to xeric coastal bluffs. It exhibits extreme drought tolerance, while also providing showy, long-lasting, and highly pollinator-attractive blooms. We also found that Pacific aster (*Symphyotrichum chilense*) fills a unique ecological role as one of California's most reliable late-season-blooming wildflowers, flowering into summer and autumn when few other pollen and nectar resources are available. The perennial lifecycle of Pacific aster results in a deep and extensive root system with a greater ability to persist through variable or irregular precipitation.

The southern plains are also challenged by periodic drought, and while a relatively good supply of native seed is available in the in the region, attention to the needs of pollinators is a relatively new focus for the region's seed industry. We identified white rosinweed (*Silphium albiflorum*), a perennial species that is extremely deep-rooted, long-lived and able persist in extended periods of drought, and Leavenworth's eryngo (*Eyringium leavenworthii*), a rapid-growing showy annual that can quickly establish and provide prolific flowers following bursts of precipitation.

In the dry climate of eastern Washington and Oregon, there has been strong interest in USDA conservation programs targeting pollinators, such as CP-42, the pollinator enhancement option available through the Conservation Reserve Program. With less than 12 inches of annual rainfall in some areas, however, planting options have been extremely limited. Working with a seed producer in eastern Oregon, we located wild sources of foundation seed for yellow beeplant (*Cleome lutea*), and Columbia tickseed (*Coreopsis tinctoria var. 'atkinsonia'*). After several years of seed amplification, reliable sources of these species are now available to support dry-climate habitat projects across the inland Northwest.

While drought is a growing concern in parts of the West, other regions are increasingly subject to extreme rain events and flooding. In looking for new commercially viable pollinator plants for the Southeast and Midwest that could thrive in these conditions, we focused on floodplains and similar plant communities where conditions could range from dry sand deposits to complete seasonal inundation. One species, wingstem (*Verbesina alternifolia*), was found across these types of locations and consistently attracted some of the greatest pollinator abundance and diversity of any plants found within the same plant communities.

Also in the Midwest, we identified meadow blazingstar (*Liatris ligulistylis*) as an unparalleled monarch resource. We repeatedly detected the presence of large numbers of monarchs on meadow blazingstar flowers, and in many cases the numbers of monarchs attracted to this species appear disproportionately high given the limited amount of flowering biomass, and the presence of other monarch-attractive plants flowering in close proximity (such as various species of Joe Pye weed and other *Liatris* species). Along with the need to increase milkweed as a larval host plant, recent monarch butterfly conservation efforts are highlighting the need to identify and increase monarch nectar resources of significant importance, such as this species.

Objective 4: Assessing Pollinator Conservation Effectiveness

Goal 1 (California): Develop seeding and maintenance plans; conduct site preparation; document costs (UCD, collaborator).

Wildflower establishment and persistence: Severe drought and unusual timing of precipitation in the fall and winter of 2013–2014 resulted in unusually high weed pressure, but despite this, wildflowers established and continued to persist with a trend to increasing over time (Figure 5). Species richness in the new mix was high, as all seeded species germinated to some degree. *Grindelia camporum* trends to increase in dominance in both mixes, and the relative proportion of many species declines over time, even with overseeding each fall. *Asclepias eriocarpa* averaged less than 2% cover in both spring and fall of 2014 even when it had been sown in a monoculture. These *Asclepias* monoculture strips became very weedy so we overseeded them with the New Mix in fall 2014. Transplanted *Helianthus californicus* established poorly and seems to require wetter soil conditions than we could achieve with the ongoing drought and minimal irrigation.

Two previously untested species, *Phacelia ciliata*, and *Clarkia williamsonii*, established and persisted well, while *Monardella villosa, Asclepias eriocarpa*, and *Helianthus californicus* struggled to take hold. Using the higher species-specific seeding rate we trialed here resulted in better establishment for two species that had not performed well in previous attempts: *Trifolium fucatum* and *Trichostema lanceolatum* (Ward and Williams unpublished data).

Performance of individual forb species in supporting wild bees: Provision of floral resources from each sown forb species was quantified using percent cover (2014) or flower counts multiplied by average corolla area to calculate total floral area (2015 and 2016). Floral resources were dominated in the first year of establishment by early-blooming annuals *Phacelia ciliata* and *P. tanacetifolia* and these species persisted in the plantings into the second and third year (Figure 6). *Eschscholzia californica* and *Grindelia camporum* become increasingly dominant over time. *Clarkia williamsonii* varied from year to year, but increased overall in the three-year study period. Despite this tendency for perennial species to become more prominent in the strips, species richness remains high, with consistently three or more species blooming at every sample from March through August. Quantification of the New Mix and Old Mix separately in 2016 shows the New Mix tends to provide higher floral area than the Old Mix. Further study is needed to determine the relative roles of higher diversity, species composition and seeding rate in achieving this.

Wild bee abundance increased later in the season each year, following typical patterns as bee populations build during the growing season. Plants varied in their ability to support both abundance and diversity of wild bees (Figures 7 and 8). *Phacelia ciliata*, *P. tanacetifolia*, and *P. californica* support abundant and diverse bees early in the season, while *Grindelia camporum* and *Trichostema lanceolatum* perform strongly in both regards later in the season. Species that stand out in supporting more abundant and diverse bees than expected based on floral resource provision include *T. lanceolatum* and *P. californica* (Table 7). Conversely, *Clarkia williamsonii* and *Eschscholzia californica* appear to support fewer bees than their floral abundance would suggest. Further examination of the species composition of bees supported by individual plants may suggest some species that appear to make a small contribution to overall abundance and diversity of bees may in fact be important for bee groups of interest such as bumble bees or important crop pollinators.

Goal 2 (California): Monitor bee communities and floral and nesting resources at 25 hedgerow and 20 control sites (UCB, collaborator).

Occupancy and persistence in hedgerows: Occupancy analyses conducted on eight years of field collection data show that hedgerows promote pollinator persistence and colonization in intensively managed agriculture (M'Gonigle et al. 2015). Analyzing occupancies of native bees and syrphid flies from 330 surveys across 15 sites over eight years, we found that hedgerow restoration promotes higher rates of between-season persistence and colonization as compared with unrestored field edges. Enhanced persistence and colonization, in turn, led to the formation of more species-rich communities. We also find that hedgerows benefit bees that are floral resource specialists more than generalists, specifically by enhancing colonization of specialists, emphasizing the value of this restoration technique for conservation of biodiversity in agricultural landscapes.

Beta-diversity and functional diversity of hedgerows: Another analysis of the long-term hedgerow dataset shows that they counter biotic homogenization in intensively managed agriculture (Ponisio et al. 2015). While other analyses have shown that hedgerows increase occupancy, persistence, and species diversity, it was unclear whether habitat restoration with hedgerows could re-establish spatial turnover in species composition (β-diversity, or regional species richness). Currently, agriculture tends to produce homogenized communities that are similar from place to places, and is thus associated with low β-diversity. We show that hedgerows, when replicated across a landscape, can boost β-diversity by approximately 14% relative to unrestored field margins, to levels similar to some natural communities. Hedgerows restore β-diversity by promoting the assembly of functionally diverse communities. In contrast, intensively managed agriculture imposes a strong ecological filter that negatively affects several important dimensions of community trait diversity, distribution, and uniqueness. However, by helping to restore functionally diverse pollinator communities, small-scale restorations such as hedgerows provide a valuable tool for conserving biodiversity and potentially, for promoting pollination services.

Ground-nesting bee resources and ground-nesting rates: A major challenge in habitat restoration is targeting the key aspects of a species' niche for enhancement, particularly for species that use a diverse set of habitat features. However, restoration that focuses on limited aspects of a species' niche may neglect other resources that are critical to population persistence. We evaluated the ability of native plant hedgerows, planted to increase pollen and nectar resources for wild bees in agricultural landscapes, to provide suitable nesting habitat and enhance nesting rates of ground-nesting bees (Sardiñas et al. 2016). We found that, when compared to unmanaged field edges (controls), hedgerows did not augment previously determined indicators of nest habitat quality, namely, bare ground, soil surface irregularity, and soil hardness (Sardiñas and Kremen 2014), although coarser soils were associated with higher incidence and richness of nesting bees. Further, hedgerows did not augment nesting rates when compared to control edges. Although all the bee species we detected nesting were also found foraging on floral resources, the foraging assemblage contained many ground-nesting bee species that were not detected nesting at the site. These results may reflect sampling error. Alternatively, species found foraging but not nesting in hedgerows could be utilizing hedgerows as "partial habitats," nesting outside hedgerow plantings but foraging on the floral resources they provide. We conclude that although hedgerows are known to provide critical floral resources to wild bees especially in resource-poor intensive agricultural landscapes (Morandin and Kremen 2013), simply increasing vegetative diversity and structure may not be simultaneously enhancing nesting habitat for ground-nesting bees.

Forb additions: Preliminary analyses find a strong benefit of adding forbs to mature hedgerows for wild bee abundance and richness, and a moderate benefit to wild bee diversity. Generalized linear models for abundance and richness provide evidence for the benefit of forb-enhanced hedgerows even in the face of extreme drought: in 2014 and 2015 abundance increased significantly in the forb sites from the 2013 pre-forb hedgerows, while hedgerows without forb additions showed a slight non-significant decrease in abundance from 2013 to 2014 and 2015 (Figure 9). Similarly, richness also decreases in the hedgerows without forbs between 2013 and 2015 (possibly due to drought); hedgerows with forbs increase in richness each year, with significantly higher richness in 2015 compared to the hedgerows without forbs.

A linear mixed model for Simpson index diversity reveals a significant difference between forb-enhanced hedgerows and hedgerows without forbs. There appears to be a slight decrease in the average diversity of non-forb hedgerows from 2013 to 2015, likely due to drought, while forb-enhanced hedgerows show significantly higher diversity.

While these are only preliminary results, they indicate that the addition of forbs to mature hedgerows has great benefit to wild bee populations. Despite being in the fourth year of drought, the forb-enhanced hedgerows not only increased diversity as compared to their non-forb hedgerow counterparts, but also increased from 2013, only two years into the drought. The added benefit forbs provide even when hedgerows are mature and blooming demonstrates the value of maintaining the forb component of pollinator plantings beyond the establishment phase.

One exciting outcome of this work is that several of our university partners in California, including some new Xerces Society staff, have published research that was either funded or made possible by this grant. Published research articles resulting from this project are included in Appendix C.

Goal 3 (New Jersey): Monitor mature habitat (and control sites) to record bee species, bee abundance, floral hosts, and wildflower abundance; Conduct ongoing landowner surveys to document operations and management practices (RU, collaborator).

Floral diversity through time in enhancements versus controls: A motivating concern for this project was that pollinator habitat enhancements in the mid-Atlantic quickly reverted to grass-dominated habitat within a few years of establishment. We did not find evidence that this was commonplace within the group of sites included in this study. Floral diversity was variable, but on average higher for habitat enhancements than the paired old-field control sites, and this trend did not decrease with the age of the planting (Figure 10).

Wild bees in pollinator habitat enhancements versus controls: The habitat enhancements attract more pollinators relative to the old-field control sites. There were nearly 100% more individual bees present in habitat plantings than in old-field control sites (Figure 11). There is no clear trend in overall native bee visitation in habitat enhancements through time (Figure 12). There was no overall response in the diversity of specimens collected to habitat type, nor to restoration age within plantings (height of blue lines across rows of plots, (Figure 12).

Honey bees: Honey bee visitation was not significantly different between pollinator habitat enhancements and old-field control sites. Honey bee visitation was highly variable in our study. The plants visited by honey bees were a mixture of common weeds (*Lythrum salicaria*, *Cirsium* spp. e.g. *Cirsium vulgare*, *Trifolium* spp.), plants commonly included in seed mixes (*Gaillardia, Asclepias, Rudbeckia*) and thus were found in habitat enhancements, and widely occurring natives that were present in both habitat enhancements and old-field controls (*Solidago, Eupatorium*). Our study included sites with *Rhus copallina*, a native shrub that was heavily visited by honey bees. The habitat enhancements do not typically include woody shrubs, although they may be compatible with some habitat enhancements. Outside of our study, we have noticed that *Rhus* species, especially *Rhus glabra*, are strong bee magnets for both *Apis* and wild bees.

Landowner survey: In order to assess if particular installation or management practices impacted the success of pollinator habitat enhancements, we provided eight landowners with a written survey by mail and/or email. All but one responded. We asked landowners what their motivations were for establishing pollinator habitat, what resources they used in installing them, what time of year and what techniques they used to install the habitat enhancement, and what management practices they were using to control weeds and woody plants. Most of the landowners had successful enhancements, as we only surveyed those whose property we were actively sampling in 2015.

When asked about motivation for installing pollinator enhancements, all landowners indicated that concern for native bees was a driving factor. Three landowners also listed honey bee declines. Only two respondents installed habitat enhancement near crop fields, and both listed crop pollination as a motivating factor. Landowners listed a number of site preparation techniques, including mowing (5), disking or tilling (5) and herbicide (2). Our observations suggest that herbicide-treated sites had greater success. At one of the most successful sites, the landowner hired a professional to remove exotic plants. To plant sites, landowners used a combination of seed drills (5) and/or broadcast seeding (4). Only one landowner indicated they used plugs. To maintain sites, nearly all landowners used mowing (6 of the 7). Three of the landowners used spring mowing and three used fall mowing. Only one landowner used prescribed burning, and this was a land trust that had the resources to execute this management technique. One landowner of a highly successful site reseeded in the first two years. Several landowners mentioned a desire for more support after initial planting especially in weed control and reseeding. One landowner suggested a guide to seedlings, to help growers manage weeds early in the season when target plants are not easily recognized. Finally, all landowners viewed the enhancements as successful.

Goal 4 (Minnesota): Monitor honey bee and native bee visitation to highly diverse and less diverse seed mixes; Quantify how much of the total honey bee diet is composed of the native wildflower plots relative to the surrounding area; Quantify the pollen sources collected by honey bees before adjacent wildflower plots mature (UMN, collaborator).

The results indicate a large contribution of native tree pollen in the spring and summer (e.g., *Acer* maple, *Tilia*- basswood, *Rhus*- sumac), non-native Fabaceae pollen in the summer and fall (ex. *Trifolium*- white/red clover, *Melilotus*- sweet clover, and *Lotus corniculatus*- birds-foot trefoil), and native and non-native aster pollen in the late summer and fall (e.g., *Ambrosia*-ragweed, *Arctium*- burdock) (Figure 13). In addition, we have identified several native prairie plants that contribute to colony food stores. The top 10 native prairie taxa (and genera that contain native prairie species) from the sequencing results are: *Solidago* (goldenrods), *Impatiens capensis* (spotted touch-me-not), *Dalea purpurea* (purple prairie clover), *Helianthus* (sunflowers), *Lupinus* (lupines), *Hypericum* (St. John’s wort), *Penstemon* (beard tongues), *Liatris* (blazing star), *Allium* (wild onion/chives/garlic), and *Potentilla* (cinquefoil).

Additional results from unripe honey samples indicate contributions from non-prairie species, including sweet and white clover, basswood, *Rhamnus* (buckthorn), *Raphanus* (radish), *Glycine max* (soybean), *Brassica nigra* (black mustard), and *Taraxacum* (dandelion), and several native species, including touch-me-not, *Helianthus* (sunflower), prairie clovers, and goldenrod/asters. Despite the unexpectedly low numbers of mint pollen grains, mints such as those in the genera *Agastache* (giant/anise hyssop) and *Pycnanthemum* (mountain mint) may still be an attractive source of nectar. According to Bryant and Jones (2001), species in the mint family tend to be under-represented in honey relative to species in other families. We are currently setting up experiments to test the attractiveness of several native species, including mints using observations of visitation and waggle dance mapping.

A very large proportion of the DNA sequence reads from our unripe honey samples were from non-native sweet clovers, white/alsike clovers, and birds-foot trefoil. The top native prairie taxa (and genera that contain native prairie species) from the sequencing results are: *Solidago* (goldenrods), *Impatiens capensis* (spotted touch-me-not), *Dalea purpurea* (purple prairie clover), *Helianthus* (sunflowers), and *Lupinus* (lupines).

Conclusions and Recommendations

Objective 1: Developing long-term operations and maintenance guidance for established habitats

In order to achieve the best management outcomes for the long-term health of wildflower habitat and the pollinators they support, we recommend taking an active, adaptive management approach. An active approach requires a low-level, but consistent time commitment, in which a landowner or conservation specialist frequently evaluates, prescribes, and implements management activities to maintain their wildflower plantings. This process involves monitoring, evaluation, management and re-evaluation.

Management techniques are intended to either maintain the existing diversity or control weeds in the habitat. Management techniques we recommend include mowing, hand-weeding, spot spraying, applying grass-selective herbicide, weed removal around site edges, conservation haying, irrigation, prescribed fire, and grazing. We also recommend interseeding and plug planting to reintroduce wildflower diversity. Our guide *Maintaining Diverse Stands of Wildflowers Planted for Pollinators: Ongoing Management of Pollinator Habitat* describes each of these techniques in detail and contains decision trees to help identify appropriate management technique(s) for a variety of conditions.

In order to maximize management effectiveness, it is important to use the appropriate tools and schedule management actions to be implemented at a time when they are likely to have the highest impact. Timing of techniques varies by region, but is often connected to growth stages of unwanted weedy plants, which may change annually given local weather conditions. In general, paying close attention to when weeds or dominant species are growing, flowering, or setting seed will help time management activities to avoid missing a critical window that could cause problematic species to increase their populations.

Objective 2: Testing habitat restoration practices for organic producers

For sunny areas less than 0.5 acre in size, we recommend using solarization to prepare sites for habitat restoration. Solarization is a non-herbicidal method of controlling weeds by placing a clear plastic sheet on moist soil during periods of high ambient temperature. It is most effective in hot climates, and can be used in areas with moderate to high weed pressure.

For small sites where solarization is impractical due to plastic unavailability, unaffordability, or shade, we recommend using sheet mulching, a low-maintenance and no-till method of weed management that kills existing vegetation and prevents seed bank germination by smothering. This method can prepare new habitat or enhance existing habitat. It is ideal where transplants will be used, but can also be planted with wildflower seeds. For very small areas (<⅛ acre), we recommend sod removal as an excellent method for quickly converting areas such as patches of lawn to native wildflower plantings.

For large sites greater than 0.5 acre, we recommend soil inversion as an effective method where moderate to high weed pressure is present, and where appropriate equipment and experienced operators are available. Soil inversion is conducted by using a moldboard plow to invert the soil, followed by secondary tillage such as shallow disking. For large areas with low to moderate weed pressure, smother cropping is recommended when farmers and operators are already experienced with successful cover-cropping. Smother cropping is a method of weed control in which temporary cover crops are grown for the purpose of weed suppression, and is generally inexpensive to implement. Repeated shallow cultivation is also recommended when transitioning crop fields or sites with low weed pressure. This method uses shallow cultivation to encourage germination of weed seeds in the top layer of the soil (i.e., germination zone), following which weed seedlings emerge in response to the soil disturbance and are killed by subsequent shallow cultivation, flame weeding, shallow hoeing, or other methods.

We found organic herbicide applications to be less effective than other methods. We recommend using organic herbicide in situations where weeds are at the seedling stage, and when organic herbicides already being used on the farm have been found to be effective against common weeds on-site. For further information on each method please see *Wildflower Establishment: Organic Site Preparation Methods* in Appendix C.

Objective 3: Increasing the availability of critical plant materials

This project resulted in new commercial sources for 10 wildflower species that had been completely absent from the market or in limited supply. These species are highly attractive to pollinators, fit unique ecological niches such as tolerance to extreme drought, and support a wide diversity of pollinators. By focusing on overcoming the production challenges for these species, we have helped boost yields, with nearly 250 pounds of seed produced for this group of species. Four additional species are currently in the early stages of production and will be harvested in the coming years.

In addition to expanding commercial sources of these plants, we also recommend seed saving and sharing as a low-cost method for creating pollinator habitat. The costs of obtaining seeds can be a barrier to some producers; however, if native plant areas are already established on the farm, these plantings can provide a readily available source for additional seed. Saving and replanting seeds has long been a tradition in farming, and saving and spreading native wildflower seeds to expand pollinator habitat is a conservation legacy that can be passed down on the farm. Sharing these seeds among farmers can spread pollinator habitat, connect neighbors, and benefit pollinators and entire farming communities. Our guide *Expanding Pollinator Habitat on Farms: Collecting and Using Your Own Wildflower Seed* outlines the basic steps of collecting native plant seed using readily available, non-specialized equipment.

During this project, we concluded that there is a great need for expanding the use of native thistle species in pollinator plantings, which have been in very limited supply. We identified five species of native thistles with high value to pollinators but limited commercial availability: field thistle (*Cirsium discolor*), tall thistle (*C. altissimum*), Hill's thistle (*C. pumilum* var. *hillii*), Flodman's thistle (*C. flodmanii*), and swamp thistle (*C. muticum*). Thistles attract and support a wide range of pollinators, including several declining species of bumble bees and butterflies, and provide food for seed-feeding birds as well as several butterfly and moth caterpillars. Yet, native thistle seed sources are currently scarce to nonexistent and there is a significant need to increase thistle seed availability for wildlife habitat restoration efforts.

The benefits of native thistles are significant yet not well recognized, and they are often confused with invasive non-native thistle species. To increase awareness of these species and encourage their conservation and use in pollinator plantings, we developed a guide, *Native Thistles: A Conservation Practitioner's Guide. Plant Ecology, Seed Production Methods, and Habitat Restoration Opportunities*, which describes their pollinator value and conservation status, and describes best practices for thistle propagation and use in conservation plantings. We have also been approved to present on the value of native thistles for pollinators in the NRCS science and technology webinar series. This July 2017 webinar will discuss the importance of native thistles to supporting pollinators and other beneficial insects on farms and restoration plantings.

This project also confirmed that meadow blazingstar (*Liatris ligulistylis*) is of significant importance to attracting monarch butterflies and providing nectar. To maximize yields, we recommend additional efforts to develop more effective management of root disease and weed control in production stands. We recommend including meadow blazingstar in mass plantings on farms and corporate campuses in the Upper Midwest. We see this species as an important potential "homing beacon" to attract monarchs to safe, restored breeding habitats where they can also find milkweed host plants and a refuge from pesticides.

There continues to be a crucial need for species that offer robust drought or flood tolerance, as well as species that provide bloom at critical times of the year when few other native plants are still flowering. While the species identified through this project are adding an important new range of options for habitat restoration, there is still much important work to be done. Looking ahead, this emphasis on highly adaptive pollinator attracting plants is expected to become a large part of our research and development support for the native seed industry.

The popularity of several of these plants is now propelling the expansion of these enterprises and improvement of production methods. Our partner growers are expanding production of species such as *Liatris ligulistylis*, which have become incredibly popular in restoration plantings. We have helped market this species by highlighting it in e-newsletters and social media distributed to an audience of approximately 35,000 people.

As we advance production technologies that boost and protect yield, this work will continue to increase availability of high-value wildflowers for conservation plantings. In turn, the growing recognition of the value provided by diverse, flowering habitat will drive the demand for more seed and wildflower species. The end result is to firmly establish a much broader diversity of high-value pollinator plants in production farms, markets, and conservation plantings.

Objective 4: Assessing Effectiveness of Restoration for Pollinator Communities

Goal 1(California): Develop seeding and maintenance plans; conduct site preparation; document costs (UCD, collaborator)

Our data show that long-term maintenance of forb plantings in pollinator hedgerows is worthwhile in terms of the abundance and diversity of wild bees supported (Figure 14), and that forbs increase in their ability to support bees even while planted shrubs decline during drought (Figure 15).

A more diverse mix of forbs tended to provide greater bloom and support a higher abundance of wild bees in spring than a simpler mix in the third year of establishment (Figures 6 and 7) and further study is needed to tease apart the relative roles of diversity, species composition, and seeding rate in achieving this ecological function.

Incorporating forbs into shrubby hedgerow pollinator plantings can increase support of wild bees, but we provide the following recommendations for practice:

1. Practitioners should take care to avoid planting too close to untrimmed shrubs that may harbor herbivores, or should plan to cover the plot with reemay until seedlings have their first true leaves;

2. Forbs should be planted in a solid strip as wide as possible to minimize edge effects where weeds can encroach;

3. Planting should be avoided in years with unfavorable weather conditions such as late precipitation, because resulting weed dominance reduces cost-effectiveness; and

4. Individual plant species differ in their ability to support abundant and diverse wild bee communities.

Goal 2 (California): Monitor bee communities and floral and nesting resources at 25 hedgerow and 20 control sites (UCB, collaborator)

Hedgerows are an effective tool to support bee diversity in agricultural areas. They increase beta-diversity and support more specialized bees than control sites. The benefit to crop pollination may be context- and crop-dependent—so while the installation of hedgerows has shown to benefit pollinator assemblages, the benefit to crops needs more research in different systems. While forbs are often added to hedgerows to provide more immediate pollinator resources during maturation, our preliminary results of mature hedgerows with forbs show that the addition of forbs can help boost pollinator abundance, diversity, and richness above the levels of hedgerows without forbs, even in the face of drought.

Goal 3 (New Jersey): Monitor mature habitat (and control sites) to record bee species, bee abundance, floral hosts, and wildflower abundance; Conduct ongoing landowner surveys to document operations and management practices (RU, collaborator)

Our results demonstrate that NRCS practices for installing pollinator habitat enhancements successfully attract native pollinators. Contrary to our earlier prediction, as well-established habitat enhancements aged, they continued to attract a diverse assemblage of native bees. Plant communities within habitat enhancements varied with time, but did not generally become more or less diverse. It is important to note that we studied successful plantings with landowners that exhibited a high interest in native bees and biodiversity. These landowners may have been more likely to put more effort into establishing and maintaining enhancements.

We found that honey bees use, but do not prefer, habitat enhancements. This may be due to the fact that honey bees typically recruit colony members to large, mass flowering blooms. The enhancements we studied were primarily high diversity plantings, and thus were not more likely than the control sites to have dense, single species blooms. This suggests that there may be trade-offs in creating habitat enhancements for honey bees and native bees.

Goal 4 (Minnesota): Monitor honey bee and native bee visitation to highly diverse and less diverse seed mixes; Quantify how much of the total honey bee diet is composed of the native wildflower plots relative to the surrounding area; Quantify the pollen sources collected by honey bees before adjacent wildflower plots mature (UMN, collaborator).

Results of this project seem to indicate that even in the presence of diverse and abundant native wildflower species, honey bees have an ability to find abundant, non-native legumes upon which they preferentially forage. These are typically weedy species in the Upper Midwest and northern Great Plains, and because of the combination of their abundance and prolific nectar production, they are known to be preferred by honey bees.

Some standout native wildflower species used by honey bees in this study include spiderwort, Culver’s root, sumac, basswood, goldenrod and aster. If a habitat project’s primary goal is to provide forage resources for honey bees, plant choices can be simplified, but other objectives, such as longevity of planting, diversity of other pollinator species, and plant weediness need to be considered.

Appendix A. Figures and Tables

Figures

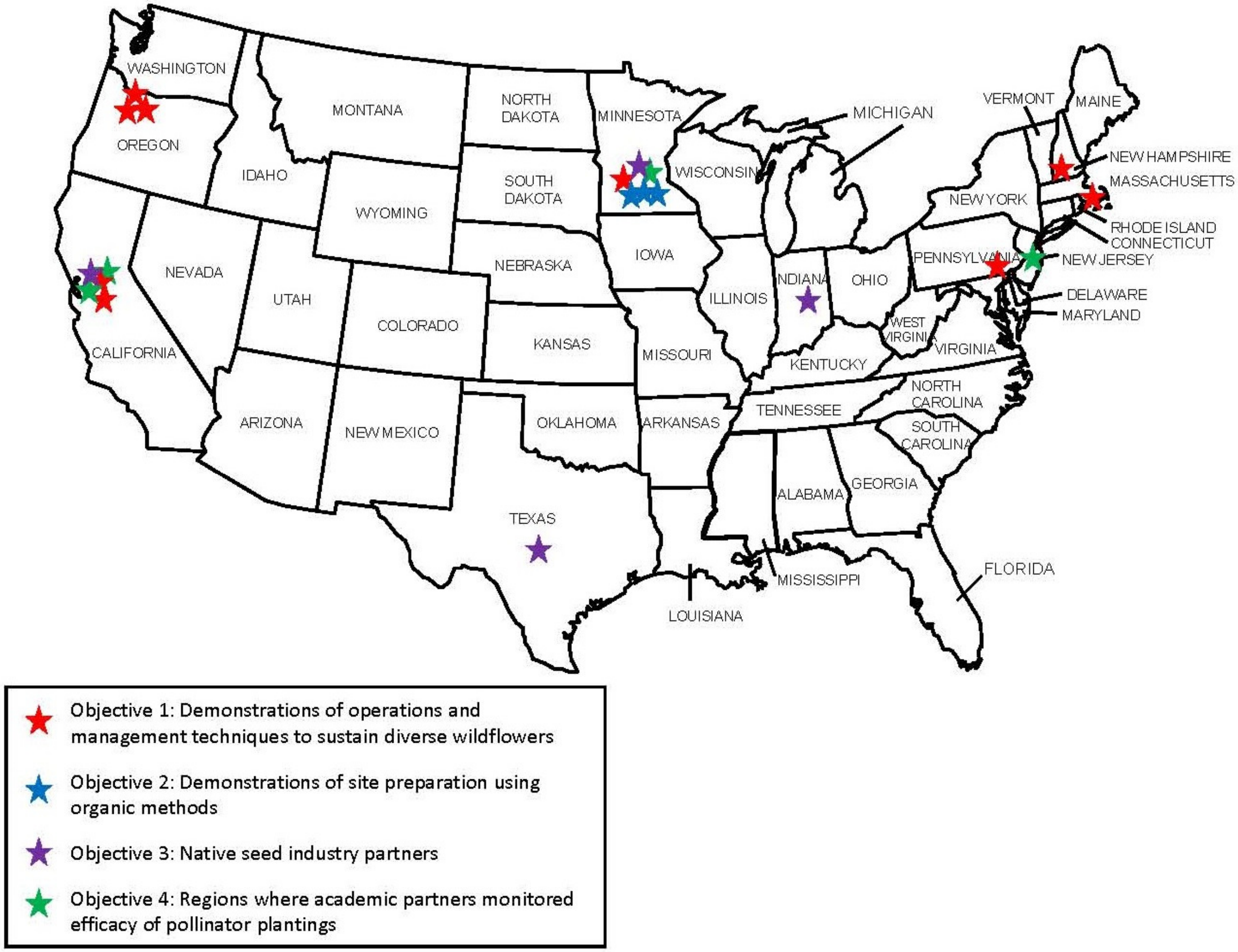


Figure 1. *Next Steps in Pollinator Conservatio*n project locations.

Figure 2. Forbs-enhanced and control hedgerows sampled in Yolo County, CA.

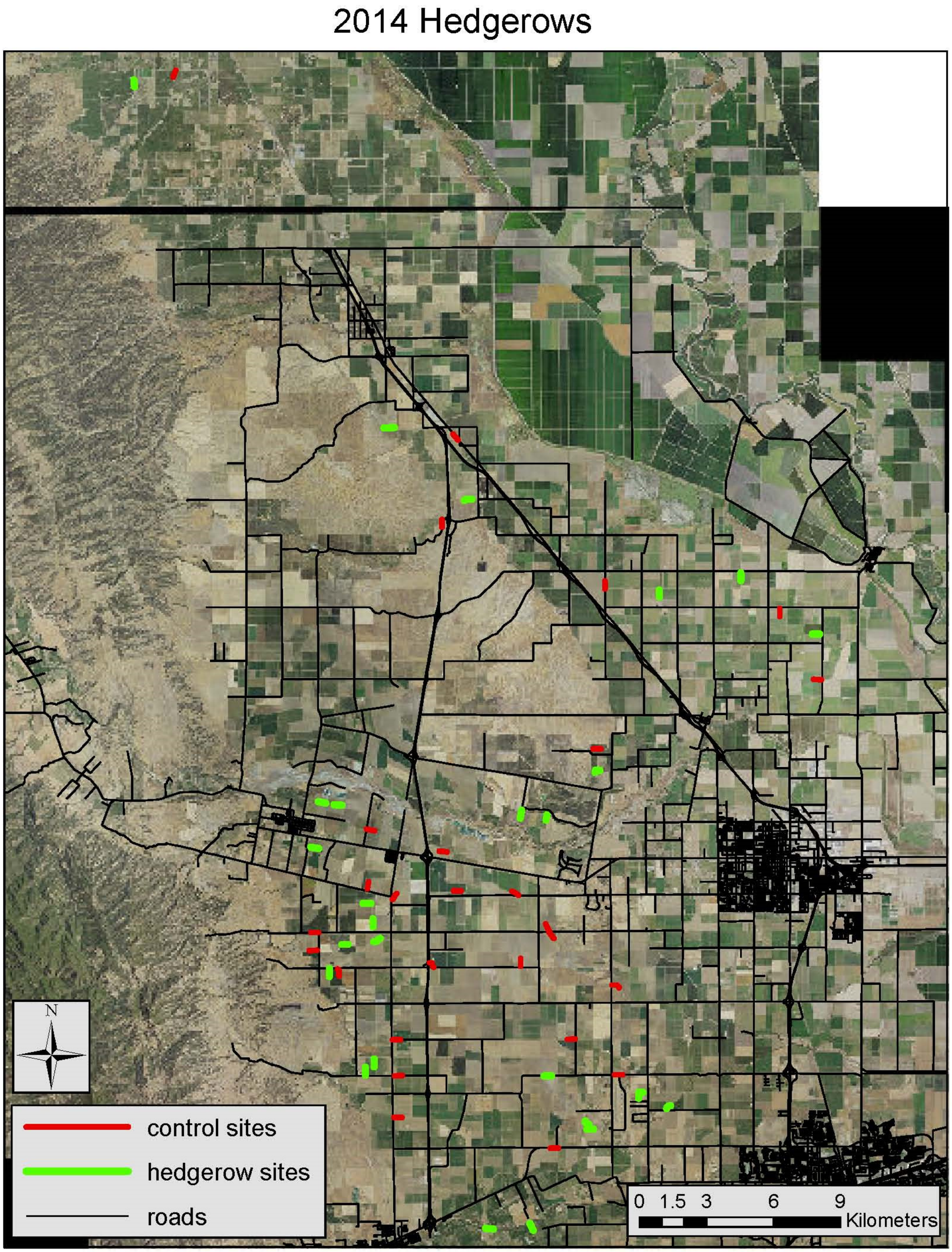


Figure 3. 2014 hedgerow and control sites.

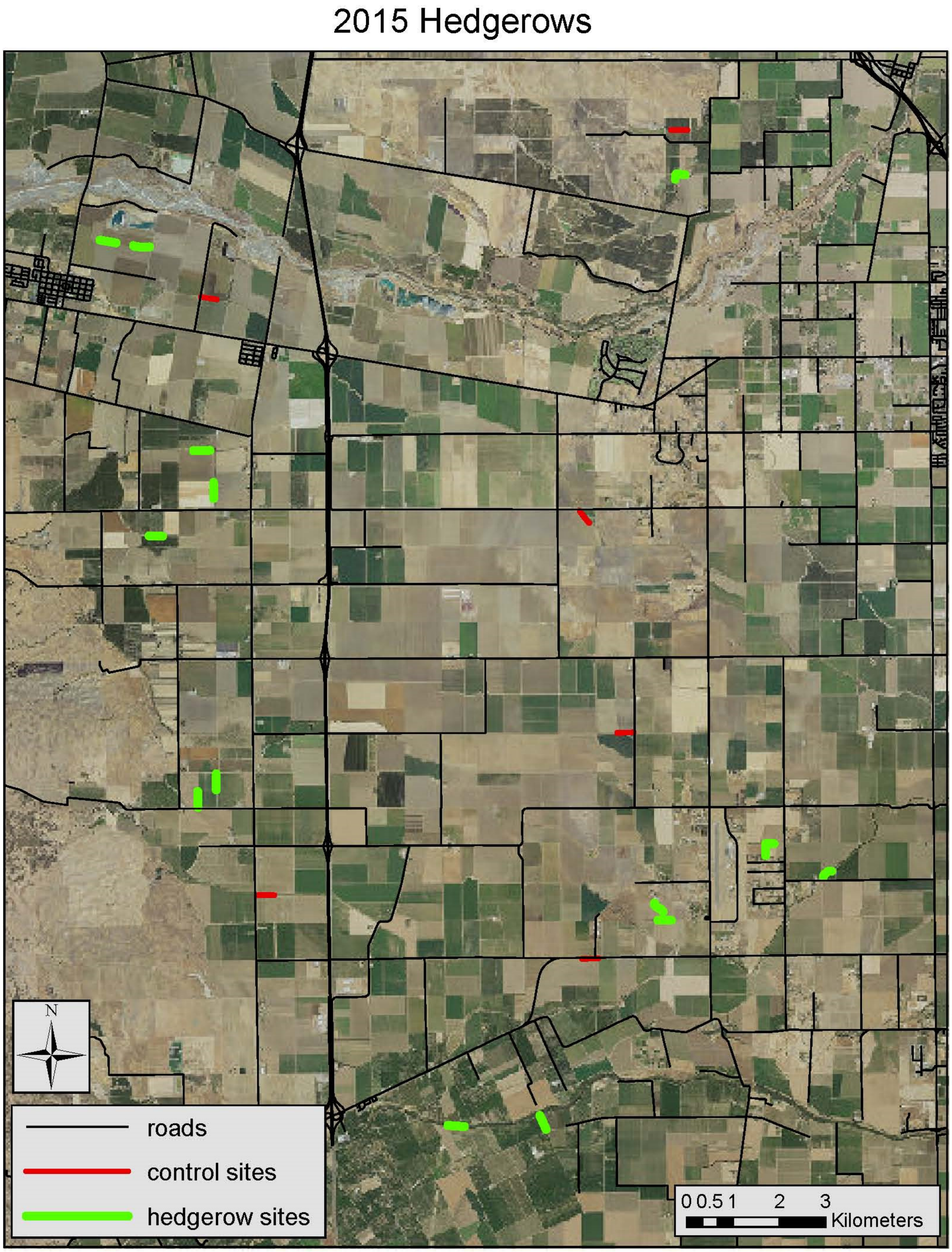
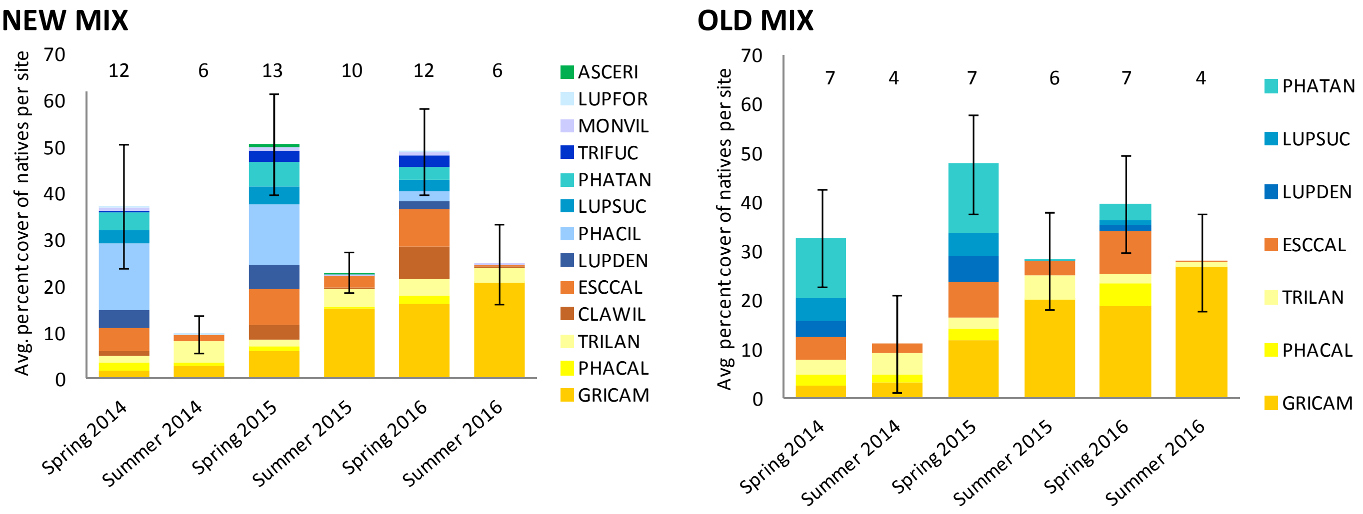


Figure 4. 2015 hedgerow and control sites.



NEW MIX

OLD MIX

Figure 5. Average cover of sown native forbs across five sites (or 4 sites in 2016) in the new mix (left) and old mix (right) in spring and summer vegetation assessments. Error bars are standard error of total percent cover of natives. Relative proportion of each sown species is shown by color, with spring-blooming species in cool tones and summer-blooming species in warm tones. Numbers above error bars give the number of species represented.

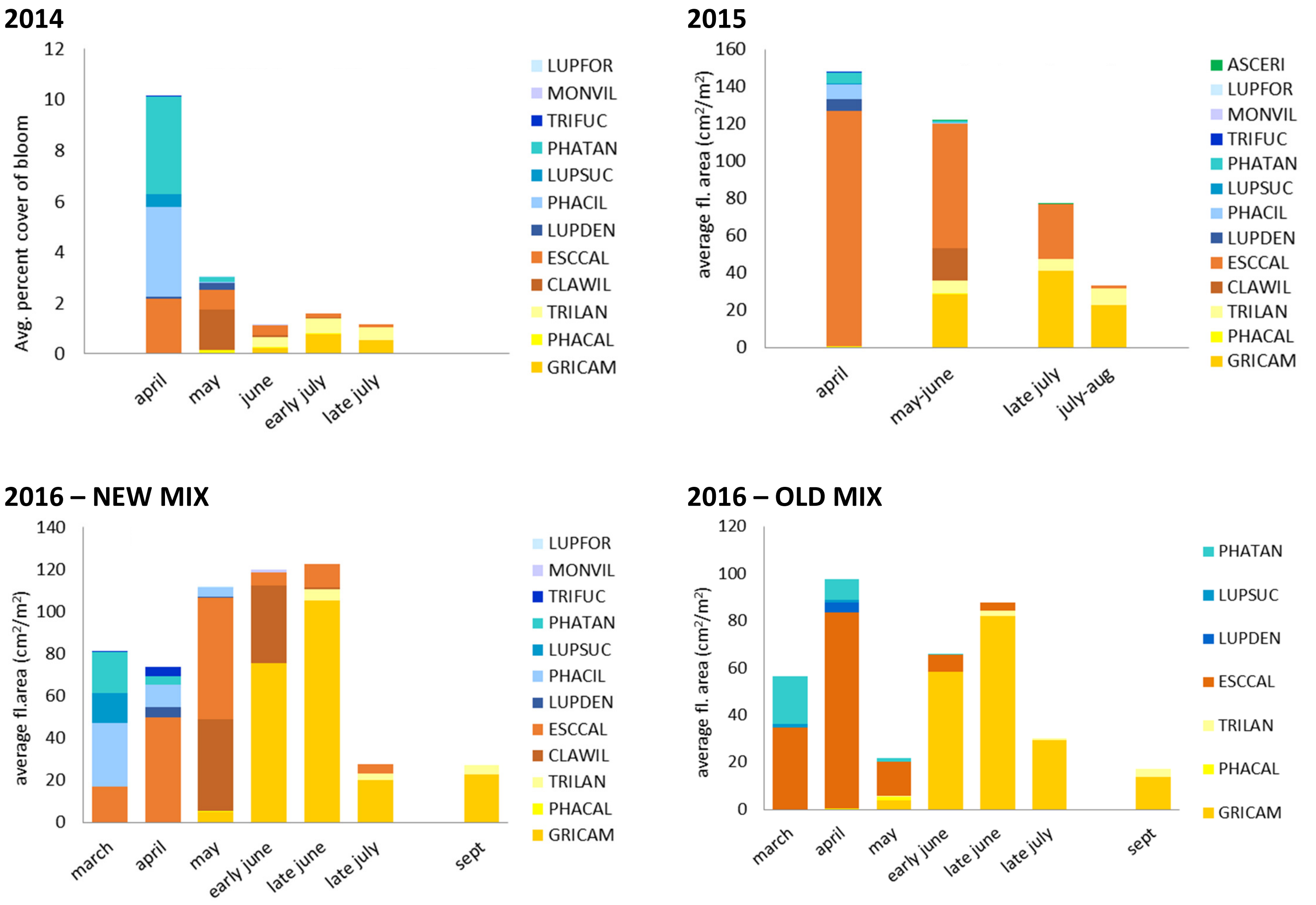


Figure 6. Average floral abundance across five sites (or 4 sites in 2016). In 2014 (upper left), only percent cover data was collected for flower species. In 2014 and 2015, floral area was not quantified separately for old and new mix. In 2016, floral area is shown for the new mix (bottom left) and old mix (bottom right). Relative proportion of each sown species is shown by color, with spring-blooming species in cool tones and summer-blooming species in warm tones. Sample dates varied with staff availability and weather but are aligned for comparison between years.

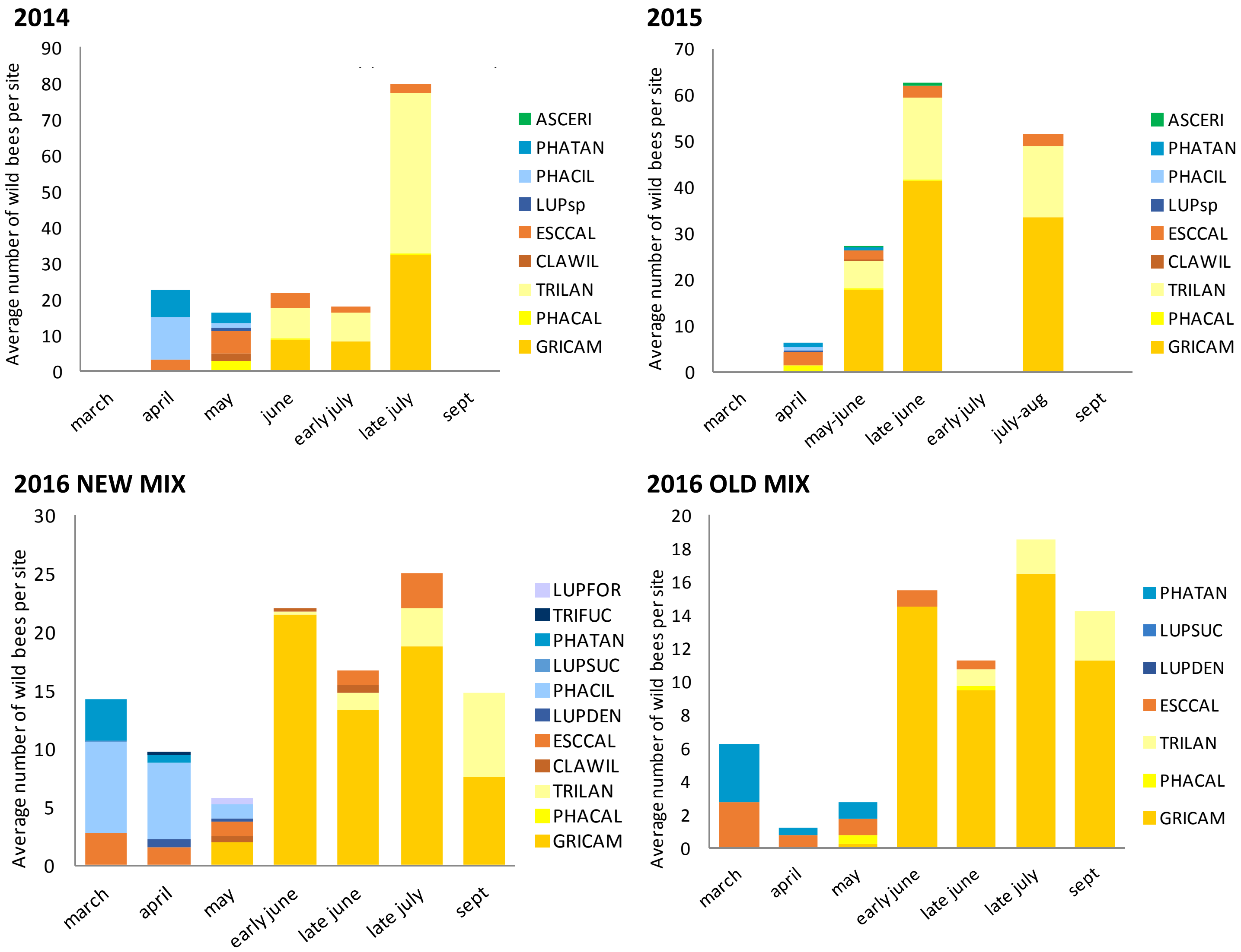


Figure 7. Average wild bee abundance across five sites (or 4 sites in 2016). The two wildflower mixes were not quantified separately in 2014 and 2015. Relative proportion of bee abundance on each sown forb species is shown by column with spring-blooming species in cool tones and summer-blooming species in warm tones. Sample dates varied with staff availability and weather but are aligned for comparison between years.

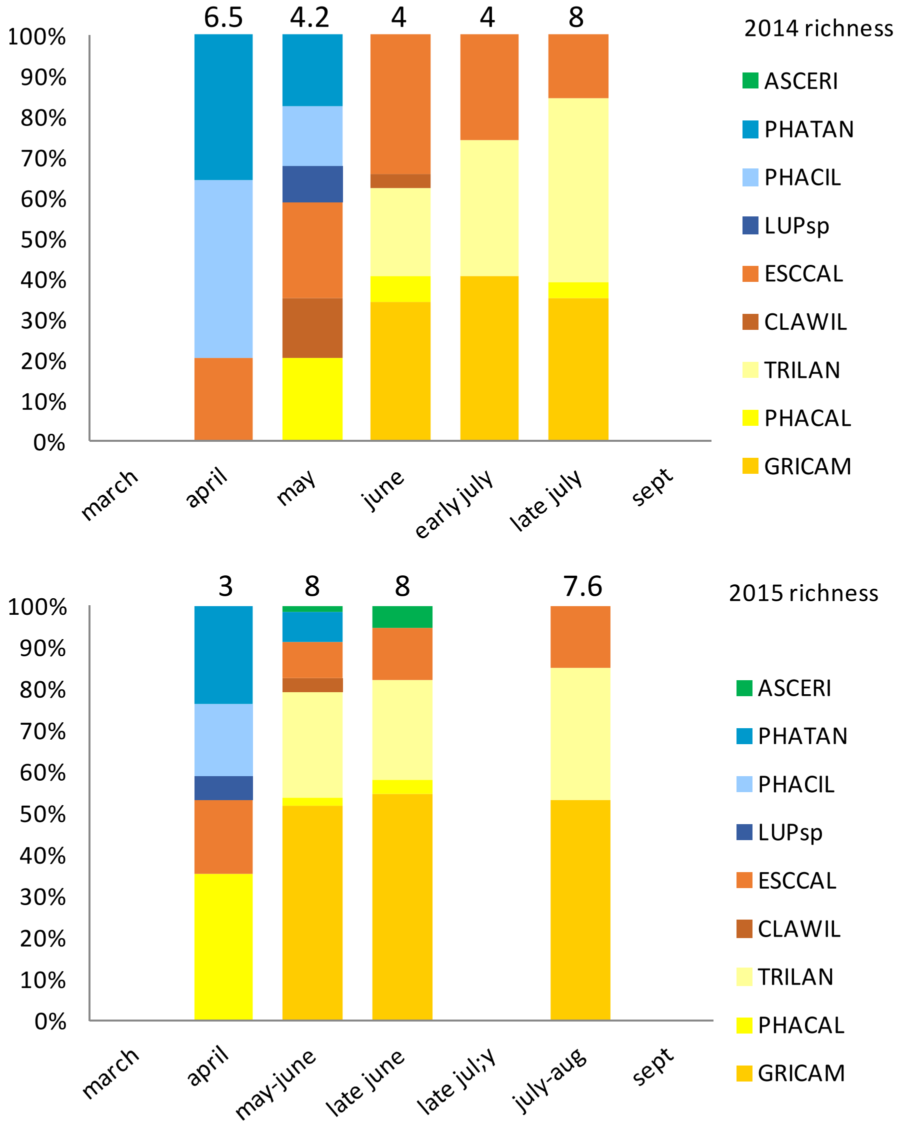


Figure 8. Average wild bee richness across five sites in 2014 and 2015 (bees are not yet identified for 2016). Total richness per site is given by the numbers above each bar; total richness per plant species (where bee species may be overlapping between plants) is represented by the proportional color patch, with spring-blooming species in cool tones and summer-blooming species in warm tones. Sample dates varied with staff availability and weather but are aligned for comparison between years.

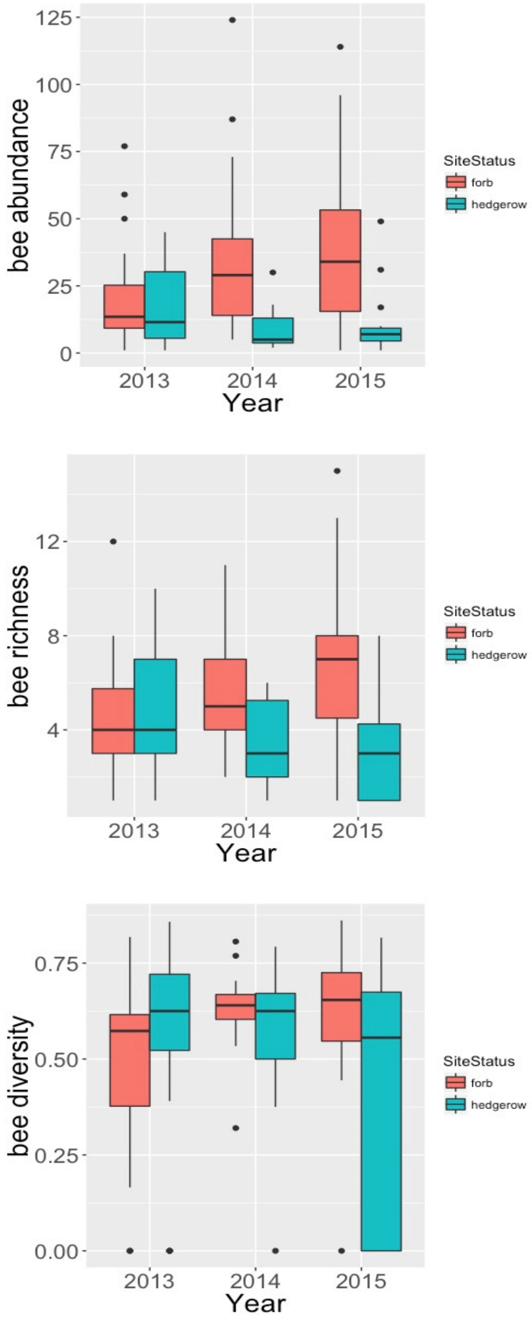


Figure 9. Wild bee abundance, richness, and diversity at mature hedgerows with and without the addition of forbs. We monitored five pairs of mature hedgerows in 2013 pre-planting and 2014 and 2015 post-forb planting at five of the sites.

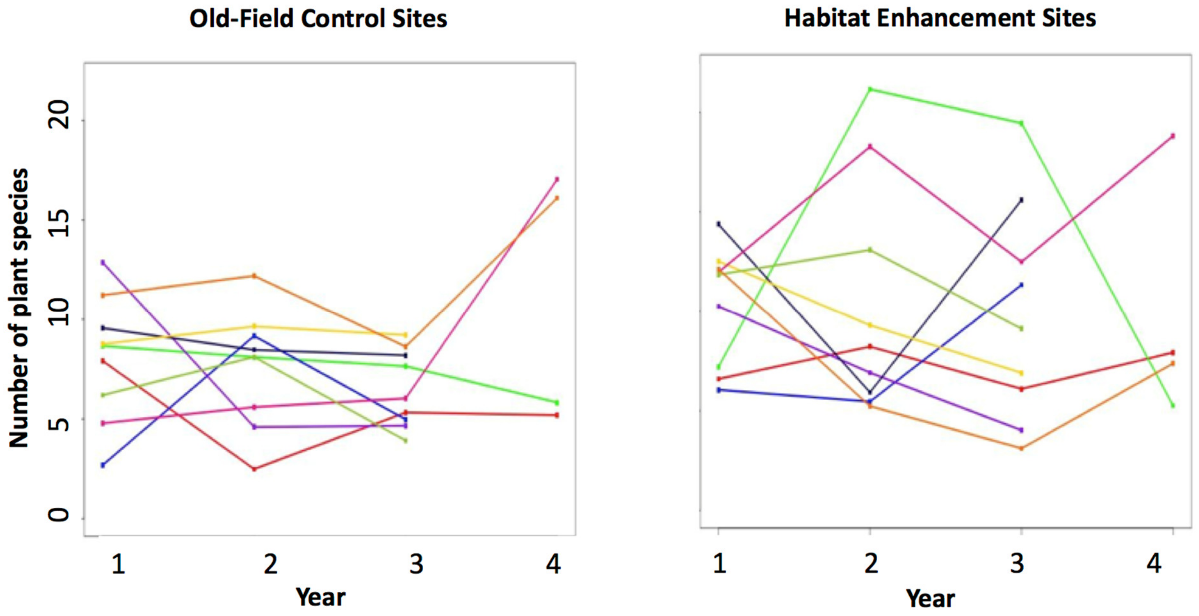


Figure 10. Trends in bloom diversity through time. Each colored line represents a single old-field control site (left) or habitat enhancement site (right), with colors representing site pairs. The y-axis is diversity, expressed as the number of species. The x-axis represents year of sampling. The points are shown without error estimates for clarity, but plant communities were typically undersampled. Despite this, habitat enhancement plant diversity is higher (about 30% on average) and more variable than old-field control plant communities. We did not detect an overall change in plant diversity with the time since planting of enhancements.

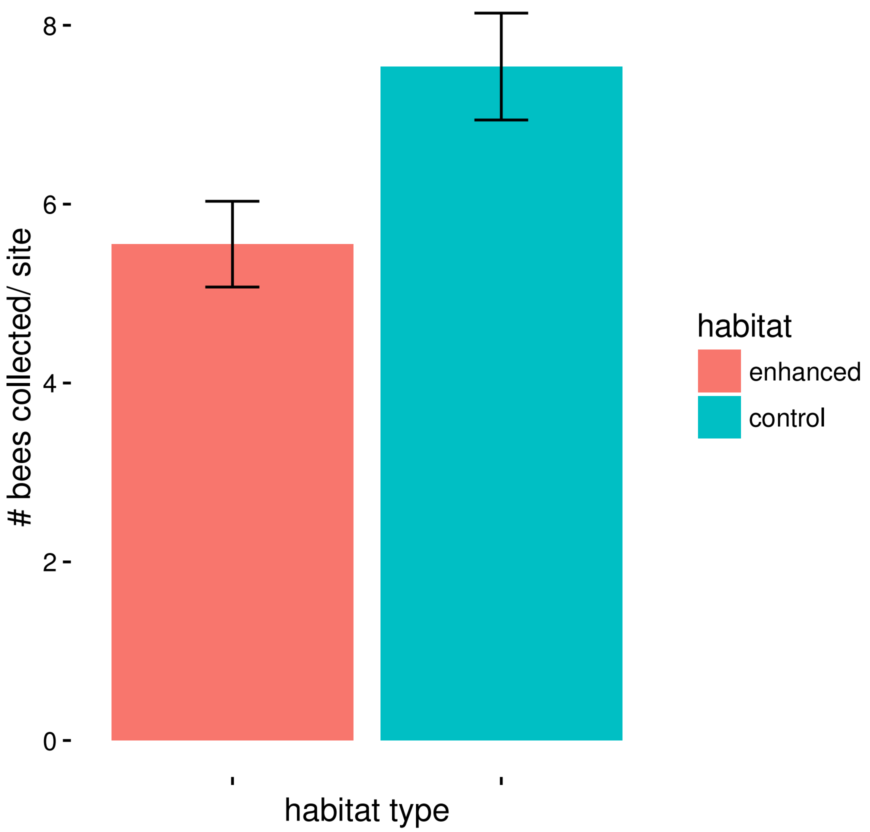


Figure 11. Wild bee visitation is greater in pollinator habitat enhancements than old-field controls. Bars represent mean # of wild bees collected in each site, error bars represent standard error. The difference in means is significant (paired Student's t-test, t = -4.06, df = 28, p = 0.0004).

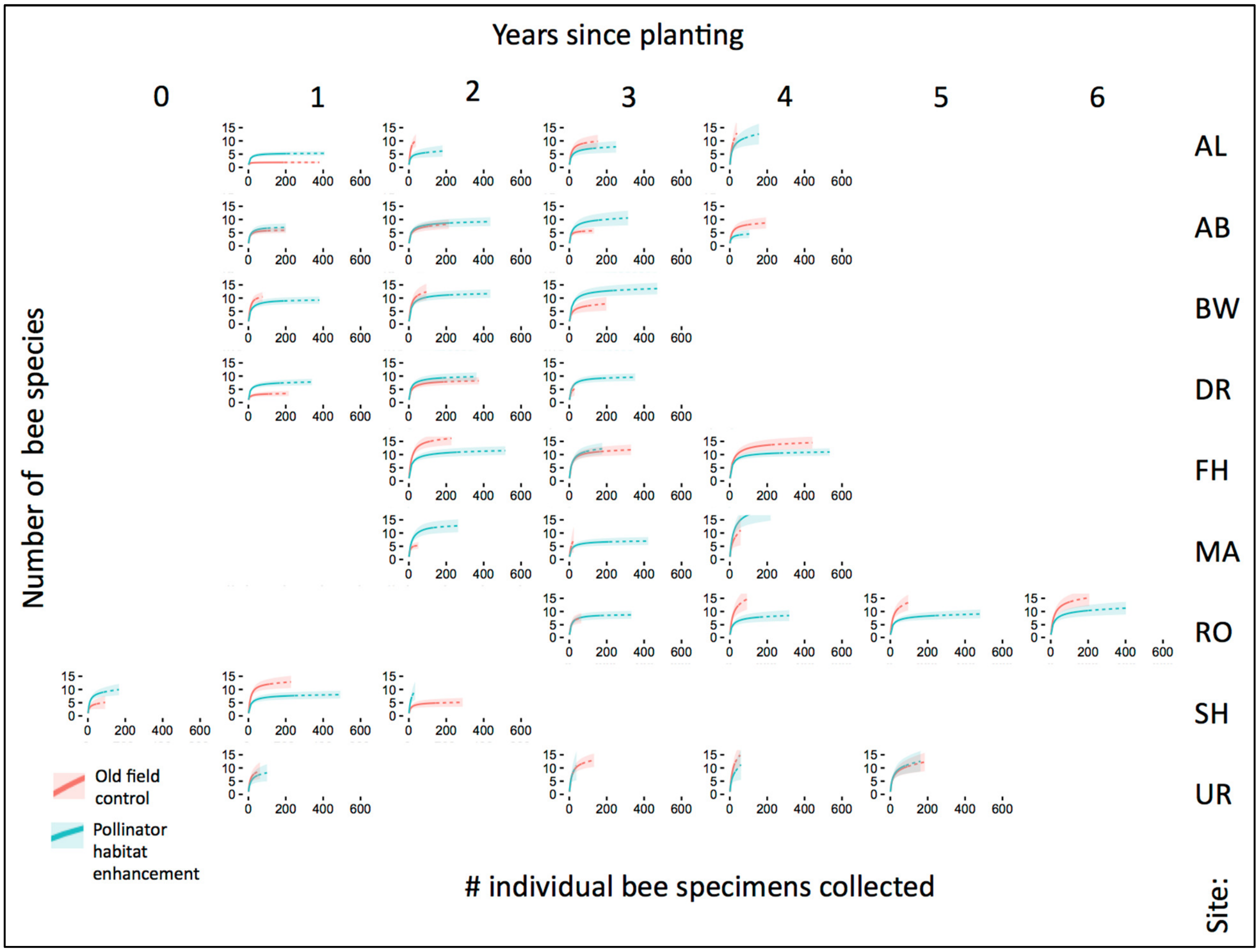


Figure 12. Trends in wild bee visitor diversity and abundance through time.
Because diversity estimates increase with the number of individuals included in the sample, we present the number of individuals collected at each site and year, with the corresponding diversity estimates for each sample size. Each row of plots corresponds to a single site, each column to the age of the site in years since the pollinator habitat planting was established. Estimated diversity (y-axis) increases with the number of individuals collected (x-axis). It is possible to compare the diversity of the pollinator habitat plantings (blue lines) to the old-field controls (red lines) when diversity no longer increases with additional sampling. Overall, there is no detectable difference in diversity between the pollinator habitat enhancements and the old-field controls, nor are there detectable changes in the diversity of wild bee visitors to pollinator habitat enhancements over time (reading across rows). Solid lines represent estimated diversity, the surrounding cloud represents estimated 95% confidence interval, and dotted lines represent the diversity estimate extrapolating to double the sample size.

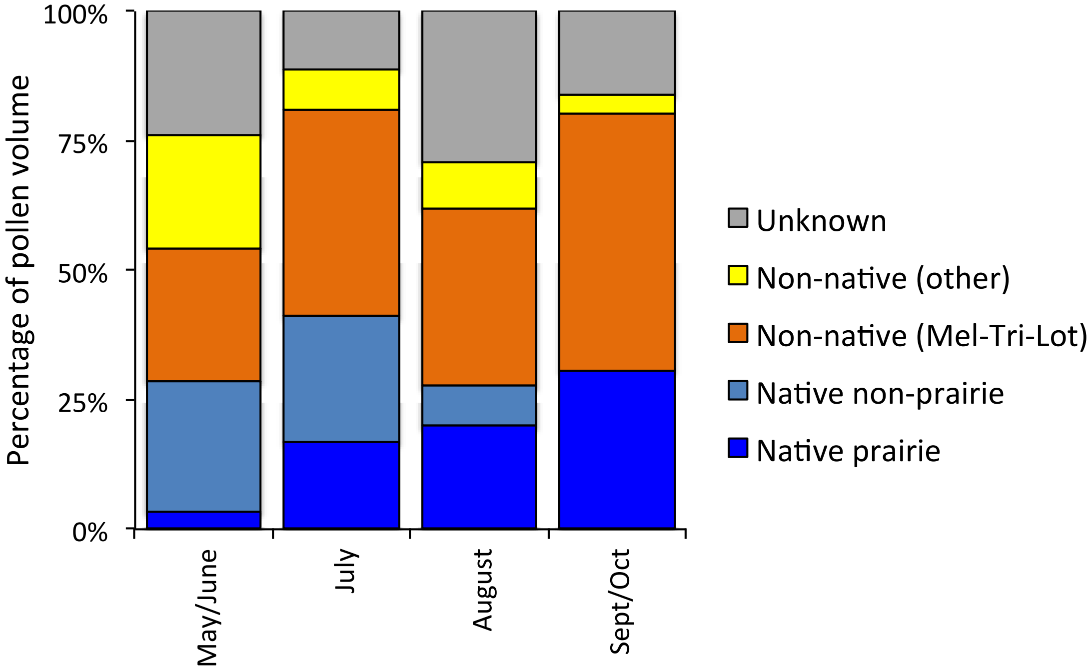


Figure 13. Average contributions of different categories of taxa to the pollen coming into our colonies at different times of year. These data are averaged across all four sites.

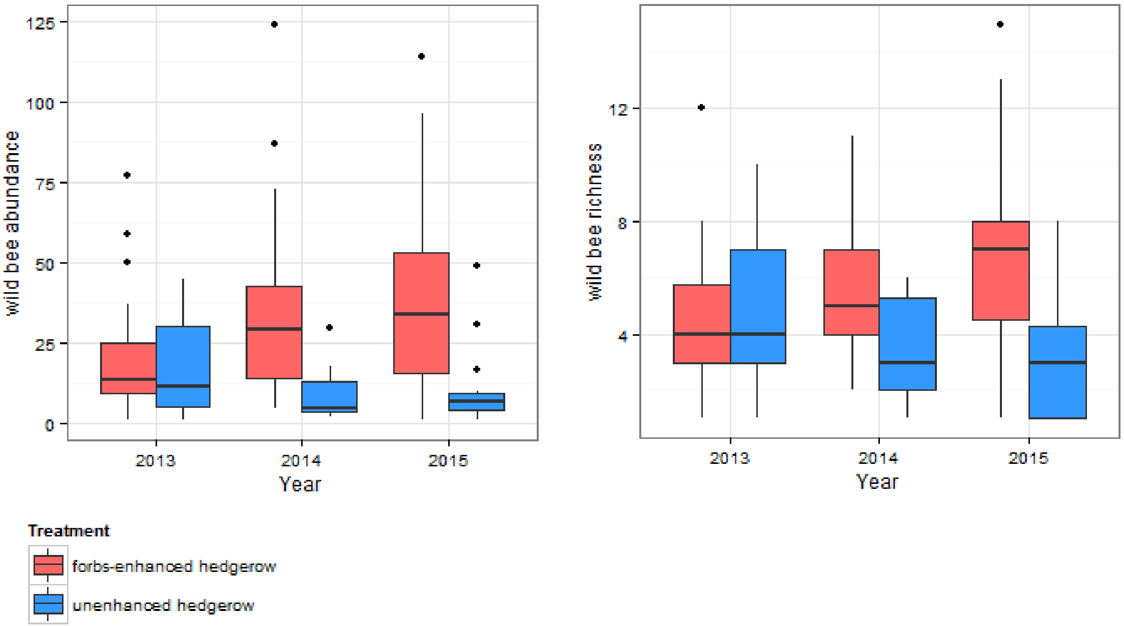


Figure 14. Wild bee abundance (left) and species richness (right) at forbs-enhanced and unenhanced control hedgerows in 2013 before forbs installation and the first two years of forbs establishment. Both hedgerow types had matured to blooming.

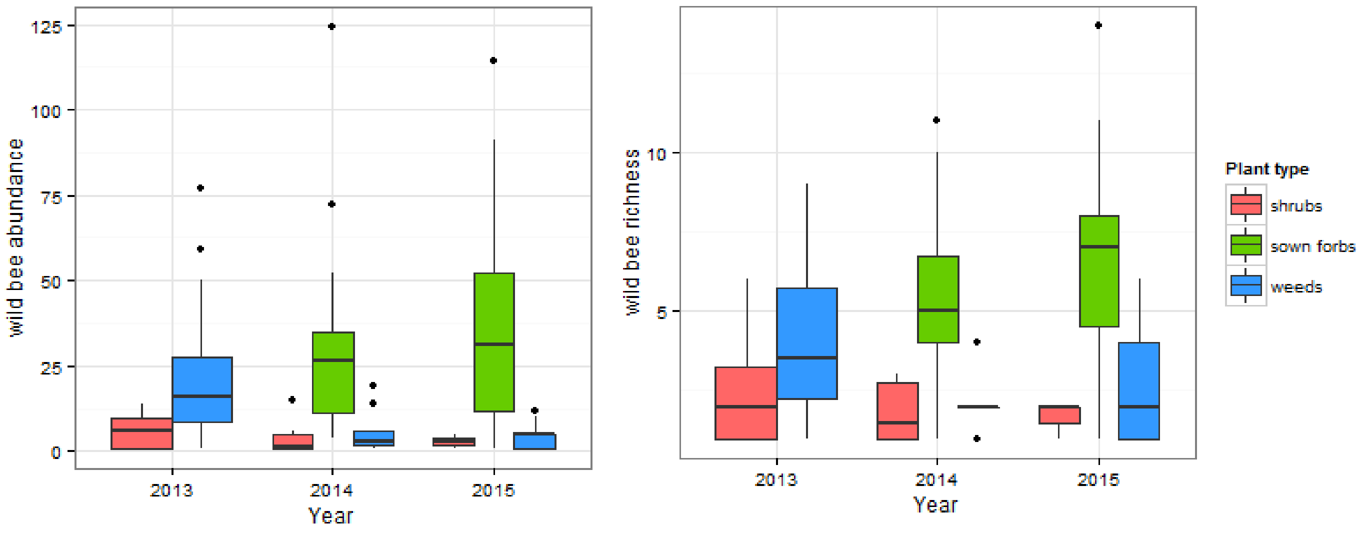


Figure 15. Wild bee abundance (left) and species richness (right) on shrubs, sown forbs and weeds in the forbs-enhanced hedgerows in 2013 before forbs installation, and during the first two years of forbs establishment.

Tables

Table 1. Establishment costs 2013

Sum of Person-hours						Site				
Year	Category	Activity	Method	Subactivity	Sub-subactivity	Gilmer	Muller	Parcell	Putah Creek	Rominger
2013	Establishn	Seeding	Dropseeder	harrowing/sowing/ringrolling	NA	4.5	8	4	5	
			Handscatter	raking/sowing	NA					11
			Hoe-ASCERI	NA	NA	3	6	7	2.5	3
	Site_Prep	Clearing_Vegeta	mowing	NA	NA	1	2	1	1	1
		Weed_Control	Chemical	broadcast spray	NA		0.5			
				spot spray	NA	0.5	1	1.5	1	1.5
			Mechanical	weedwhack	NA				0.5	
				hand pull	NA					2
			Solarize	Disc	NA	2	1.5	1	1	3
				Irrigation	Infrastructure - drip tape				10	61.5
					Infrastructure - microsprinklers	19.5		16		
					Watering-Drip tape	3			7	26
					Watering-microsprinklers		1	1		
				Making furrows	NA	1	0.5	1	1	4
				Laying plastic	NA	33	48	40	74.5	80
				check and tape plastic	NA	4.5	13.25	7	7.25	8.25
				weedwhacking plastic edges	NA		4			
				Pulling plastic	NA	6.75	12.5	12	10.5	6.5
2013 TOTALS - SITE PREP AND SEEDING					Hours - total	78.75	98.25	91.5	121.25	207.75
					Labor costs @ $18/hr	$ 1,417.50	$ 1,768.50	$ 1,647.00	$ 2,182.50	$ 3,739.50
					Cost per 1,000 sf	$ 162.71	$ 203.00	$ 189.05	$ 250.52	$ 429.24

Table 2. Maintenance Costs in first year - 2014

Sum of Person-hours						Site				
Year	Category	Activity	Method	Subactivity	Sub-subactivity	Gilmer	Muller	Parcell	Putah Creek	Rominger
2014	Establishn	Overseeding	Belly_Grinder	harrowing/sowing/r	NA	1		4		
			Handscatter	harrowing	NA				0.5	
				raking	NA					10.5
				sowing/ringrolling	NA	1			3.5	5.5
	Site_main	Fencing	NA	NA	NA	1		3	0.5	
		Irrigation	NA	NA	Infrastructure-microsprinklers					
					Watering-microsprinklers	3	0.5	1.5		
		Weed_Control	Chemical	broadcast spray	NA					5
				spot spray	NA	7.668	11.25	19.468	12.168	18
			Mechanical	cut and bag	NA	0.3	9.85	3.1	2.45	8.7
				hand pull	NA	26		66	45.5	83
				weedwhack	NA		3.5	1	2	3.75
	Site_Prep	Clearing_Vegeta	mowing	NA	NA			1		0.5
2014 TOTALS - SITE MTCE INCLUDING OVERSEEDING					Hours - total	39.968	25.1	99.068	66.618	134.95
					Labor costs @ $18/hr	$ 719.42	$ 451.80	$ 1,783.22	$ 1,199.12	$ 2,429.10
					Cost per 1,000 sf	$ 82.58	$ 51.86	$ 204.69	$ 137.64	$ 278.82

Table 3. Maintenance costs Year 2, 2015

Sum of Person-hours						Site				
Year	Category	Activity	Method	Subactivity	Sub-subactivity	Gilmer	Muller	Parcell	Putah Creek	Rominger
2015	Establishn	Overseeding	Belly_Grinder	harrowing/sowing/r	NA	7				8
			Dropseeder	harrowing	NA				12	
			Handscatter	harrowing	NA		2.75			
				raking	NA	7				6
				ringrolling	NA		2.75			
				sowing	NA	6	3.5			5
				stomping	NA	7				
		Reemay	Reemay	Reemay	3 events at Muller (place winter 2015, remove spring, replace in fall)		14		2.5	5.5
	Site_main	Irrigation	Irrigation	Irrigation	Infrastructure-microsprinklers	6		3		
					Watering-microsprinklers	1.5	0.5	1.5		
		Weed_Control	Chemical	broadcast spray	NA		1			
				spot spray	NA	9.968	3.5	9	4.5	1.5
			Mechanical	hand pull	NA	36.375	16.5	46.5	3	27.5
				weedwhack	NA			2		
	Site_Prep	Clearing_Veget	clearing_brush	NA	NA				14	
			mowing	NA	NA				1	5
			weedwhackin	NA	NA		7			
2015 TOTALS - SITE MTCE INCLUDING OVERSEEDING					Hours - total	80.843	51.5	62	37	58.5
					Labor costs @ $18/hr	$ 1,455.17	$ 927.00	$ 1,116.00	$ 666.00	$ 1,053.00
					Cost per 1,000 sf	$ 167.03	$ 106.40	$ 128.10	$ 76.45	$ 120.87

Table 4. Maintenance costs partial Year 3, 2016

Sum of Person-hours						Site				
Year	Category	Activity	Method	Subactivity	Sub-subactivity	Gilmer	Muller	Parcell (dropped Aug 2015)	Putah Creek	Rominger
2016	Establishn	Reemay	Reemay	Reemay removal	NA		8.5		2.5	
	Site_main	Weed_Control	Chemical	spot spray	NA	4	4		8.5	5.5
			Mechanical	hand pull	NA		1		2	
				weedwhack	NA		2.5		2	
2016 TOTALS - SITE MTCE					Hours - total	4	16	0	15	5.5
					Labor costs @ $18/hr	$ 72.00	$ 288.00	$ -	$ 270.00	$ 99.00
					Cost per 1,000 sf	$ 8.26	$ 33.06	$ -	$ 30.99	$ 11.36

Table 5. Establishment and maintenance costs overall (March 2013-Aug 2016)

	Gilmer	Muller	Parcell (Ending 2015)	Putah Ck	Rominger
TOTAL COST PER 1,000 SF: ESTABLISHMENT	$ 420.58	$ 394.32	$ 521.83	$ 495.60	$ 840.29
TOTAL COST PER 1,000 SF: MTCE 2.5 YRS	$ 257.87	$ 191.32	$ 332.79	$ 245.08	$ 411.05

Table 6. Species composition and seeding rate of two seed mixes sown at each forbs-enhanced hedgerow site. A monoculture of *Asclepias eriocarpa* was hand-seeded between the two mixes and *Helianthus californicus* was plug-planted into the New Mix area at each site.

Old Mix seeding rate	
Species	**Sown live seed/ft^2**
Eschscholzia californica	3.5
Grindelia camporum	3.0
Lupinus densiflorus	1.0
Lupinus succulentus	2.0
Phacelia californica	3.0
Phacelia tanacetifolia	1.5
Trichostema lanceolatum	10.0
	24.00

New Mix seeding rate	
Species	**Sown live seed/ft^2**
Clarkia williamsonii	8.8
Eschscholzia californica	5.3
Grindelia camporum	4.5
Lupinus densiflorus	1.5
Lupinus formosus	1.7
Lupinus succulentus	3.0
Monardella villosa	11.0
Phacelia californica	4.5
Phacelia ciliata	8.3
Phacelia tanacetifolia	2.3
Trichostema lanceolatum	15.0
Trifolium fucatum	13.20
	78.90

Table 7. Native forbs trialed in forbs plots added to existing mature shrubby hedgerow plantings, with rationale for inclusion of novel species and notes on each species initial establishment as well as persistence, contribution to floral resources for bees and support of wild bee abundance and diversity over time.

Common Name	Species	Annual/ Perennial	Bloom Season	Old Mix	New Mix	Rationale for inclusion of novel species	Establishment	Persistence	Contribution to bloom at site	Wild bee abundance	Wild bee richness (2014 and 2015 only)
Indian milkweed	*Asclepias eriocarpa*	P	Jun-Aug			Hand-seeded in 10% of the plot as a monoculture. Attracted bumble bees in a pilot study.	Poor	Poor	Small due to poor establishemtn	Negligible	Small
Fort Miller Clarkia	*Clarkia williamsonii*	A	May-Jul		X	Fills a mid-summer gap in bloom and attracted diverse bees in pilot study.	Good	Increasing	Increasing	Small	Small
California poppy	*Eschscholzia californica*	P	Apr-Jul	X	X		Good	Good	Increasing	Moderate	Moderate
valley gum plant	*Grindelia camporum*	P	Jun-Oct	X	X		Good	Overdominant	Increasing	Large	Large
California sunflower	*Helianthus californicus*	P	Jul-Sep		X	Hexaploid species that **cannot cross with cultivated sunflower**. Therefore it **cannot contaminate hybrid sunflower production fields**.	Poor (transplants)	Too few to assess	None	None	None
golden lupine	*Lupinus densiflorus*	A	May-Jun	X	X		Good	Declining	Inconsistent	Small	Small (lupines combined)
summer lupine	*Lupinus formosus*	P	Jun-Oct		X	Previously tested species but included in just one-third of the plot because of cost.	Poor (seeded at very low rate)	Good	Small but increasing	Small	
arroyo lupine	*Lupinus succulentus*	A	Feb-May	X	X		Good	Declining	Inconsistent	Very small	
coyote mint	*Monardella villosa*	P	Jun-Aug		X	Fills a mid-summer gap in bloom.	Poor	Too few to assess	Negligible	Negligible	None
California phacelia	*Phacelia californica*	P	Jun-Jul	X	X		Poor in drought year	Increasing	Small	Small	Small-Moderate
Great Valley phacelia	*Phacelia ciliata*	A	Feb-May		X	Provides early season bloom and attracted diverse bees in pilot study, including queen bumble bees.	Good	Good but declining	Large	Moderate-Large	Moderate-Large
lacy phacelia	*Phacelia tanacetifolia*	A	Mar-May	X	X		Good	Good but declining	Large	Moderate	Moderate-Large
vinegar weed	*Trichostema lanceolatum*	A	Aug-Oct	X	X		Good	Good but declining	Inconstistent	Large	Large
bull clover	*Trifolium fucatum*	A	Apr-Jun		X	Attracts bumble bees in natural areas.	Poor	Fair	Snall	Negligible	None

Appendix B. Landowner Survey

Implementation

1) What year and month did you plant your pollinator habitat?

2) How many acres of pollinator habitat did you plant (approximate)?

3) Was this planting in one location or were plantings at multiple locations?

4) Was weed pressure in planting area before seeding high, moderate, or low? (Circle answer below)

A) **High weed pressure is characterized by**: persistent year-round cover of undesirable plants (covering the entire surface of the planting area); sites where invasive weeds have been actively growing and producing seed for multiple years; sites dominated by sod-forming grasses and rhizomatous forbs (e.g., Canada thistle)

B) **Moderate weed pressure is characterized by**: persistent, partial cover of undesirable plants (covering up to 50% of the planting area); sites where sod-forming grasses and rhizomatous forbs (e.g., Canada thistle) are present, but not the dominant cover.

C) **Low weed pressure is characterized by**: previously cropped lands that have been cultivated for several years or where consistent weed abatement activities were performed; site is a crop field being converted to permanent cover; or site may have some annual weeds growing.

5) How did you prepare the planting area? (Check all that apply)

A) Herbicide
B) Cultivation
C) Smother crop
D) Solarization
E) Mowing
F) Other (please specify)

6) Approximately how many hours did it take to prepare the planting area?

7) How did you plant? (Check all that apply)

A) Broadcast seeding
B) Spreader
C) Seed Drill
D) Plant plugs
E) Other (please specify)

8) Did you receive technical assistance? If yes, from whom?

9) Did you received financial assistance through USDA NRCS conservation programs?

Maintenance

10) What management activities were used during ***first*** year of establishment? (Check all that apply)

A) Manual weed removal
B) Herbicide spot treatment,
C) Spring mowing
D) Midseason mowing
E) Late fall mowing
F) Reseeding
G) Other (please specify)

11) What management activities were used during ***second*** year of establishment? (Check all that apply)

A) Manual weed removal
B) Herbicide spot treatment,
C) Spring mowing
D) Midseason mowing
E) Late fall mowing
F) Reseeding
G) Other (please specify)

12) What management activities were used during ***third*** year of establishment? (Check all that apply)

A) Manual weed removal
B) Herbicide spot treatment,
C) Spring mowing
D) Midseason mowing
E) Late fall mowing
F) Reseeding
G) Other (please specify)

13) What control material did you follow to install and maintain the pollinator habitat?

A) NRCS or Xerces officer’s written plans
B) Anything specific?
C) Other (please specify)

Assessment

14) What were your overall goals in installing habitat for pollinators? (Check all that apply)

   A) Supporting honey bees
   B) Increase native bee diversity
   C) Improve crop pollination on your farm
   D) Aesthetics
   E) Other (please specify)

15) Do you think the planting was successful?

16) Are there any resources (e.g., documents, online tools, professional consultation) that would have helped you install and maintain your pollinator habitat?

17) Considering all of the steps involved in installing and managing the habitat planting, what worked especially well?

18) Considering all of the steps involved in installing and managing the habitat planting, what could have been improved?

Appendix C. References and Publications

- Works Cited
- Xerces Society Publications (project deliverables)
- Published Research

Works Cited

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Sardiñas, H.S., L.C. Ponisio, and C. Kremen. 2016. Hedgerow presence does not enhance indicators of nest-site habitat quality or nesting rates of ground-nesting bees. *Restoration Ecology*. DOI: 10.1111/rec.12338

Xerces Society Publications

The following publications were produced by the Xerces Society as a result of the *Next Steps in Pollinator Conservation* Conservation Innovation Grant. Copies of all publications can be downloaded from http://www.xerces.org/final-documents-nov-2016/.

1. Estimated Costs to Establish Wildflower Plantings Using Chemical Fallow
2. Estimated Costs to Establish Pollinator Hedgerows
3. Estimated Costs to Establish Wildflower Plantings Using Solarization
4. Maintaining Diverse Stands of Wildflowers Planted for Pollinators: Ongoing Management of Pollinator Habitat
5. Wildflower Establishment: Organic Site Preparation Methods
6. Expanding Pollinator Habitat on Farms: Collecting and Using Your Own Wildflower Seed
7. Increasing Seed of Wildflowers Valuable to Pollinators: Xerces Society and Seed Producer Partnerships
8. Native Thistles: A Conservation Practitioner's Guide. Plant Ecology, Seed Production Methods, and Habitat Restoration Opportunities (draft document and publication design sample)

Published Research

The following publications are based on research that was part of *Next Steps in Pollinator Conservation* and previous Conservation Innovation Grants. Listed articles are included in following pages.

Kremen, C., and L.K. M'Gonigle. 2015. Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. *Journal of Applied Ecology* 52: 602–610. [Selected as Editor's Choice]

M'Gonigle, L.K., L. Ponisio, K. Cutler, and C. Kremen. 2015. Habitat restoration promotes pollinator persistence and colonization in intensively-managed agriculture. *Ecological Applications* 25: 1557–1565.

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Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2015, **52,** 602–610 doi: 10.1111/1365-2664.12418

Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species

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Summary

1. Agriculture now constitutes 40–50% of terrestrial land use globally. By enhancing habitat suitability and connectivity, restoration within agricultural landscapes could have a major influence on biodiversity conservation. However, habitat management within intensive agricultural landscapes may primarily boost abundances of common, highly mobile generalists, rather than vulnerable or endangered species. We studied pollinator community response to small-scale habitat restoration in the intensively farmed Central Valley of California to determine whether restoration could also promote more specialized, less common and/or less mobile species.

2. Composition of pollinator communities was assessed in five experimental and 10 control (unrestored) sites before and after restoration of native plant hedgerows over an 8-year period, using a before-after control-impact design.

3. We characterized bee and fly species based on functional response traits [floral specialization, habitat specialization, abundance, body size and sociality (bees only)] known to influence the response to habitat change.

4. We modelled how species occurrences changed with habitat restoration over time as modulated by their response traits.

5. We found that hedgerows not only significantly enhanced occurrences of native bee and syrphid fly species, but that as hedgerows matured, they had a greater positive effect on species that were more specialized in floral and nesting resources and smaller (less mobile).

6. *Synthesis and applications*. Unlike previous studies that suggest habitat restoration in agricultural landscapes only benefits mobile, generalist species, our results suggest that small-scale habitat restoration can promote species whose traits likely render them particularly vulnerable to habitat degradation. Thus, even within highly intensive agricultural landscapes, small-scale habitat restoration can be a conservation management tool. However, tailoring habitat enhancements to promote certain species or guilds may be critical for their success as a conservation intervention in agricultural landscapes.

Key-words: Apoidea, bee, before-after control-impact, conservation, hedgerow, land-use change, pollination service, response traits, syrphid fly

Introduction

Two primary goals of restoring natural habitat are to conserve biodiversity and restore ecosystem functions and services (Benayas *et al*. 2009). Agriculture is the world's largest land use and constitutes a principle driver of biodiversity loss, increased homogenization and decreased ecosystem services (Foley *et al*. 2011; Karp *et al*. 2012). Agricultural lands also constitute much of the matrix that surrounds protected patches of natural habitat. Managing this matrix both to provide resources for species in these patches and to improve connectivity among patches is perhaps the most important current task for biodiversity conservation (Driscoll *et al*. 2013).

While restoring habitat within agricultural areas might enhance species abundances in the matrix or promote

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movement through the matrix, such schemes are thought to primarily promote common and resilient species and thus provide few conservation benefits for species of concern (Kleijn *et al.* 2006). Such species, it is thought, are likely to have specific functional traits ('response traits') like high mobility and generalist habits (Ewers & Didham 2006; Schweiger *et al.* 2007) that permit them to survive even in intensive agricultural landscapes (Flynn *et al.* 2009). Thus, trait composition could be used to assess whether restoration simply bolsters populations of such species or, alternatively, promotes species that are sensitive to habitat loss, fragmentation and degradation (hereafter, 'land-use changes'). Here, we examine how restoration of native plant hedgerows in an intensive agricultural setting influences the response trait composition of flower visitor communities, as an indicator of conservation effectiveness of this technique.

For bees and syrphid flies, two dominant groups in many flower visitor communities (Morandin & Kremen 2013; Winfree *et al.* 2014), abundance, body size, specialization in diet or microhabitat, and sociality are response traits that are sensitive to land-use changes and might, therefore, differentiate flower visitor communities in response to restoration (i.e. reversal of land-use changes). Abundance was the single most important trait influencing persistence in a study of bees and flies (Winfree *et al.* 2014), while population size, but not habitat area, was related to persistence in a solitary bee species (Franzén & Nilsson 2010). Diet specialization was associated with sensitivity to land-use changes for both bees (Bartomeus *et al.* 2013; Burkle, Marlin & Knight 2013; but see Williams *et al.* 2010) and syrphid flies (Schweiger *et al.* 2007). Microhabitat specialization also influenced flower visitor response to land-use changes. In flies, Schweiger *et al.* (2007) found that larval habitat specialists (i.e. living on water plants or in the root zone of trees) were most sensitive to land-use changes. In bees, several studies found that cavity nesters were more affected by land-use changes (Williams *et al.* 2010; Burkle, Marlin & Knight 2013; but see Bartomeus *et al.* 2013), as are above-ground nesters that either used existing cavities or excavated their own nests (Williams *et al.* 2010).

Body size, sociality and parasitism displayed conflicting responses to land-use changes in different studies. Body size is a proxy for mobility in bees (Greenleaf *et al.* 2007) and flies (Schweiger *et al.* 2007). Larger-sized individuals may be more resilient to land-use changes because they can disperse further through inhospitable landscapes in search of resources. However, large-bodied species may also have larger resource needs and smaller population sizes, reducing their resilience to land-use changes. These opposing tendencies may explain the wide variation found in the responses of body size to land-use changes which include non-significant for bees (Williams *et al.* 2010), significant positive for bees (Larsen, Williams & Kremen 2005; Bartomeus *et al.* 2013) and significant negative for bees (Jauker *et al.* 2013) and flies (Öckinger *et al.* 2010). Social bees responded more strongly to land-use changes than solitary bees in several studies (Williams *et al.* 2010; Bommarco *et al.* 2010), but others found no effect of sociality (Bartomeus *et al.* 2013) or effects that varied by bee family (Jauker *et al.* 2013). Cleptoparasitic bees, which are generally specialized on their hosts and are considered to occur at a higher trophic level because they feed on the nest provisions and/or larvae of other bees (Bommarco *et al.* 2010), were found to be more sensitive to land-use changes than non-parasitic bees in one study (Burkle, Marlin & Knight 2013), but less sensitive in another (Jauker *et al.* 2013). These discrepancies among studies may reflect not only true differences among study systems, but also methodological differences, such as coding of qualitative traits.

While many studies have examined how traits of flower visitor communities change as communities disassemble in response to land-use changes (e.g. Steffan-Dewenter & Tscharntke 2000; Larsen, Williams & Kremen 2005; Schweiger *et al.* 2007; Bommarco *et al.* 2010; Bartomeus *et al.* 2013; Burkle, Marlin & Knight 2013; Winfree *et al.* 2014), only a few studies have used a trait-based approach to examine how restoration influences the reassembly of flower visitor communities (Alanen *et al.* 2011; Merckx, Marini & Feber 2012). If restoration in intensive agricultural landscapes merely promotes common generalist species, then we would expect to see increases in mean occurrence (i.e. presence) of species between restored and unrestored sites, but no relative increases in the occurrence of species that are more sensitive to land-use changes. Here, we present results from a long-term restoration study. Specifically, we examine (i) how restoration of native plant hedgerows within an intensive agricultural landscape in California's Central Valley influences species occurrences of bees and flies and (ii) how these effects on species occurrences are modulated by response traits. We predict that hedgerows promote species more sensitive to land-use changes and thus will disproportionately increase occurrence of species that have some or all of the following response traits: (i) less abundant, (ii) narrow larval and/or adult diet breadths, (iii) cavity-nesting bees, (iv) large body size for bees (based on Larsen, Williams & Kremen 2005 from the same study region), (v) small body size for flies and (vi) parasitic bees. We predict no difference in sociality for bees, however, since in our study system, some social bees are least responsive to agricultural intensification (i.e. *Halictus* and *Lasioglossum*), whereas others (*Bombus*) are most sensitive to agricultural intensification (Larsen, Williams & Kremen 2005; see also Jauker *et al.* 2013). If hedgerows promote species with these response traits disproportionately relative to controls, then hedgerows may be partially reversing the community disassembly that has occurred in response to agricultural intensification in this region (Kremen, Williams & Thorp 2002; Larsen, Williams & Kremen 2005).

Materials and methods

STUDY LANDSCAPE AND SAMPLING

Our study landscape, located in the Central Valley of California (Yolo County), is an intensively managed agricultural landscape comprised principally of conventional row crops, vineyards and orchards (Fig. 1a). The 1-km buffers around our sites contained on average $<0{\cdot}6 \pm 0{\cdot}2\%$ (SE) natural habitat cover; thus, these areas are examples of 'cleared landscapes' (*sensu* Tscharntke *et al.* 2005). We utilized a before-after control-impact (BACI) design (Underwood 1994) to assess the impact of hedgerows on pollinator communities, as recommended for evidence-based assessment of conservation and agri-environment management schemes (Potts *et al.* 2006). We selected five farm edges to be restored and paired these with 10 control sites that would not be restored. As recommended, we selected a larger number of controls than restoration sites ('beyond BACI', Underwood 1994).

Monitoring began in 2006 prior to restoration and continued through 2013. Hedgerows were planted in 2007 or 2008 with native perennial shrubs and trees (e.g. *Cercis occidentalis*, *Ceanothus* spp., *Rosa californica*, *Heteromeles arbutifolia*, *Sambucus mexicana*, *Eriogonum* spp., *Baccharis* spp., *Salvia* spp. and others). Hedgerows are approximately 350 m long and 3–6 m wide, bordering an irrigation ditch or slough and adjacent to large (*c.* 80 acre) crop fields. After initial planting, hedgerows were irrigated and weeded for 3 years until well-established (see Fig. 1b and 1c for an example of a restoration site prior to and 6 years post-restoration).

Control sites (Fig. 1a) were selected to roughly match conditions surrounding paired restoration sites, including adjacency to an irrigation ditch or slough and similar crop system (row, orchard, pasture or vineyard), within the same landscape context (i.e. within 1–3 km of the restoration site, but >1 km from all other study sites to maintain independence). Controls reflect the variety of potential conditions on edges of crop fields that could be restored (see Fig. S1, Supporting information). Such edges may at times be tilled, treated with pesticides or left alone; plants on these edges include predominantly non-native forbs and grasses, with occasional shrubs and trees. The most common flowering plants at these sites are the non-native weeds: *Convolvulus arvensis*, *Brassica* spp., *Lepidium latifolium*, *Picris echioides* and *Centaurea solstitialis*. Many of these weeds also occurred at restoration sites.

We sampled flower visitor communities at each site a minimum of three times between April and August each year, except for two sites which were sampled only twice in the first year (Table S1). For logistical reasons, no sampling was conducted in 2010. In each sample round, sites were sampled in random order during allowed weather conditions, which were bright overcast to clear skies, wind speed $<2{\cdot}5$ m s^{-1}, temperature >21 °C. Beginning in the morning, all flower visitors that contacted the reproductive parts of the flower (except *Apis mellifera*) were netted along a 350-m transect for 1 h, pausing the timer while handling specimens and recording the plant species on which each specimen was collected. Honeybees (*A. mellifera*) were not collected because their abundance is determined largely by the placement of hives throughout the region by bee-keepers. Here, we focus our analyses on the two most abundant and effective wild pollinator groups in the data set: bees and syrphid flies (representing 47% and 20% of records, respectively). Bee specimens were identified to species or morpho-species by expert taxonomist Dr. Robbin Thorp (Professor Emeritus, University of California, Davis), and syrphid specimens were identified to species by expert taxonomist Dr. Martin Hauser (California Department of Food and Agriculture).

RESPONSE TRAITS

Qualitative traits for bees included sociality, nesting location and nesting habit. Following Burkle, Marlin & Knight (2013), we classified bees as social (including primitively social to eusocial), solitary or cleptoparasitic, based on Michener (2000). Following Williams *et al.* (2010), we classified nesting location as above- or below-ground or mixed and nesting habit as constructing a nest (excavator) or using a pre-existing cavity

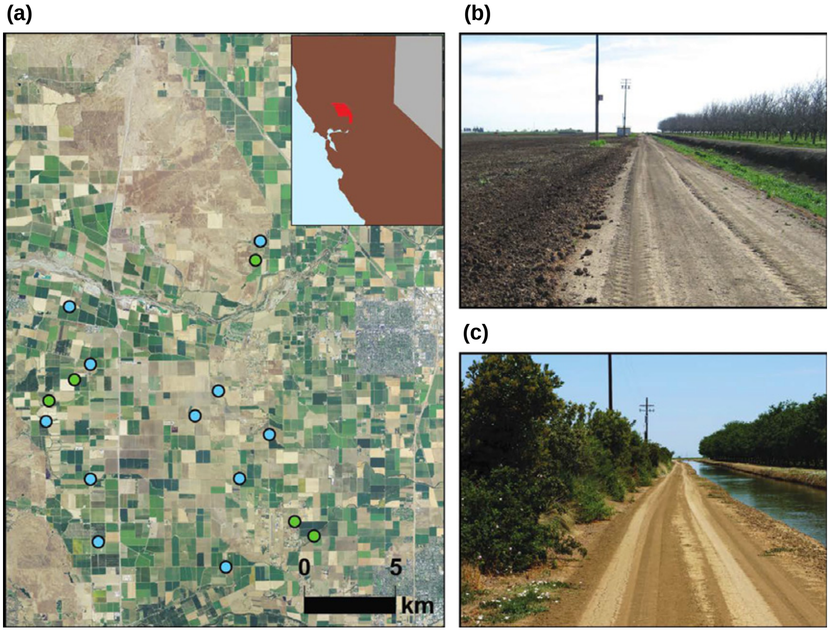

Fig. 1. Study region and sites. (a) Location of hedgerow and control sites in California (inset) and surrounding land cover (Data available from the U.S. Geological Survey, National Aerial Imagery Program). Green dots are restored sites and blue are control sites. (b) A hedgerow site prior to restoration. (c) Same site 6 years post-restoration.

(renter). Nesting location was based on Krombein *et al.* (1979), Michener (2000), Cane, Griswold & Parker (2007), Sheffield *et al.* (2011), and nesting habit was based on Michener (2000). Cleptoparasitic bees were not scored for nesting habit since they do not collect pollen or construct nests. For flies, we assessed the type of larval diet (aphids, detritus/bacteria, oozing tree sap, rotting cactus), but dropped the latter two classes because they were utilized by only one species each. Fly traits were provided by taxonomists Dr. Martin Hauser (California Department of Food and Agriculture) and Dr. Francis Gilbert (University of Nottingham).

Quantitative traits for bees and flies included mean body size, abundance and floral resource specialization. We used intertegular distance for bees and wing length for flies as proxies for mobility (Greenleaf *et al.* 2007; Rotheray *et al.* 2014), measuring from one to five specimens under a dissecting microscope. We calculated floral resource specialization and abundance, using not only the data from this study, but also data collected in the same study area on an additional 56 hedgerow and control sites using identical sampling methods during the same sample years (Morandin & Kremen 2013). For floral resource specialization, for each pollinator species in our data, we calculated the metric d', which measures the deviation of the observed interaction frequency from a null model in which all partners interact in proportion to their abundances (Bluthgen, Menzel & Bluthgen 2006); thus, it is not confounded with abundance as is linkage (Winfree *et al.* 2014). It ranges from 0 for generalist species to 1 for specialist species. Body size metrics and abundance were log-transformed.

For syrphid flies, larval diet is entirely distinct from adult floral resource use; thus, larval diet type and d' provide non-overlapping information. However, for bees, measurements of d' include floral visits both for pollen to provision larvae and for nectar and pollen for adult food, reflecting both larval and adult diet breadth. We therefore used only d' and not assessments of lecty classes (specialization in larval diet of bees within plant taxa), since these traits would constitute overlapping measurements. Since d' is measured from our network data, it is available for all of our bee species, whereas data on lecty are poor or absent for a number of our species.

We were able to measure or obtain all traits for 80 of 97 bee species in our data set (Table S4) and for 26 of 30 syrphid fly species (Table S5).

ANALYSES

To evaluate the effect of habitat restoration over time on bee communities and traits, we model species occurrence data (presence = 1 or absence = 0 of species at a given site and sample date) as a function of the number of years post-restoration (*ypr*) for a particular site in a particular year. *ypr* values for restoration sites begin at 0 and increase each year following restoration, but remain at 0 for controls in all years. Thus, sites restored in 2007 have a value of *ypr* = 0 in 2006 and 2007 and a value of 6 in 2013. Use of the continuous *ypr* variable permits more flexibility in analyses then a classic before–after coding scheme. The before–after coding is better suited for analysing a pulse disturbance, whereas we studied a press disturbance (the maturation of hedgerows and their effects on flower visitor communities and traits). Further, since different sites were restored in different years, the *ypr* variable permits us to isolate changes associated with restoration from annual fluctuations in insect population dynamics.

Bee and syrphid fly data sets were analysed separately. In order to maximize the number of species that could be included in analyses, we first analysed each trait separately (see also Williams *et al.* 2010) and then considered the subset of species with full trait data in a multitrait analysis. All quantitative traits were centred and scaled ((u − û)/2 SD) to facilitate comparison of effect sizes (Gelman & Hill 2006, p. 54). All analyses were conducted in R v. 3.1.1. (R Core Team 2013) using 'LME4' (Bates *et al.* 2014).

For single-trait analyses, we used generalized linear mixed effect models with a binomial error and a logit link function to model species occurrences for each site and date, with *ypr* (years post-restoration), a trait and the interaction between *ypr* and that trait as fixed effects. We were specifically interested in this interaction because, for a given trait, a significant interaction indicates that restoration differentially affects species differing in that trait. Site, species and year were all included in each analysis as random effects. Using Akaike information criterion (AIC) values, we compared each single-trait model to a 'no-trait' model based on the same species set (the subset of species analysed for that trait), constructed as before but with only *ypr* included as a fixed effect. Comparison of these two AIC values enabled us to assess whether the trait or its interaction with *ypr* contributed substantially to the model. We considered models with ΔAIC ≤ 4 to be equivalent (Burnham & Anderson 2002).

Using the same basic model structure, we also constructed multitrait models using the subset of species for which we had a complete set of trait values. Here, we included each trait and an interaction between that trait and *ypr* in a single model, with species, site and year as random effects, as above. The advantage of including all traits within the same model is that one can assess the relative importance of each trait while also accounting for their combined effects. However, since functional traits are intercorrelated (Table S2), we used variance inflation factors (VIF), calculated using the AED package (Zuur *et al.* 2009) to remove collinear variables from the model. We successively removed the covariate with the largest VIF exceeding 3 and recalculated VIFs until all VIFs were <3 (Table S3), following Zuur *et al.* (2009). This covariate set was then used in the multitrait model.

By combining data from all of our species into a single analysis and including species identity as a random effect, we were able to accomplish our goal of making inferences at the community level. While some species occurred infrequently in the data, such species only exert a small influence on the estimation of effect sizes. Analyses with infrequent species removed (defined as <than five site–date occurrences in the entire data set) produced similar results to analyses including all species, except for lack of convergence in one of the 12 analyses; therefore, we present only the analyses with all species included.

Since no species-level phylogeny of our specific taxa yet exists, we could not fully account for potential phylogenetic non-independence in our analyses. However, Bartomeus *et al.* (2013) recently showed that, for bees, nesting species within genus and genus within family as random effects produced essentially the same results as a more sophisticated analysis that accounted for phylogenetic non-independence using generic-level phylogenetic trees created from GenBank sequences. Therefore, we also conducted analyses nesting species within higher-order taxonomy (genus and family for bees, and genus and tribe for syrphid flies). For all single-trait models, these analyses yielded equivalent outcomes. Multitrait models fit the data much better without the inclusion of taxonomy (i.e. ΔAIC ≥20). Therefore, for all analyses, we present only the analyses without taxonomy.

Results

We collected 6145 bees from 97 species resulting in 1349 occurrences (i.e. presences) and 2744 syrphid flies from 30 species in 899 occurrences (Tables S4 and S5). Species occurrences of bees and flies increased significantly with *ypr* (no-trait model, bees, $N = 97$, effect size for *ypr* ± SE = 0·08567 ± 0·02653, $P = 0{\cdot}00124$; flies, $N = 30$, effect size for *ypr* ± SE = 0·14956 ± 0·02783, $P = 7{\cdot}68\text{e-}08$).

The addition of many of the single traits and their interactions with *ypr* improved models for both bees and syrphid flies (Tables 1 and 2, see ΔAIC values). We found significant positive interactions between *ypr* and the level of floral specialization (d') for both bees and flies (Figs 2a and 3a), indicating that hedgerow maturation favours specialized flower visitors. For bees, *ypr* interacted significantly with nesting habit, favouring renters that rely on pre-existing cavities over bees that excavate their own nests (Fig. 2b). We also found that restoration favoured occurrence of above-ground-nesting bees over below-ground-nesting bees (Fig. 2c), although the model including nest location was equivalent to a model without it (ΔAIC = −4). We found no significant interaction for abundance, body size or sociality in bees. For flies, we also found a significant negative interaction with wing length (Fig. 3b) but no significant interactions with larval diet or abundance. Significance and trends of trait main effects are also noted in Tables 1 and 2.

Traits were intercorrelated (Table S2). Cavity-nesting bees had higher floral specialization, lower abundances and larger body size than excavators. Solitary bees were more specialized (d') and less abundant than social bees. Parasitic bees were less abundant than solitary bees but similar in floral specialization to social bees. Body size and floral specialization were positively correlated in bees. Nest location and nesting habit were non-randomly associated with each other and with sociality. In flies, aphid feeders had smaller wing sizes. Wing size was negatively correlated with abundance.

Multitrait models, adjusted to remove correlated traits using VIF (Table S3), largely supported the single-trait models (Tables 1 and 2). For bees, we again found a significant positive interaction between *ypr* and both floral specialization and nesting habit (favouring renters). In addition, we found a significant negative interaction between *ypr* and body size. For flies, we found only a significant negative interaction with body size (wing length) but no longer an interaction with floral specialization.

Discussion

If habitat restoration chiefly benefits the common generalists that are able to survive in intensive agricultural landscapes, then we would expect to see increased occurrence of species between restored and control sites, but no increases in the occurrence of the species that are more sensitive to disturbance. In contrast, our results show that hedgerows not only significantly enhanced occurrences of native bee and syrphid fly species but differentially promoted occurrence of species with greater floral specializa-

Table 1. Bees: single- and multitrait models of species occurrence data showing Akaike information criterion (AIC) values compared to the corresponding no-trait model; effect size for the interaction between years post-restoration (*ypr*) and trait, standard error (SE) and *P*-value; and the direction of significance (+/−) if the trait's main effect was significant

Bees	Number of species	AIC (no traits, no taxonomy)	AIC (traits, no taxonomy)	ΔAIC	Interaction effect (*ypr**trait)	SE	*P*-value	Trait main effect, significance and trend
Single-trait models								
Abundance	97	7080	7027·9	−52	−0·0525	0·0406	0·1951	+
Nesting habit (rent)	82	6628·7	6601·1	−28	**0·1654**	0·0301	**3·950E-08**	−
Floral specialization (d')	97	7080	7044·6	−35	**0·1411**	0·0229	**7·410E-10**	−
Body size	91	6955·6	6952·1	−4	0·0297	0·0267	2·662E-01	−
Sociality	93	6966·6	6962·8	−4				
Social					−0·0495	0·0754	5·119E-01	+
Solitary					−0·0241	0·0739	7·446E-01	
Nest location	85	6730·6	6726·2	−4				
Below					−**0·1129**	0·0321	**4·340E-04**	
Mix					−0·0901	0·0499	7·083E-02	
Multitrait model	80	6597·4	6507·9	−90				
Abundance					0·0181	0·0524	7·293E-01	+
Nesting habit (rent)					**0·1465**	0·0369	**7·340E-05**	
Floral specialization (d')					**0·1721**	0·0328	**1·550E-07**	−
Body size					−**0·1164**	0·0347	**7·840E-04**	
Sociality (solitary)					−0·0690	0·0385	7·270E-02	

Bolded interaction effects are significant. Both single- and multitrait models have significant positive interactions with *ypr* for floral specialization and more specialized nesters (cavity nesters).

Table 2. Flies: single- and multitrait models of species occurrence data showing Akaike information criterion (AIC) values compared to the corresponding no-trait model; effect size for the interaction between years post-restoration (*ypr*) and trait, standard error (SE) and *P*-value; and the direction of significance (+/–) if the trait's main effect was significant

Flies	Number of species	AIC (no traits, no taxonomy)	AIC (traits, no taxonomy)	ΔAIC	Interaction effect (*ypr**trait)	SE	*P*-value	Trait main effect, significance and trend
Single-trait models								
Abundance	30	5107	5090·5	–16	0·0507	0·0365	0·165	+
Floral specialization (*d′*)	30	5107	5102·2	–5	**0·0755**	0·0277	**6·35E-03**	
Larval diet (detritus/bacteria)	28	4984	4986·2	2	–0·0020	0·0323	9·51E-01	
Wing length	28	5070	5062·3	–8	**–0·0708**	0·0313	**0·0238**	–
Multitrait model	26	4947	4930·7	–16				
Abundance					0·0289	0·0453	5·24E-01	+
Floral specialization (*d′*)					0·0252	0·0332	4·49E-01	–
Larval diet (detritus/bacteria)					0·0384	0·0364	0·2904	
Wing length					**–0·0889**	0·0361	**0·0137**	

Bolded interaction effects are significant. Both single- and multitrait models show a significant negative interaction between *ypr* and wing size. Single-trait models also show a positive interaction with floral specialization.

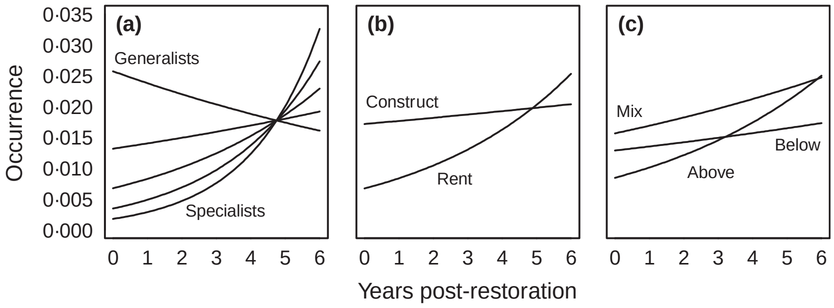

Fig. 2. Response of the mean occurrence of bee species with different traits to years post-restoration (*ypr*) based on single-trait models. Only significant relationships from Table 1 are displayed. Raw occurrence data (0 or 1 corresponding to the presence or absence of each species at each site and sample date) not shown. (a) Floral generalists vs. specialists. Five evenly spaced values of *d′* (specialization index from least specialized to most specialized) that fully span the range of observed values are shown. (b) Nesting habit, cavity nesters vs. excavators. (c) Nest location, above-ground, below-ground or mixed. These graphs show that as hedgerow restorations mature, they promote more specialized bees, including floral specialists and cavity nesting bees.

tion, more specialized habitat requirements (cavity nesting as opposed to ground-nesting bees) and smaller body sizes (lower mobility). These results suggest that small-scale habitat restoration within intensive agricultural landscapes has the most positive effects on species whose response traits may render them more vulnerable to habitat degradation, namely more specialized and less mobile species. (We were not able to evaluate red-listing status of these species since very few bee or syrphid species have been evaluated for threatened or endangerment status in the United States.) Thus, these plantings may be partially reversing the community disassembly that has occurred in response to agricultural intensification in this region (Kremen, Williams & Thorp 2002; Larsen, Williams & Kremen 2005).

It is important to note, however, that we did not compare communities at hedgerows with a reference natural or semi-natural community and, therefore, we cannot say to what extent hedgerows promote more specialized or less mobile species relative to the full complement of species from the region. A study on bee functional trait composition in the same biogeographic region found that farms impose strong environmental filters limiting species occurrences relative to semi-natural habitats (Forrest *et al.*, in press). This finding, coupled with our finding of enhanced success of cavity nesters with restoration, suggests that providing shrubs and trees on farms is the key to re-establishing the cavity-nesting component of native bee communities.

We found support not only for our general hypothesis that habitat enhancements differentially promote species that may be more sensitive to disturbance, but also for some of our specific predictions on response traits. For bees, however, several specific predictions were not borne out. We predicted that hedgerows might differentially promote large-bodied species, based on previous work in this

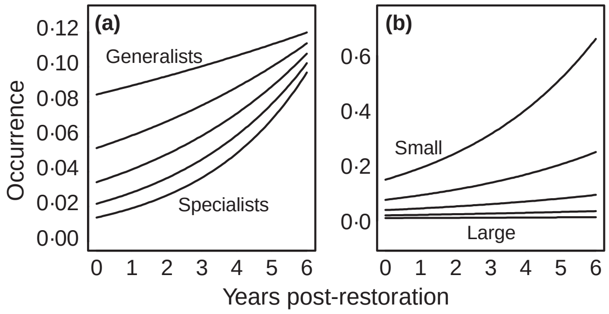

Fig. 3. Response of the mean occurrence of syrphid fly species with different traits to years post-restoration (*ypr*) based on single-trait models. Only significant relationships from Table 2 are displayed. Raw occurrence data (0 or 1 corresponding to the presence or absence of each species at each site and sample date) not shown. (a) Floral generalists vs. specialists. Five values of d' (specialization index from least specialized to most specialized) are modelled to cover the range of values in the data set. (b) Body size. Five values of wing size are modelled to cover the range of values in the data set. These graphs show that as hedgerow restorations mature, they promote floral specialists more than generalists and smaller-bodied (less mobile) flies more than more mobile flies.

region (Larsen, Williams & Kremen 2005). Instead, we found either no interaction with body size (single-trait analysis) or that smaller bees were promoted (multitrait analysis). However, both of the other traits that were promoted by hedgerow maturation, cavity nesting and floral specialization were strongly associated with larger body size (Table S2). These results suggest that, for bees, body size alone may not be an ideal indicator of species responses to small-scale habitat restoration, although it may be correlated or interacted with other traits (see also Bommarco *et al.* 2010). Also contrary to our prediction, we did not find that hedgerows differentially supported parasitic (higher trophic level) bees. Parasitic bees tend to be uncommon in our collections (2% of occurrences, Table S4), so it is possible that we are simply unable to detect such a trend, if it occurs, or that insufficient time has elapsed post-restoration for a trophic-level trend to emerge. Finally, we did not find that hedgerows differentially supported less common bee species, although cavity-nesting bees tended to be less common (Table S2), and a previous study in the same area did find greater abundances of less common species at mature hedgerows (i.e. >10 years old) than at controls (Morandin & Kremen 2013).

For bees, our principle finding – that hedgerows differentially promote more specialized flower visitors with more specialized nesting requirements – was consistent between single- and multitrait analyses. The importance of both variables in the multitrait models was evident even though cavity-nesting bees also were more specialized in floral resource use (Table S2). For flies, hedgerows differentially promoted more specialized flower visitors, but only the body size effect was consistent between single- and multitrait analyses. In bees, the main effect of hedgerow maturation became non-significant or marginally significant when traits with significant interactions were included in the single- or multitrait analyses, suggesting that hedgerows do not promote abundances of bees uniformly, but rather, a subset of bees with specific traits. In flies, the main effect of hedgerow maturation remained significant even when significant interactions were included in the models, suggesting either that our analysis failed to include some key response traits of the fly community, or that hedgerows promote the abundances of all fly species, while promoting species with certain response traits more than others. For both bees and flies, significant interactions between hedgerow status and various response traits emerged between 4 and 5 years post-restoration (Figs 2 and 3).

Some evidence suggests that the European Union's (EU's) 'agri-environment schemes', which subsidize growers to implement small-scale habitat enhancements and other presumed wildlife-friendly farm management techniques, increase species richness and abundance on farms primarily by promoting common and/or resilient species rather than uncommon or endangered species (Kleijn *et al.* 2006) and are effective in simple (1–20% semi-natural habitat in surrounding landscape) but not in cleared (<1% semi-natural habitat) landscapes (Scheper *et al.* 2013). In the United States, Farm Bill conservation programmes are the analogue to the EU's agri-environment schemes. Several of these programmes, such as the Environmental Quality Incentives Program and the Wildlife Habitat Incentives Program, include specific provisions to promote pollinator conservation through habitat enhancements like native plant hedgerows or insectary strips. Our results suggest that such programmes can promote not just common, resilient species, but also some disturbance-sensitive species, even in cleared landscapes. It is important to note, however, that the hedgerow plantings we studied here were specifically designed to support flower visitor communities in the region. Plant palettes were selected using bee–flower network data from the same area (Williams *et al.* 2011) to obtain bee-attractive plant species that would provide a sequence of floral resources throughout the flight season. Therefore, the conservation benefits that we observed from farm-scale habitat enhancement in our study area might only be realized in other regions if planting palettes are specifically tailored for the flower visitors found there. Similar conclusions about the need for tailoring agri-environment schemes to specific conservation objectives were reached through assessments of EU agri-environment schemes (Kleijn *et al.* 2006).

Flower-rich patches in intensive agricultural landscapes may simply concentrate existing flower visitors from the surrounding landscape, rather than promote their population growth (Scheper *et al.* 2013). Studies of species abundances or occurrences cannot distinguish between concentration vs. population effects, and demographic data instead would be needed. However, several lines of evidence suggest that our results are not simply due to concentration effects. First, on other native plant hedgerows in the same landscape, we observed increases, not decreases, in the abundances of flower visitors in fields immediately adjacent to hedgerows, a pattern consistent with exportation, rather than concentration, of flower visitors from hedgerows (Morandin & Kremen 2013). Secondly, in multiseason occupancy analyses of this same data set, we found that, relative to controls, hedgerows enhance rates of persistence and colonization, particularly for more specialized species, suggesting that hedgerow resources promote the establishment of populations at these sites (M'Gonigle *et al.* 2015).

Restoring habitat for flower visitors in agricultural landscapes might also promote important ecosystem functions and services on adjacent farm fields like pollination and pest control (Blaauw & Isaacs 2014; Morandin, Long & Kremen 2014). While some direct evidence supports a positive role of native plant restoration in promoting pest control and crop pollination in adjacent fields (Morandin & Kremen 2013; Blaauw & Isaacs 2014; Morandin, Long & Kremen 2014), it remains to be determined whether this differential effect of restoration on response traits of flower visitor communities would translate into measurable improvements in ecosystem services. Some of the favoured traits may promote pest control or pollination services in adjacent fields (i.e. small-bodied species are likely to forage nearby; aphidophagous syrphids can provide pest control), but other traits may not (e.g. floral specialists may not visit crop flowers; small species deliver less pollen per visit). Even if these particular bee and fly species are not contributing substantially to pollination or pest control services now, they could become important in the future if environmental conditions change – for example, as a result of changes in farm management, climate or altered biotic relationships (Isbell *et al.* 2011). Further work is needed to elucidate how small-scale restoration influences pollination services (Menz *et al.* 2011) via their effects on species' response and effect traits (Suding *et al.* 2008). Meanwhile, this study shows that these habitat enhancements provide clear conservation benefits for sensitive species in flower visitor communities, even in highly intensively managed agricultural landscapes.

Acknowledgements

We thank Kerry Cutler, Sara Kaiser, Christina Locke, Katharina Ullman, Hannah Wallis and others for data collection. Neal Williams, Jessica Forrest, Robin Thorp, Martin Hauser and Francis Gilbert provided trait data. Funding was provided by the Army Research Office (W911NF-11-1-0361 to C.K.), the Natural Resources Conservation Service (CIG-69-3A75-12-253, CIG-69-3A75-9-142, CIG-68-9104-6-101 and WLF-69-7482-6-277 to the Xerces Society/C.K.), the National Science Foundation (DEB-0919128 to C.K.), the U.S. Department of Agriculture (USDA-NIFA 2012-51181-20105 to Rufus Isaacs, Michigan State University) and the Natural Sciences and Engineering Research Council of Canada (PDF to L.K.M).

Data accessibility

Species traits: uploaded as Supporting Information.

Sites information: uploaded as Supporting Information.

Species occurrences by site and sample date: doi: 10.5061/dryad.8n4p8 (Kremen & M'Gonigle 2015).

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Received 2 October 2014; accepted 27 February 2015
Handling Editor: Sarah Diamond

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Samples per site and year.

Table S2. Correlations among traits.

Table S3. Variance inflation factors.

Table S4. Bee species traits.

Table S5. Fly species traits.

Fig. S1. Variation among control sites.

Ecological Applications, 25(6), 2015, pp. 1557–1565

Habitat restoration promotes pollinator persistence and colonization in intensively managed agriculture

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Abstract. Widespread evidence of pollinator declines has led to policies supporting habitat restoration including in agricultural landscapes. Yet, little is yet known about the effectiveness of these restoration techniques for promoting stable populations and communities of pollinators, especially in intensively managed agricultural landscapes. Introducing floral resources, such as flowering hedgerows, to enhance intensively cultivated agricultural landscapes is known to increase the abundances of native insect pollinators in and around restored areas. Whether this is a result of local short-term concentration at flowers or indicative of true increases in the persistence and species richness of these communities remains unclear. It is also unknown whether this practice supports species of conservation concern (e.g., those with more specialized dietary requirements). Analyzing occupancies of native bees and syrphid flies from 330 surveys across 15 sites over eight years, we found that hedgerow restoration promotes rates of between-season persistence and colonization as compared with unrestored field edges. Enhanced persistence and colonization, in turn, led to the formation of more species-rich communities. We also find that hedgerows benefit floral resource specialists more than generalists, emphasizing the value of this restoration technique for conservation in agricultural landscapes.

Key words: agro-ecosystem; habitat restoration; hedgerows; occupancy; persistence; pollinators.

Introduction

By restoring habitat, conservation biologists and restoration ecologists seek to promote the reassembly of diverse ecological communities, while also enhancing the ecosystem services these communities provide (Funk et al. 2008, Rey Benayas et al. 2009). Restoration of pollinator communities is of particular concern because pollinators play a critical role in plant reproduction in both natural and agricultural systems (see Plate 1; Ollerton et al. 2011, Garibaldi et al. 2013). With managed honey bees (*Apis mellifera*) declining at unprecedented rates in many regions of the world (Neumann and Carreck 2010) and increasing evidence of declines in populations of native pollinators (Biesmeijer et al. 2006, Cameron et al. 2011, Carvalheiro et al. 2013, Weiner et al. 2014), conservation and restoration of native pollinator communities has become a conservation imperative (Potts et al. 2010, Garibaldi et al. 2011). Little is known, however, about how effectively current restoration methods are curtailing or reversing the declines of native pollinators (Menz et al. 2011, Winfree 2010).

In agricultural landscapes, where pollinators are at risk from pesticides (Brittain et al. 2010) and habitat loss (Kennedy et al. 2013), multiple studies have shown that increasing vegetative diversity locally boosts pollinator species richness and abundance (e.g., Kohler et al. 2008, Kennedy et al. 2013, Morandin and Kremen 2013*a*). However, it is unknown from these snapshot studies whether such techniques contribute to the conservation of these pollinators by enhancing population persistence or if they simply attract pollinators from the surrounding landscape, leading to transient increases in local abundance and/or richness. Additionally, earlier work in intensively managed agricultural landscapes has found that local floral enhancements increase pollinator richness but do not promote the conservation of rare, endangered, or specialized species (Kleijn et al. 2006). Thus, small-scale floral enhancements alone may fail to conserve biodiversity adequately and, consequently, not fully restore functioning communities and the services they provide (Klein et al. 2009, Isbell et al. 2011).

In order to assess whether restoration promotes pollinator conservation (i.e., via enhancing population persistence), it is necessary to examine temporal trends in species occurrence or occupancy by tracking individual species across multiple seasons. Recently developed occupancy models are designed for this task (MacKenzie et al. 2006, Royle and Kéry 2007). These models account for imperfect species detection, and thus permit inferences about species occupancy that might otherwise be obscured by differences in species-specific detectabilities. In order to estimate species persistence, occupancy

Manuscript received 1 October 2014; revised 9 December 2014; accepted 9 January 2015. Corresponding Editor: A. K. Brody.

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models require substantially more data than models that do not account for the detection process; specifically, they require that multiple surveys or collection episodes take place at each site in each year. Due, in part, to the high data requirements, these occupancy models have seldom been applied to invertebrates (although, see Pellet et al. 2007, Dorazio et al. 2011) and, to our knowledge, have never been applied to insect pollinators, leading to a critical knowledge gap.

The most widely used restoration technique to promote pollinators in agricultural landscapes is the planting of flowering native shrubs and forbs along farm edges, where they do not remove arable land from production. These hedgerows are designed to include a variety of plant species which provide a continuous or near continuous sequence of floral resources over the flight seasons of many pollinators (Menz et al. 2011). Plantings may also create nesting habitat and function as refuges from pesticides and soil disturbances such as tilling (Morandin and Kremen 2013*a*, *b*). Here we show how restoration of hedgerows facilitates assembly and long-term temporal stability of native pollinator populations and communities. We do this by tracking five hedgerows from their inception through their maturation and comparing them against 10 non-restored control sites in a hierarchical multi-season, multi-species occupancy model. To determine whether hedgerows promote pollinator conservation or simply function as transient pollinator sinks, we tested (1) whether the establishment of diverse native plant hedgerows increased pollinator occupancy, (2) whether this increase was a consequence of reduced extinction, enhanced colonization, or both, (3) whether hedgerow restoration had differential effects on specialist vs. generalist species, and (4) if effects on occupancy translated into species richness patterns. We found, as expected, that restoration led to increases in species richness and, furthermore, that it did this by increasing both rates of between season persistence and colonization. Additionally, we found that this latter effect was most pronounced for more specialized foragers which are less likely to survive in highly modified environments (e.g., Burkle et al. 2013). These findings suggest, therefore, that restoration via hedgerows is an important conservation technique effecting the temporal stability of pollinator populations and communities, including more specialized species.

Materials and Methods

Study sites and collection methods

Our study landscape, located in the Central Valley of California (Yolo County), USA, is an intensively managed agricultural landscape comprising conventional row crops, vineyards, and orchards (Fig. 1). We selected five farm edges to be restored as hedgerows and 10 non-restored control edges. Because hedgerow sites require significantly greater financial and time investments, it was not feasible to restore more than five sites. However, because some parameters in our model (such as the rates of species detections) are shared between control sites and hedgerows, including more control sites than hedgerows increases our ability to detect trends associated with restoration. Hedgerows were planted in 2007 and 2008 with native perennial shrubs and trees (e.g., *Cercis occidentalis*, *Ceanothus* spp., *Rosa californica*, *Heteromeles arbutifolia*, *Sambucus mexicana*, *Eriogonoum* spp., *Baccharis* spp., *Salvia* spp., and others; see Appendix: Table A1 for a complete list of plantings by site). Hedgerow restorations were approximately 350 m long and 3–6 m wide and border large crop fields (~30 ha). After initial planting, hedgerows were irrigated and weeded for three years, after which no further management was needed (see Fig. 2 for an example of a restoration prior to and six years after restoration). Pollinator sampling at each restoration site began one year prior to restoration (see Table 1 for an overview of our sampling history).

Control sites were selected to match conditions surrounding restoration sites. For each restoration site, we selected two control sites adjacent to the same crop type (row, orchard, pasture, or vineyard), within the same landscape context (i.e., within 1–3 km of the restoration site), but >1 km from all other study sites. Control sites were generally weedy field edges and reflect a variety of unmanaged crop field edges found in the region and the pre-restored condition (Appendix: Fig. A1). Such edges typically contain a variety of nonnative forbs, grasses, shrubs, and trees and may at times be tilled, treated with pesticides, or left alone. The most common flowering plants at these sites are *Convolvulus arvensis*, *Brassica* spp., *Lepidium latifolium*, *Picris echioides*, and *Centaurea solstitialis*. Many of these species have also established at restoration sites.

We sampled pollinator communities at each restoration and control site three to five times each year from 2006 until 2013 (with some exceptions; see Table 1). All sampling was conducted between April and August. Dates of sampling were spread evenly across this time period. Sites were selected in random order for sampling and, once all sites had been sampled, the process began again for the next sample round. For logistical reasons, no sampling was conducted in 2010. In 2012 and 2013, the number of rounds of sampling was increased to satisfy data requirements for other projects (Table 1). However, because we use analyses here that account for imperfect detection and also temporal turnover of pollinators over the duration of the field season (described in detail below), different numbers of visits to sites across years do not bias parameter estimates.

Flower-visiting insects were netted along a 350-m transect for one hour, pausing the timer while handling specimens and identifying the plant species from which each specimen was collected. Pollinators were only surveyed under sunny conditions when the temperature was above 21°C and wind speed was below 2.5 m/s. While all insect visitors that contacted the reproductive

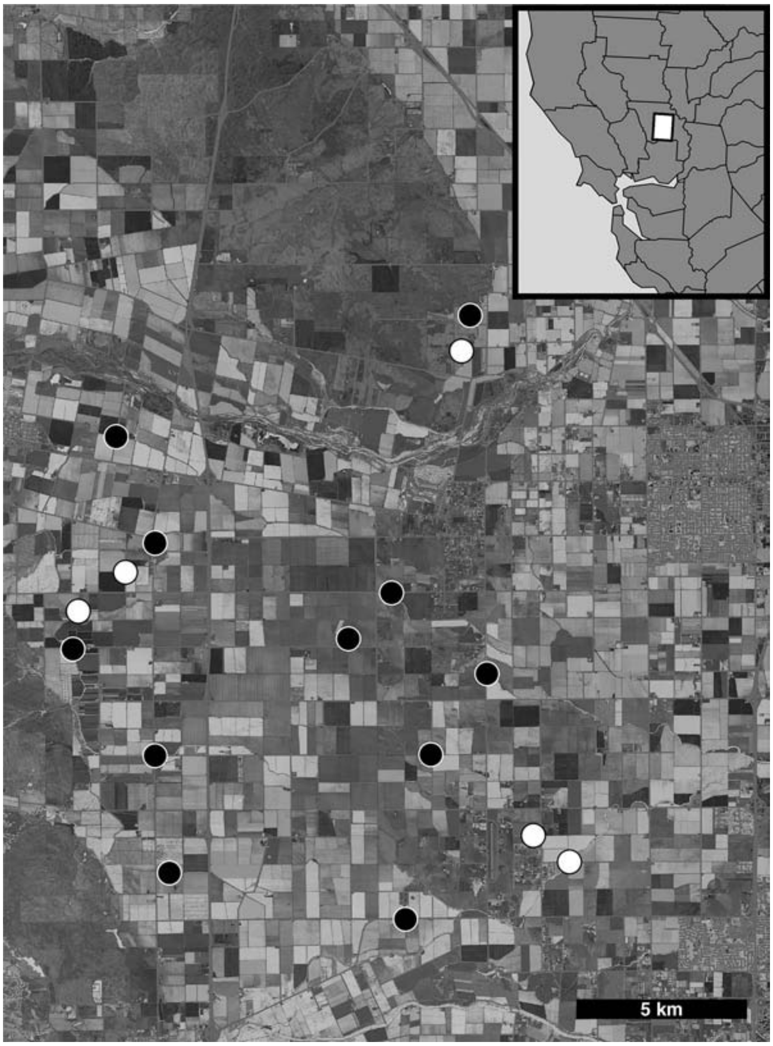

FIG. 1. Location of hedgerow and control sites in California (inset) and surrounding landcover (National Aerial Imagery Program, 2012). White dots are restored sites and black dots are control sites.

FIG. 2. Photographs of a restoration site (H1) (a) immediately prior to its restoration in the early spring of 2008 and (b) in its sixth year post-restoration in late summer of 2013. Photo credits: K. Ullman (a) and L. K. M'Gonigle (b).

TABLE 1. Number of samples per year at each site.

Site	2006	2007	2008	2009	2010	2011	2012	2013
Hedgerows								
H1	2	3	3†	3		3	4	5
H2	4	3†	3	3		3	4	5
H3		3	3†	3		3	4	5
H4	2	3†	3	3		3	4	5
H5		3	3†	3		3	4	5
Controls								
C1a	4	3	3	3		3	4	5
C1b		3	3	3		3	4	5
C2a	4	3	3	3		3	4	5
C2b		3	3	3		3	4	5
C3a		3	3	3		3		
C3b	4	3	3	3		3	4	5
C4a		3	3	3		3	4	5
C4b		3	3	3		3	4	5
C5a	4	3	3	3		3	4	5
C5b		3	3	3		3	4	5

Note: Sampling was not conducted in 2010 because resources were allocated to other projects.

† Year of planting for each restoration site.

parts of the flower were collected, here we focus our analyses only on wild bees and syrphid flies (for more information about the efficacy of syrphids as pollinators; see Kearns 2001, Rotheray and Gilbert 2011). Bee and syrphid specimens were identified to species (or morpho-species for some bee specimens in the genera *Lasioglossum*, *Nomada*, and *Sphecodes*) by expert taxonomists.

Using plant–pollinator interaction data from a more extensive data set from Yolo County (18 000 interaction records) that included both the data collected in this study and additional data from sites where we collected flower visitors with identical methods (Morandin and Kremen 2013*a*, *b*; C. Kremen, *unpublished data*), we quantified each pollinator species' level of floral resource specialization by calculating the metric d' for each pollinator species in our data set (Blüthgen et al. 2006). This metric measures the deviation of the observed interaction frequency from a null model in which all partners interact in proportion to their abundances. It ranges from 0 for generalist species to 1 for specialist species. The distribution of specialization values for the species investigated here are shown in Appendix: Fig. A2 and a full list of species with specialization scores is provided as an supplementary data file, along with the rest of our raw data (see Data Availability). To simplify interpretation of model coefficients, specialization values were standardized prior to running analyses.

Statistical model

To analyze our data, we employed a hierarchical framework that explicitly incorporated uncertainty in the detection process into the estimation of occupancy parameters (MacKenzie et al. 2006, Royle and Kéry 2007). Because our goal was to draw conclusions about communities, rather than individual species, we used a model that linked species-specific parameter estimates together by assuming they come from common community-level distributions (Dorazio et al. 2006). By doing this, we were able to include data for species that were seldom observed and thus not amenable to analysis on their own.

We developed a multi-season, multi-species model to compare occupancy dynamics between restoration and non-restoration sites over time. For species i, we let $z_{i,j,t}$ denote its true occupancy state in year t at site j. We then let $x_{i,j,t,k}$ indicate whether we detected ($x_{i,j,t,k} = 1$) or did not detect ($x_{i,j,t,k} = 0$) that species in the kth visit to site j in year t. We assumed that the occupancy of the ith species at the jth site in the tth year is a Bernoulli random variable $z_{i,j,t} \sim \text{Bern}\ (\psi_{i,j,t})$ with probability $\psi_{i,j,t}$. In the first year, all sites were equivalent with respect to restoration status and so we assumed that a species probability of occupancy, $\psi_{i,j,1}$, was equal to the fraction of times we observed that species at that site. Because a species' occupancy in subsequent years is the net outcome of its ability to colonize vacant sites and persist in already colonized sites, we investigated how habitat restoration affects these two processes. Letting $\phi_{i,j,t}$ denote the probability that species i persists at site j from years t to $t+1$ (provided it was present at site j in year t, $z_{i,j,t} = 1$) and $\gamma_{i,j,t}$ denote the probability that species i colonizes site j in year $t+1$ (provided it was not present at site j in year t, $z_{i,j,t} = 0$), we then computed the probability of occupancy for species i at site j in subsequent years as

$$\psi_{i,j,t+1} = \phi_{i,j,t} \times z_{i,j,t} + \gamma_{i,j,t} \times (1 - z_{i,j,t}). \qquad (1)$$

In order to investigate the effect of habitat restoration, we defined the following species-specific persistence and colonization models:

$$\begin{aligned}\text{logit}(\phi_{i,j,t}) &= \phi_0[i] + \phi_1 \times d'[i] + \phi_2 \times \text{ypr}[j,t] \\ &\quad + \phi_3 \times \text{ypr}[j,t] \times d'[i] \\ \text{logit}(\gamma_{i,j,t}) &= \gamma_0[i] + \gamma_1 \times d'[i] + \gamma_2 \times \text{ypr}[j,t] \\ &\quad + \gamma_3 \times \text{ypr}[j,t] \times d'[i]. \end{aligned} \qquad (2)$$

Here $\phi_0[i]$ and $\gamma_0[i]$ denote species-specific effects on persistence and colonization, respectively, ϕ_1 and γ_1 denote the effect of species specialization on persistence and colonization, respectively, and $d'[i]$ denotes the specialization level of species i. Positive values of ϕ_1 and γ_1 would indicate that specialist species have higher rates of persistence and colonization, respectively, than generalist species. For restoration sites, prior to restoration, and for control sites in all years, $\text{ypr}[j,t] = 0$. The variables ϕ_2 and γ_2 denote the effect of habitat restoration on persistence and colonization, respectively, with $\text{ypr}[j,t]$ indicating the number of years post-restoration for site j in year t. Positive values of ϕ_2 and γ_2 would indicate that rates of persistence and colonization, respectively, are higher as sites mature after restoration. Last, ϕ_3 and γ_3 denote the interaction effects between years post-restoration and species specialization on persistence and colonization, respectively. Positive values of ϕ_3 and γ_3 would, respectively, indicate that rates of persistence and colonization for specialists are more positively affected by maturation of hedgerows than are rates of persistence and colonization for generalists.

For simplicity, both colonization and persistence in our model depended linearly on the number of years post-restoration (on a logit scale). Because the number of years post-restoration will continue to grow indefinitely, a saturating function (that requires an additional parameter) would be more appropriate here for modeling rates of persistence and/or colonization over the longer term. However, here we were interested in quantifying the effects of restoration in the years immediately following restoration and thus a linear response was appropriate.

We also assumed that detection was distributed according to be a Bernoulli random variable such that $x_{i,j,t,k} \sim \text{Bern}(p_{i,j,t,k} \times z_{i,j,t})$, where $p_{i,j,t,k}$ is the probability that the ith species was detected at site j in the kth sample period of the tth year, given that it was present. When species i was absent, $z_{i,j,t} = 0$, and thus $x_{i,j,t,k}$ was 0. We allowed detection probabilities to vary by species and also to change over the course of the year in a species-specific manner. Specifically, the detection probability of the ith species at the jth site in the kth replicate of the tth year was specified as

$$\text{logit}(p_{i,j,t,k}) = p_0[i] + p_1[i] \times \text{date}_{j,t,k} + p_2[i] \times (\text{date}_{j,t,k})^2 \quad (3)$$

where $p_0[i]$ denotes a species-specific effect and $p_1[i]$ and $p_2[i]$ denote the effect of day of the year on detectability of species i. In addition to their low rates of detection, another difficulty in working with communities of pollinators is that many species' flight seasons do not span the entire duration of the field season (i.e., not all species are active during some of the early or late season samples). By including $\text{date}_{j,t,k}$ and $(\text{date}_{j,t,k})^2$ in the above model, the detection probability of each species was allowed to vary over the season according to that species' phenology. The inclusion of the quadratic term allowed species-specific rates of detection to peak at some point during the season.

We used a hierarchical community model that links together species-specific parameter estimates by assuming that they come from a common distribution. Specifically, the values for ϕ_0, γ_0, p_0, p_1, and p_2 were each drawn from common distributions whose defining parameters were also estimated. We assumed that each of the aforementioned quantities was distributed normally such that $x_i \sim \mathcal{N}(\mu_i, \sigma_i)$ where $\mu_i \sim \mathcal{N}(0,1000)$ and $\sigma_i \sim \mathcal{U}(0,100)$. Pollinator specialization scores were standardized before analysis to facilitate interpretation of coefficients and convergence of parameter estimates.

We analyzed the model in a Bayesian framework using uninformative priors throughout. Markov chain Monte Carlo (MCMC) chains were run for 10^5 iterations after an initial burn-in of 10^3 iterations. Each of 10 independent chains was sampled every 10^3 iterations to create samples for analyses. Models were run in R, version 3.1.0 (R Core Team 2014) using JAGS (Plummer et al. 2003). JAGS code and data are available online (see Data Availability. Model parameters were considered to be significantly different from zero if the 95% credible interval did not overlap zero.

RESULTS

Across all of our samples and all 15 sites, we observed 1347 bee and 893 syrphid fly occurrences which, in total, comprise 6143 specimens from 97 bee species and 2732 specimens from 30 syrphid species. For bees, 553 of the 1347 occurrences and 73 of the 97 species were observed at the five hedgerow sites compared to 794 and 79 at the 10 control sites (note that the latter numbers are higher due to the greater number of control sites). For syrphids, 353 of the 893 occurrences and 27 of the 30 species were observed at the hedgerow sites compared to 540 and 26 at the control sites. Despite substantial sampling effort (330 collection days across 15 sites over eight years), many species were detected only a few times. For example, 63% of bee species and 27% of syrphid species were detected fewer than five times. For this reason, we analyzed bee and syrphid species in a single multi-species analysis; we did not have sufficient data to analyze each of these groups on their own.

Restoration increased both rates of pollinator persistence and colonization and, for the latter, this effect was most pronounced for specialist pollinators (see Fig. 3 and Appendix: Table A2). Years post-restoration had a significantly positive effect on rates of persistence. (i.e., the estimate of ϕ_2 was positive and its 95% Bayesian credible interval did not include zero; Fig. 3a, Table A2). For colonization, on the other hand, there was no evidence for a strong main effect of years post-restoration (the 95% CI for the parameter γ_2 overlapped zero) but there was a positive interaction between years post-restoration and the level of pollinator resource specialization (Fig. 3b, Table A2). While there was no evidence for a main effect of pollinator specialization on rates of persistence, rates of colonization were much lower for more specialized species (Fig. 3, Table A2). Species-specific rates of persistence and colonization for sites at zero and five years post-restoration are shown in Figs. A3 and A4.

By substituting model estimates for parameters into Eq. 2, we can compute the expected change in a species' rate of persistence and/or colonization for sites of different maturities. For example, for a species with mean intercept $\phi_0[i] = \bar{\phi}_0$ and a specialization value of $d'[i] = 0.5$, we compute its rate of persistence at non-restored sites (i.e., those with ypr = 0) as $\text{logit}^{-1}(\bar{\phi}_0 + \phi_1 \times 0.5 + \phi_2 \times 0 + \phi_3 \times 0 \times 0.5) = \text{logit}^{-1}(1.32 - 0.14 \times 0.5 + 0.47 \times 0 + 0.16 \times 0 \times 0.5) = 0.78$ We can then compare this to its rate of persistence at sites that have matured

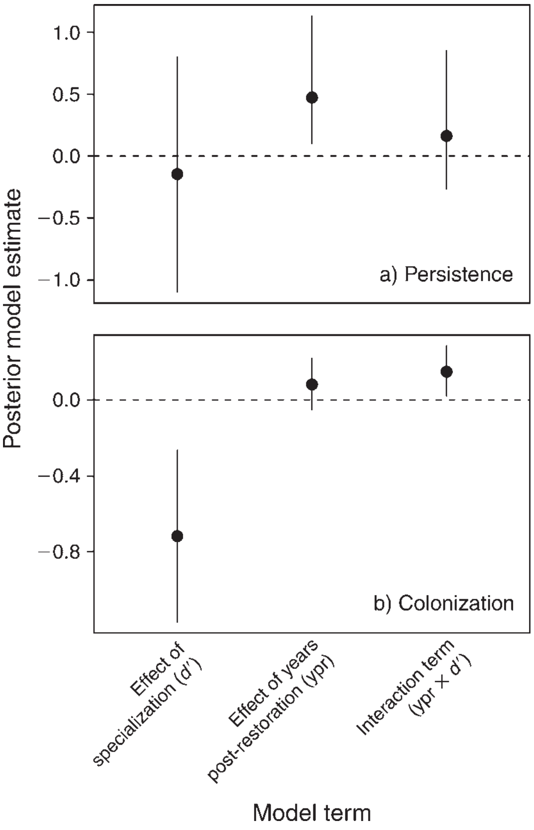

FIG. 3. Posterior estimates for model coefficients for both (a) persistence and (b) colonization. The effects of species specialization corresponds to the parameters ϕ_1 (panel a) and γ_1 (panel b). The effects of years post-restoration corresponds to the parameters ϕ_2 and γ_2. The terms corresponding to the interaction effects between these two quantities correspond to parameters ϕ_3 and γ_3. Positive values can be interpreted to mean that the corresponding explanatory variable has a positive effect on rates of either persistence (a) or colonization (b) and vice versa. Vertical bars denote Bayesian 95% credible intervals. When 95% credible intervals do not overlap zero, those coefficients can, in some sense, be considered to be "significantly different from zero" with a type 1 error rate of 0.05.

for a single year, $\text{logit}^{-1}(\bar{\phi}_0 + \phi_1 \times 0.5 + \phi_2 \times 1 + \phi_3 \times 1 \times 0.5) = 0.86$. Thus, we would expect this species to see an increase in its rate of persistence by approximately 8% after just one year of restoration.

Increased rates of persistence and colonization at restoration sites led to more species-rich pollinator communities in later years (Fig. 4). While restoration and non-restoration sites exhibited similar levels of richness in the early years of our study (especially prior to restoration), species richness in later years increased at restored sites compared to non-restored sites.

DISCUSSION

Habitat restoration increases rates of between-season persistence and, for more specialized wild bee and syrphid fly pollinators, colonization (Fig. 3). This, in turn, leads to the assembly of more species-rich pollinator communities at restored sites (Fig. 4). Furthermore, these restorations do not simply facilitate recolonization from an external source population but, rather, they create the conditions that promote population persistence. It follows that they do not simply concentrate floral visitors transiently, but instead create temporally stable pollinator populations. This has also been suggested by our earlier findings that mature hedgerows (i.e., >10 years old) enhance abundances in adjacent fields, rather than dilute them through concentration (Morandin and Kremen 2013*b*) That these restorations could eventually even act as source populations into other parts of the landscape is an important possibility for a landscape such as California's Central Valley where there is little remaining undeveloped habitat and thus few potential source populations.

Our results corroborate recent findings that small, florally enhanced patches in agricultural areas can increase pollinator richness, although these former studies did not distinguish between transient effects on species occurrences vs. enhancement of persistence (Kohler et al. 2008, Batáry et al. 2011, Carvell et al. 2011, Pywell et al. 2011). Importantly, and unlike some earlier work (Kleijn et al. 2006), we found that restoration particularly benefits more specialized bees, likely because the critical floral resources that specialists need are at low densities or altogether absent in conventional field edges. Similarly, others have found that leguminous floral enhancements led to higher abundance and richness of legume-specialist bumble

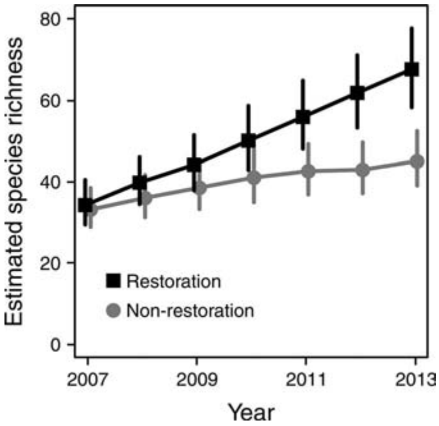

FIG. 4. Estimated mean number of species present in restoration sites (squares) and non-restoration sites (circles). The estimate of the species richness for site j in year t is computed by summing $z_{i,j,t}$ across all i. Points denote means and vertical bars 95% credible intervals. Note that because a species' occupancy at a site in any given year depends, via the process of persistence and colonization, on its occupancy in the previous year, estimates shown here are not independent between years, thus creating roughly monotonic trends. In addition, because we have focused our entire analysis only on species we have actually detected, these estimates do not include species that were potentially unobserved from our study, altogether.

PLATE 1. Native bee (*Melissodes robustior*) pollinating sunflower. Photo credit: L. K. M'Gonigle.

bees (Carvell et al. 2011), and that availability of particular pollen resources plays a critical role in enabling long-term persistence of populations of the specialist solitary bee, *Andrena humilis* (Franzén and Nilsson 2013). In line with these findings, our results demonstrate that small-scale restorations are an important conservation tool for sustaining diverse pollinator populations in intensively managed landscapes.

Here we have considered the age of a habitat restoration as a predictor of pollinator population responses. However, hedgerow age is only a crude proxy for the many potentially important factors that contribute to making more mature hedgerows better habitats for insect pollinators. Identifying specifically which attributes of these hedgerows (e.g., abundance of floral resources vs. quality of nesting substrates) are most critical in creating the trends we report here will provide important additional insights. We are currently in the early stages of investigating this.

More diverse pollinator communities can provide higher quality and more stable levels of pollination services to a greater variety of crops (Klein et al. 2009). Thus, by enhancing richness, hedgerow restorations may also positively affect the provisioning of pollination services. Theoretical work has also predicted that diverse communities provide more consistent levels of pollination services than less diverse communities, because these services are less sensitive to temporal fluctuations in composition (e.g., the "portfolio effect" [Tilman et al. 1998] and the "biodiversity insurance hypothesis" [Lawton and Brown 1993]). The few empirical studies that have been conducted on pollination services support these theoretical predictions (Klein et al. 2003, Steffan-Dewenter et al. 2006, Bartomeus et al. 2013). Our results indicate that restoration increases pollinator diversity by enhancing species colonization and persistence between seasons and thus may lead to communities that provide more stable pollination services.

The primary goal of conservation is the maintenance of biodiversity. Our findings demonstrate that restoration benefits specialized pollinators species more than generalists (Fig. 3, Appendix: Figs. A3, A4). Such pollinators may be lower in abundance and/or less likely to contribute to the pollination of crops (although they still could be important for selected crops that attract specialists, such as sunflower or squash; Hurd et al. 1974, 1980). In a separate work, we have examined the effects of restoration on species that are likely more vulnerable to agricultural intensification, including species that are less common, less mobile, and more specialized in floral and/or nesting resource needs (Kremen and M'Gonigle 2015). There we have shown that hedgerow restoration has the most beneficial effects on the species that are more vulnerable to habitat degradation. Thus, hedgerow restoration provides a critical avenue for promoting the long-term conservation of biodiversity.

This study is one of the few to model the population dynamics of insect species in an occupancy framework. Unlike more traditional statistical methods, such a framework enables us to explicitly disentangle uncertainty associated with imperfect rates of species detection from actual species' presences and absences. Insect pollinators are notoriously difficult to sample due to their small size and also high rates of spatial and temporal turnover (e.g., Minckley et al. 1999). The low rates of detectability of many bee species makes the use of such a framework even more important. In our case, low detectability led to high degrees of uncertainty in species-specific estimates of occupancy, colonization, and persistence (e.g., see large credibility intervals in Figs. S3 and S4). However, by using a *multi-species* modeling framework that pools data across species, we were able to make inferences about communities with relatively high certainty. Additionally, we were able to detect these patterns despite our relatively low number of restoration sites (five).

Restoration of native habitat presents a promising avenue for conserving pollinator communities in intensive agricultural landscapes, currently in precarious decline due to land use change, pesticides, diseases, and invasive species (Potts et al. 2010). Maintaining native pollinator communities is vital for ensuring reproduction of both native plants (Ollerton et al. 2011) and crops (Garibaldi et al. 2013). Especially as resource demands on our planet continue to grow, restoration efforts within intensive agricultural landscapes that enhance biodiversity and stabilize yields will likely prove critical.

Acknowledgments

We thank the growers and land owners that allowed us to work on their property and Robbin Thorp (Professor Emeritus, University of California–Davis) and Martin Hauser (California Department of Food and Agriculture) for identifying our bee and syrphid specimens, respectively. We also thank D. Karp, C. Kennedy, and P. de Valpine for providing valuable comments on the manuscript and C. Crossman, S. Kaiser, H. Sardiñas, and all the field and lab assistants that have helped over the many years of data collection and specimen processing. This work was supported by funding from the Army Research Office (W911NF-11-1-0361 to C. Kremen), the Natural Resources Conservation Service (CIG-69-3A75-12-253, CIG-69-3A75-9-142, CIG-68-9104-6-101 and WLF-69-7482-6-277 to The Xerces Society), the National Science Foundation (DEB-0919128 to C. Kremen), The U.S. Department of Agriculture (USDA-NIFA 2012-51181-20105 to Michigan State University) and the Natural Sciences and Engineering Research Council of Canada (PDF to L. K. M'Gonigle).

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-1863.1.sm

Data Availability

Data associated with this paper have been deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.2vj67

Conservation Letters
A journal of the Society for Conservation Biology
Open Access

LETTER

A Tool for Selecting Plants When Restoring Habitat for Pollinators

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Keywords
Conservation support tool; networks; plants; pollinators; restoration.

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Received
7 January 2016
Accepted
7 April 2016

Editor
Mark Brown

doi: 10.1111/conl.12261

Abstract

Native pollinators and, particularly bees, are a critical component of agricultural systems. Unfortunately, many factors are leading to their declines, including habitat loss. Consequently, approaches have emerged that aim to restore pollinator habitat in managed landscapes. A widely adopted technique in Europe and North America is the planting of flowering shrubs and forbs along field edges. These habitats usually include a variety of species, chosen because they are attractive to pollinators and because they flower continuously over those pollinators' flight seasons. Because there are many potential plant species with different flowering times and pollinator preferences, selecting a subset is challenging. Here, we develop a tool that identifies a plant mix that optimizes some assessment criteria (e.g., pollinator visitation, richness, or phenology). We test our tool by showing that it identifies mixes that better satisfy these criteria than ones found using conventional expert-driven methods, when applied to a plant–pollinator dataset.

Introduction

The honey bee (*Apis mellifera*) is experiencing increased colony losses (van Engelsdorp *et al.* 2009) and there is evidence that native pollinator populations are also declining (Biesmeijer *et al.* 2006; Potts *et al.* 2010; Cameron *et al.* 2011; Carvalheiro *et al.* 2013). Because pollinators are critical for plant reproduction—87% of flowering plant species (Ollerton *et al.* 2011) and 75% of agricultural crop species benefit from animal pollinators (Klein *et al.* 2007)—mitigating further declines has become a global conservation imperative (Potts *et al.* 2010; Garibaldi *et al.* 2013).

Little is known about how we can reverse pollinator declines (Winfree 2010; Menz *et al.* 2011). However, in agricultural landscapes, where habitat loss and pesticides threaten pollinator populations (Brittain *et al.* 2010; Garibaldi *et al.* 2011; Rundlöf *et al.* 2015), multiple studies have shown that increasing vegetative diversity can boost pollinator species richness, abundance, and spatial turnover (e.g., Carvell *et al.* 2007; Kohler *et al.* 2008; Haaland *et al.* 2011; Kennedy *et al.* 2013; Morandin & Kremen 2013; Scheper *et al.* 2013; Ponisio *et al.* 2016), promote specialized species (Pywell *et al.* 2012; Kremen & M'Gonigle 2015), and increase persistence (M'Gonigle *et al.* 2015). One widely used practice is the planting of flowering shrubs and/or forbs along field edges. These enhancements typically include a variety of species that flower in sequence, covering the flight seasons of many pollinator species (Garibaldi *et al.* 2014; Williams *et al.* 2015); gaps in flowering might prevent pollinators from completing their life cycles (Memmott *et al.* 2010; Burkle *et al.* 2013). Because there are many potential plant species, creating an optimal mix can be a computational and agronomic challenge. Here, we focus on the former.

Computational tools are increasingly being used for land-use planning (Meir *et al.* 2004; Sarkar *et al.* 2006; Turner & Wilcove 2006; Stralberg *et al.* 2009). For example, there are numerous tools for identifying and optimizing acquisition of spatial land units for conservation (e.g., Turner & Wilcove 2006; Moilanen *et al.* 2009). When the goal of restoration is the assembly of a group of species, a restoration design must take into account the full needs of those species over the duration of their life cycles. For obligate mutualists, this means taking into account the interaction network between the planted species and the restoration targets (e.g., pollinators), as well as factors such as nesting or breeding resources (Menz *et al.* 2011).

Simultaneously optimizing multiple criteria is common to many conservation planning problems (Nicholson *et al.* 2006; Sarkar *et al.* 2006). Surprisingly, however, no tool exists for optimizing criteria, single or multiple, when planning restoration for pollinators. Here, we develop such a tool for identifying plant mixes that optimize a range of criteria. For example, a planner might want a phenological sequence of blooms appropriate for pollinators of a specific crop or, alternatively, a plant mix that supports the greatest pollinator species richness or visitation. We test our tool by applying it to a dataset from California's Central Valley.

Methods

Data requirements and model description

We develop a genetic algorithm to find the mix (or mixes) of plants (defined as a list of k plants, $M = \{p_1, p_2, \cdots, p_k\}$) that maximizes some "objective function." All code developed here is available at https://github.com/leithen/plant_selection_tool. Our tool requires three data as inputs:

1. A record of pollinator collections and corresponding plants on which they were collected.
2. An optimality criterion.
3. In some cases, trait information about the plants or pollinators (e.g., floral bloom period or timing of plant–pollinator interactions).

Details of the genetic algorithm are described in the Supplementary Materials (Section S1). In brief, the algorithm subjects an initial "population" of plant mixes to several iterations of "selection," "recombination," and "mutation," keeping track of the best mixes encountered. In any run, we require that mixes contain the same number of plants. However, by comparing across different mix sizes (i.e., different k values), we can also optimize k.

Objective functions

The objective function, f, defines the optimization criteria and allows us to compare plant mixes M_i and M_j by evaluating $f(M_i)$ and $f(M_j)$. Construction of this function will depend on the goals. For example, one could maximize pollinator visitation (the total number of visits) or target particular pollinators. Alternatively, because pollinator flight seasons are often longer than individual plant species' bloom periods, one might want plants whose combined bloom periods span the flight seasons of the relevant pollinators. In our framework, more complex objective functions can be constructed by combining simpler ones.

In the Supplementary Materials (Section S2), we develop four simple objective functions that optimize, respectively, pollinator visitation, f_{V}, pollinator species richness, f_{R}, and phenology based on either the timing of plant–pollinator interactions, f_{T}, or the bloom periods of plants, f_{B}. The "visitation" metric, f_{V}, closely mimics the criterion that has been used by planners in the past, and thus we use it as a baseline against which we compare the performance of other metrics. Because we are ultimately interested in maximizing pollinator visitation and richness, while also providing coverage of the pollinators' flight seasons, we use our tool to compare the performance of plant mixes that optimize these simple criterion to mixes that optimize them in combination. Specifically, we let $f_{\mathrm{VRT}}(M) = f_{\mathrm{V}}(M) * f_{\mathrm{R}}(M) * f_{\mathrm{T}}(M)$ denote the objective function that optimizes pollinator visitation, pollinator species richness, and the timing of plant–pollinator interactions. Similarly, we let $f_{\mathrm{VRB}}(M) = f_{\mathrm{V}}(M) * f_{\mathrm{R}}(M) * f_{\mathrm{B}}(M)$ denote the objective function that optimizes visitation, species richness, and floral bloom periods.

Data collection

We test our tool using a dataset comprising $\sim 8,000$ wild bees netted on flowers at sixteen ~ 1.8 hectare sites in Northern California's Central Valley. Sites were situated in mixed native vegetation, vegetable farms, and orchards and were sampled eight times at regular 3-week intervals between March and August within a single season. All collections were made on days with clear skies, temperatures $> 20^\circ$C and wind speeds < 2.8 m/s using timed collections (for a full description, see Forrest *et al.* 2015). Plants were identified to species and bees were identified to species or to morphospecies (~ 800 specimens to morphospecies, primarily in the genera *Lasioglossum* and *Nomada*). Records were filtered to include only collections on native plants. Additional filters could be applied here (e.g., plants could be filtered based on perceived weediness or availability/desirability).

We compare our optimized mixes to ones created using expert opinion and the same dataset described above. These mixes were created using a set of simple rules: the first three plant species were chosen by selecting the early, middle, and late blooming species that had the largest number of occurrences of crop-visiting species, over unique combinations of sites, seasons, and bee visitors (similar to Kremen *et al.* 2002), the next three were selected in the same manner, and so on. Plant mixes based on a similar process have been used to create hedgerow enhancements at several sites in California (Kremen & M'Gonigle 2015). Comparisons to independently compiled "off the shelf" plant mixes would be helpful, but presently there are no such mixes in our study region for which we have sufficient pollinator visitation data.

Results

Our dataset contains 76 plant and 181 pollinator species. Assuming equal plant frequencies within mixes, there are 70,300 mixes containing three plants, 218,618,940 mixes containing six plants, and 142,466,675,900 containing nine plants. Should one wish to vary plant frequencies, these numbers would become even larger. Thus, exhaustively examining potential mixes becomes computationally intractable as the mix size and complexity increase.

We first demonstrate that our method correctly identifies the optimal plant mix for scenarios where that mix can be found exhaustively. We do this in two ways. First, for our dataset, we can do this for mixes containing up to five plants. In doing so, we found perfect congruence between these mixes and those found using our model. Second, it is possible for some criteria to find the optimal plant mix of any size. For example, the mix that maximizes pollinator visitation, f_V, can be found by ranking plants according to their total occurrence and then selecting the top k. Again, we found perfect congruence between these mixes and those found using our model. For the remaining cases, we evaluated performance by comparing tool-selected mixes to a large number of randomly generated mixes. Our tool identified mixes that outperformed all randomly generated plant mixes by a large margin (Figure 1).

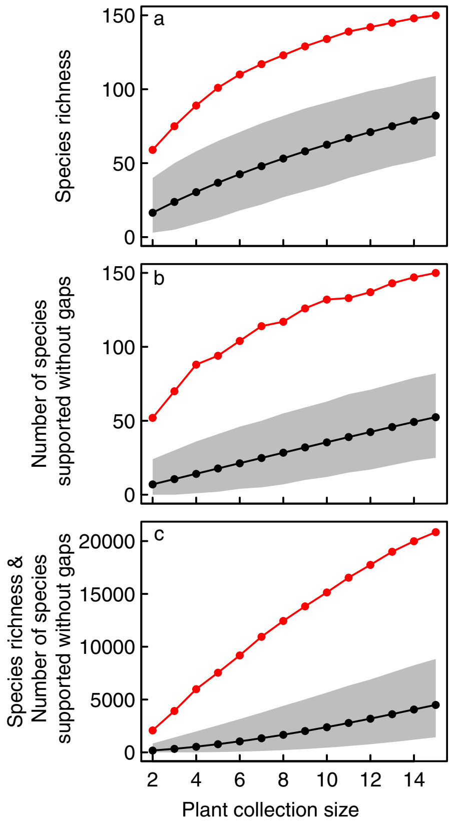

Figure 1 Performance of our tool against randomly selected plant mixes when attempting to maximize (a) pollinator richness, (b) the number of fully supported pollinators, or (c) both pollinator richness and the number of fully supported pollinators. Black curves and shaded regions show means and 95% quantiles for performance of 10^5 randomly generated models of the corresponding mix size, whereas the red curves show model scores for best models found using our tool. The algorithm was run, in each case, for $1,000$ generations with a population size, N, equal to 100, probability of mutation, μ, equal to 0.01, probability of sex, ψ, equal to 1, probability of recombination, r, equal to 0.25, and strength of selection, s, equal to 5 (see Supplement S1 for descriptions of these parameters).

We found that mixes that optimize f_{VRT} and f_{VRB} perform almost as well in maximizing their constituent components (visitation, richness, and the timing of interactions, in the case of f_{VRT}, or phenological bloom continuity, in the case of f_{VRB}) as plant mixes that optimize only those components (Figure 2). For example, a nine species mix found by maximizing pollinator visitation, species richness, and the timing of plant–pollinator interactions (f_{VRT}) provides resources to 97.7% as many pollinator species as one that maximizes only pollinator species richness, f_R. Similarly, a mix that optimizes visitation, species richness, and the floral bloom periods (f_{VRB}) provides resources to 98.4% as many species as one that maximizes only pollinator richness. Analogously, mixes found by optimizing f_{VRT} and f_{VRB} support, respectively, 92.7% and 93.0% as many occurrences as one that maximizes only visitation, f_V.

Importantly, these mixes provide better phenological coverage than ones that only maximize visitation (compare blue and red curves to black curve in Figures 2b and 2c). For example, the nine species mix that maximizes visitation, species richness, and the timing of plant–pollinator interactions (f_{VRT}) or, respectively, phenological bloom continuity, f_{VRB}, can support 17.5% (respectively, 14.2%) more species across their life cycles than one that maximizes only visitation, f_V. Furthermore, in our dataset, these gains are largest for collections of smaller sizes. Thus, our tool effectively

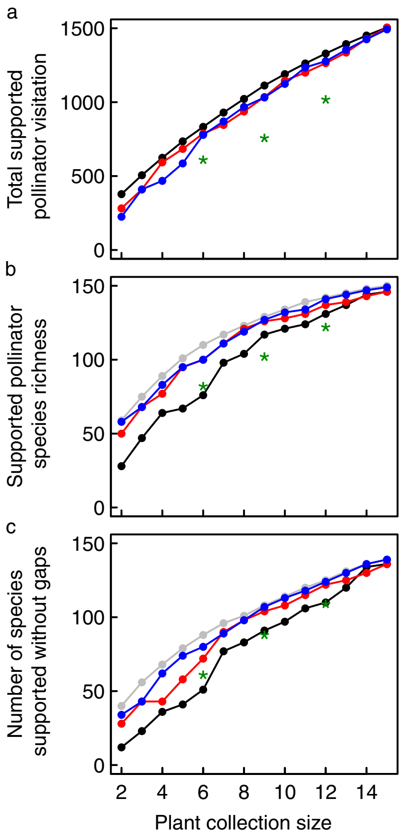

Figure 2 Performance of optimal models of varying plant size, as measured by the total supported pollinator visitation (a), the total supported pollinator richness (b), and the total number of pollinators supported for the complete duration of their flight seasons (c). Each curve corresponds to plant mixes that were selected using a different optimality criterion. In each panel, the gray curve shows the performance of plant mixes optimized for only the criteria of interest in that panel, and thus provides an upper limit. We also consider three additional criteria. The black curve denotes plant mixes optimized for only visitation, f_V, whereas the blue and red curves denote, respectively, plant mixes optimized for the more complex composite functions $f_{VRT} = f_V * f_R * f_T$ and $f_{VRB} = f_V * f_R * f_B$. Green asterisks denote plant mixes that have been created by experts using this same dataset in the past. In panel (a), the black curve obscures the gray curve because they correspond to the same objective function.

finds mixes that, in theory, support a greater number of pollinators more evenly across the duration of their flight seasons and, further, the efficiency gains are greater when only a smaller number of plants can be included, which is frequently the case due to cost and availability.

Lastly, we found that our tool identified mixes that performed noticeably better than ones created using expert opinion for this same dataset (compare asterisks to blue and red curves in Figure 2). For example, the nine species mix that maximizes visitation, richness, and the timing of plant–pollinator interactions (f_{VRT}) or, respectively, phenological bloom continuity, f_{VRB}, could, in theory, support 18.1% (respectively, 21.5%) more species across their life cycles than an expert-derived mix of the same size.

Discussion

Selecting the optimal mix of plants when restoring habitat for pollinators is a computational and logistical challenge (Menz *et al.* 2011). Here, we have developed a tool to help identify mixes of plants that, in theory, will provide floral resources capable of supporting pollinator communities. We applied our tool to a plant–pollinator dataset and showed that it identified mixes that, if established, could sustain diverse pollinator communities over the duration of those pollinators' flight seasons.

There are numerous conservation support tools for solving similar problems, such as selecting spatial land units for habitat conservation or restoration (Sarkar *et al.* 2006). These tools can be structurally similar to ours, using algorithmic methods to select an optimal subset from a larger set (e.g., see Possingham *et al.* 2000; Moilanen *et al.* 2005). However, when the targets of restoration are interaction networks, it is necessary to develop methods that explicitly incorporate species interactions. For example, here, selected plants need to flower such that their bloom periods will combine to cover the pollinator's flight seasons.

In developing our tool, we have created several simple objective functions with a focus on improving phenological coverage via bloom periods (f_B) or the timing of plant–pollinator interactions (f_T). These functions could be refined in the presence of more comprehensive datasets or more specific restoration goals. For example, the frequency of each plant species within a mix is not considered here but is likely an important factor. In order to incorporate this, a planner would need to articulate how to score different compositions of the same mix; a difficult task. A planner may also want a mix that targets pollinators of a specific crop (e.g., Kremen *et al.* 2002) or one that does not bloom while their crop is flowering (in order to promote movement of pollinators into the field). She/he might also require particular plants or pollinators be included/supported. In this case, the remaining plants would be selected to optimize the objective function, constrained by the initial choice of required species. In the reserve design literature, this is analogous to forcing the algorithm to include existing protected areas (Possingham *et al.* 2000). Such modifications could be easily accommodated in our framework.

All of our metrics are based on visitation data. This is potentially problematic for three related reasons. First, plant or pollinator species that are rarely detected will often be incorrectly inferred to have short bloom periods or flight seasons. Second, restoration may subsequently favor common species (Kleijn *et al.* 2015). Third, the list of eligible plants will not contain those on which specimens were never collected, potentially omitting interactions that are rare or have low detectability (e.g., nocturnal visitors). Additionally, visitation data do not indicate whether pollinators were foraging for pollen or nectar on a given plant species. To overcome these problems, planners would ideally begin with a list of all potential plant species across the landscape and their bloom periods and resources provided, all pollinator species and their flight periods, and an interaction matrix. While floral bloom periods could potentially be estimated, obtaining an interaction matrix is only possible using collections, as we have done here. Thus, the approach we have taken (sampling in nearby pristine and agricultural habitats) is a practical and economic option, with the acknowledgment that additional sampling might improve the end result.

In a recent paper, Russo *et al.* (2013) proposed a heuristic for restoring pollinator habitat using attributes of interaction networks to select plants. They assess the value of each plant species by considering network attributes such as "node duration," which they define as "the number of times out of the total number of samples that a species participates in the network." Such an approach, where one ranks individual species provides valuable insight into the roles played by different plant species. Our tool extends their approach by developing a formal, reproducible method for selecting mixes that optimize network metrics. With sufficient data, it would be straightforward to extend our optimization functions to use pollinator preference strengths instead of visitation rates. This might alleviate some of the problems discussed in the previous paragraph.

There are other important considerations and constraints to consider when designing a restoration such as economic costs, plant availability, compatibility of seed mixtures, local soil conditions, land-use type, perceived weediness, pest control, and the availability of preexisting foraging and nesting resources (Balzan *et al* 2014). While incorporating such constraints is beyond our scope here, these factors could certainly be included within the algorithm. For example, one could obtain nursery prices and construct an objective function that calculates the cost of a mix. This cost function could then be built into an objective function or added as a constraint.

In practice, expert opinion is critical in planning any restoration and this tool is not intended to replace it, but to support it, by providing a formal and transparent structure to a process that typically uses informal application of the logic described here. Furthermore, we found that our model-selected plant mixes performed substantially better than expert-derived ones. Thus, as the complexity of the problem grows, so does the helpfulness of conservation support tools such as this one.

The method we present marks a first step in the development of computational tools to aid in selection of plant mixes for use in the restoration of pollinator communities. Beyond the potential extensions of this method described above, it will be important to test these mixes empirically. Otherwise, it is difficult to know whether the subsets of plants identified by our tool will actually support the establishment and persistence of the target pollinator communities (M'Gonigle *et al.* 2015). Such next steps are the focus of ongoing work; we are incorporating a broader array of criteria into the development of actual plant mixes and testing these on the ground with plantings (Williams & Lonsdorf, *in prep*).

Acknowledgments

We thank the Xerces Society for their support in developing the methods presented here. We also thank the growers and land owners that allowed us to work on their property. This work was supported by funding from the Army Research Office (W911NF-11-1-0361 to CK), the Natural Resources Conservation Service (CIG-69-3A75-12-253, CIG-69-3A75-9-142, CIG-68-9104-6-101 and WLF-69-7482-6-277 to the Xerces Society/CK), the McDonnell 21st Century Fund (to CK), the Natural Sciences and Engineering Research Council of Canada (NSERC-CREATE BRITE and PDF to LKM), and DH Smith Postdoctoral Fellowship to NMW, NSF, and USDA SCRI 3-23798 - RC102039I to NMW and EL. RW Thorp provided final determinations of bee species.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Supplementary Materials S1. Genetic Algorithm
Supplementary Materials S2. Objective functions

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RESEARCH ARTICLE

Bee Preference for Native versus Exotic Plants in Restored Agricultural Hedgerows

Lora A. Morandin[1,2] and Claire Kremen[1]

Abstract

Habitat restoration to promote wild pollinator populations is becoming increasingly common in agricultural lands. Yet, little is known about how wild bees, globally the most important wild pollinators, use resources in restored habitats. We compared bee use of native and exotic plants in two types of restored native plant hedgerows: mature hedgerows (>10 years from establishment) designed for natural enemy enhancement and new hedgerows (≤2 years from establishment) designed to enhance bee populations. Bees were collected from flowers using timed aerial netting and flowering plant cover was estimated by species using cover classes. At mature hedgerow sites, wild bee abundance, richness, and diversity were greater on native plants than exotic plants. At new sites, where native plants were small and had limited floral display, abundance of bees was greater on native plants than exotic plants; but, controlling for floral cover, there was no difference in bee diversity and richness between the two plant types. At both mature and new hedgerows, wild bees preferred to forage from native plants than exotic plants. Honey bees, which were from managed colonies, also preferred native plants at mature hedgerow sites but exhibited no preference at new sites. Our study shows that wild bees, and managed bees in some cases, prefer to forage on native plants in hedgerows over co-occurring weedy, exotic plants. Semi-quantitative ranking identified which native plants were most preferred. Hedgerow restoration with native plants may help enhance wild bee abundance and diversity, and maintain honey bee health, in agricultural areas.

Key words: **agriculture, Apoidea, ecosystem services, pollinators.**

Introduction

Seventy-five percent of the leading food crops and 35% of global food production is dependent on pollinators (Klein et al. 2007). Bees are the primary crop pollinators, with managed honey bees being the most important pollinator globally (Watanabe 1994). However, recent problems with honey bee colony health (Neumann & Carreck 2010) and a greater than 300% increase in area devoted to pollinator-dependent crops in the last 50 years, has made reliance on managed honey bees a risky proposition (Aizen & Harder 2009). Native pollinators supply a significant amount of pollination to many agricultural crops. In areas with large amounts of natural or semi-natural land, native bees can fully meet pollination requirements of a crop without the need for managed honey bees (Kremen et al. 2004; Morandin & Winston 2006; Winfree et al. 2007). However, intensive agricultural systems often are lacking in native pollinators (Winfree et al. 2009) and hence native pollination services to crops (Kremen et al. 2002; Klein et al. 2003; Morandin & Winston 2006; Ricketts et al. 2008).

While growers have little or no control over amounts of natural habitat in their region, they are able to implement farm-scale habitat enhancements. Restoration of weedy field edges with native shrubs and forbs is a feasible, and increasingly popular, method for increasing semi-natural land and thus native pollinator diversity, abundance, and possibly pollination services in working farmlands (Pywell et al. 2005; Hopwood 2008; Hannon & Sisk 2009). While restoration initiatives to enhance native pollinators in agricultural lands increasingly are being promoted through incentive or outreach programs, very little is known about resource use by pollinators within such restored areas (Winfree 2010).

Habitat enhancements for wild pollinators generally aim to enhance the abundance and diversity of floral resources in order to provide a consistent supply over the flight season (Vaughan et al. 2007; Menz et al. 2011). Often, non-native annual plants are recommended for pest-control enhancement on farm sites, despite the fact that native plants are more suitable for conservation efforts that intend to also preserve native plants and the beneficial insects associated with them (see Tuell et al. 2008 and references therein). Most studies on bee use of native and exotic plants in disturbed habitats have found that exotic plants receive more visits than native plants by native bees because of greater attraction and rewards (Brown et al. 2002). In a meta-analysis of 40 studies that examined effect of exotic plants on native plant pollination and

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doi: 10.1111/j.1526-100X.2012.00876.x

reproductive success, Morales and Traveset (2009) showed a negative impact on native pollination and reproductive success in the presence of exotic plants. Vila et al. (2009) examined plant–pollinator interactions in invaded (presence of exotic species) and un-invaded networks and found that pollinators interacted more with exotic species than they did with native species in invaded areas, but found no clear effect on whether the greater visits to exotic plants negatively impacted visits to native plants. Williams et al. (2011), working in disturbed agricultural plots in California, found that wild bees did not exhibit a preference for either native or exotic plants, but utilized both in proportion to their availability. These studies beg the question as to whether native plantings provide important resources for wild bees and honey bees in agricultural settings, where exotics often are numerically dominant; yet, there is little information on whether pollinators preferentially choose to forage from native plant restoration plantings rather than co-occurring exotic species. Despite increasing funds and effort to restore agricultural areas with native plants, we know of no studies that examine pollinator use of native versus exotic plants in agricultural restorations.

We quantitatively assessed native bee preference for exotic and native plants in new and mature native plant hedgerows in an agriculturally intense area of Northern California. We asked the questions, (1) Do abundance, richness, and diversity of bee species foraging on exotic versus native plant species differ? (2) Do native bees preferentially forage on native as opposed to exotic plants in agricultural hedgerow restoration sites? (3) Is bee utilization of exotic and native plants different in mature hedgerows, where native plants dominate, versus newly planted hedgerows, where exotic plants still dominate? and, (4) Within the native plant species, are there species that are preferred or avoided relative to other native plants? We expected that native and exotic plants would be used in proportion to their availability in new and mature hedgerow sites, and would only be an important resource if availability was high.

Methods

Hedgerow Sites and Plantings

Newly established hedgerow sites were planted between 2007 and 2008 for the purpose of enhancing native bee populations. They were approximately 350 m long, located adjacent to natural or man-made sloughs, and contained a mix of native shrubs and forbs.

Mature hedgerow sites were established in 1996 and were comprised of a row of perennial shrubs, 305–550 m long, bordered by a stand of perennial grasses. While mature hedgerows were planted to promote natural enemy and reduce pest insect abundances (Bugg et al. 1998), the majority of the native flowering plant species also are part of the native planting palette that was used for the new hedgerow sites in this study.

Composition varied among sites in native plants due to differences in service focus (pollination enhancement at new hedgerows, pest control at mature hedgerows), differences in species choices made by the land owner, and differential survival among sites. All new and mature hedgerows contained varying ratios of *Ceanothus griseus* (California lilac), *Eriogonum fasciculatum* (California buckwheat), *Rosa californica* (California wild rose), *Rhamnus californica* (California coffeeberry), *Baccharis pilularis* (coyote brush), *Sambucus mexicana* (Mexican elderberry), and *Heteromeles arbutifolia* (toyon). Most, but not all sites contained *Salvia* spp. (sage), *Eschscholzia californica* (California poppy), *Grindelia camporum* (gumplant), *Achillea millefolium* (yarrow), and *Atriplex lentiformis* (quail bush).

The primary herbaceous exotic weeds found in both new and mature hedgerows were *Brassica* spp. (mustard), *Convolvulus arvensis* (field bindweed), *Malva parviflora* and *neglecta* (mallow), and *Picris echioides* (bristly oxtongue). Hedgerows were planted adjacent to rotational field crops of approximately 32 ha, that included primarily wheat, processing tomatoes, and alfalfa, which is typical of crop production in this region.

Study Design

We examined four mature hedgerows and four new hedgerow sites in Yolo County, CA, in 2009. There was a minimum of 1.5 km distance among hedgerows to ensure spatial independence.

New hedgerow sites were sampled three times over the course of the season, from late April until early August, with approximately 1.5 months between sample rounds. Mature hedgerow sites were sampled four times during the growing season, from early May until late July, with approximately 1 month between sample rounds. At each sample round, flowering vegetation was quantified using fifty 1 m^2 quadrats evenly spaced along the hedgerow. Within the quadrats, all plants with mature flowers were identified to species and flower cover of each species was estimated using a Braun-Blaunquet cover scale. Cover estimates were made by envisioning all flowers of a species within the vertical plane of the quadrat as a two-dimensional flat surface. To standardize estimates among collectors, all observers used an example "score-sheet" and were trained collectively to standardize and score in a consistent manner.

Bee communities were quantified using timed aerial netting. At mature hedgerow sites, bees were collected off of flowers for 30 minutes and at new hedgerows for 1 hour. The shorter amount of time at mature hedgerows was due to additional sampling protocols not reported here. As the collector slowly walked along the hedgerow, they checked every flower for the presence of a bee. If a bee was observed touching the reproductive parts of a flower it was netted and put into a labeled vial specific to that plant species. The timer was stopped after the bee was captured in the net, until the collector was ready to recommence flower observations, so that total observation time was standardized among collections. Because the observer examined every flower along the path for the presence of bees, time viewing each plant species was in proportion to its floral cover. Collected bees were pinned for later species identification, which was conducted by Prof. E. R. W. Thorp

(U. C. Davis, Henry B. Laidlaw Bee Biology Center). The non-native, but naturalized solitary bee species, *Megachile apicalis* and *Ceratina dallatoreana* were included in our native bee dataset; the combined total of these two naturalized bee species made up less than 2% of the total non-*Apis* bees in our samples.

In our study region, honey bees (*Apis mellifera*) primarily come from managed colonies. Because high recent colony losses of honey bees (Neumann & Carreck 2010) may partially be due to nutritional deficiencies that make bees more susceptible to disease (vanEngelsdorp et al. 2009), enhancing quality, abundance, diversity, and continuity of foraging resources may aid managed honey bee colony health. Therefore, we also examined honey bee use and preference of exotic and native plants in hedgerows. Because honey bees could reliably be identified to species in the field, honey bees were captured, recorded, and then released.

Data Analyses

Each dataset (mature sites and new hedgerow sites) was analyzed separately due to the slightly different methodologies employed. Floral cover from each quadrat, at each sample round, was summed to get a total cover score for that plant type (exotic or native) at that site for that sample round. Therefore for new hedgerow sites, there were four sites and three sample rounds, resulting in 12 records for native plants and 12 for exotic plants and at mature hedgerow sites there were four sites and four sample rounds, resulting in 16 records each for native and exotic plants. Mean floral cover of native and exotic plants was compared using a mixed model analysis of variance with a poisson distribution and log link function (GLIMMIX procedure, SAS 1999). Sample round nested within site was included as a repeated factor and site as a random factor.

We compared the response variables native bee abundance, richness, and diversity (Shannon index) on native and exotic plants (fixed factor) using a mixed model analysis of covariance with a log link function and poisson or negative binomial distribution (the poisson distribution was tried first and if the over-dispersion was not corrected than the negative binomial distribution was used) for bee abundance and richness data, and a normal distribution for diversity data. We included sample round nested within site as a repeated factor, site as a random factor, and floral cover as the covariate. We first included the interaction between cover and plant type to test the assumption of homogeneity of regression slopes. If the interaction was non-significant, we removed the interaction term from the analyses and report on the test of fixed effects for plant type. If the interaction was significant, we kept the interaction term and report least squares mean difference and the region(s) of significance between native and exotic plants along values of the covariate, flower cover (Johnson & Neyman 1936; Milliken & Johnson 2002). Including flower cover as a covariate acts to standardize for effort as flowers were observed in proportion to their cover. For bee abundance on native and exotic plants, standardizing for floral cover of natives and exotics additionally gives a measure of "preference" (Johnson 1980). That is, controlling for floral cover of plant type, preference is established if bees are more abundant on one plant type than the other (Alldredge & Ratti 1992). For preference analyses, we excluded sites that had less than 10 bees collected at that site and sample round, because sites with less than 10 bees collected would not have enough replication on exotic or native plants to give meaningful information on preference. Therefore, there are different results from "abundance" analyses controlling for cover (where all sites are included) and "preference" analyses where only a subset of sites are included.

We additionally utilized the reduced dataset to examine preference by native bees among native plant species semiquantitatively at mature hedgerow sites (where there was enough cover of mature plants to permit meaningful analyses among species). The data were not amenable to statistical analyses such as Chi-square because of a large number of samples under five for each plant species. Therefore, we used a ranking system at each site calculated by number of bees found on each plant species at a site and sample round divided by the flower cover of that plant species. We ranked species according to this ratio, with higher numbers getting higher ranks (i.e. relatively more attractive).

Results

Floral Cover

At new hedgerow sites, cover of exotic flowers was greater than native flowers ($F_{[1,19]} = 11.81$, $p = 0.005$) with mean total cover score (SE) of 35.5 (6.8) and 10.1 (6.8), respectively. At mature hedgerow sites, there was no difference in floral cover between exotic and native plants ($F_{[1,26]} = 0.34$, $p = 0.57$) with mean total cover score (SE) of 19.1 (7.3) and 25.8 (7.1), respectively.

Bee Abundance, Richness, and Diversity

Of the 23 species of native bees netted on flowers at the new hedgerow sites, 7 species were observed only on exotic plants and 7 species were observed only on native plants. Of the 30 species of native bees netted on flowers at mature hedgerow sites, 23 bee species were observed only on native plant species and only 1 bee species was found only on exotic plant species.

There was an interaction between floral cover and native bee abundance at new hedgerow sites ($F_{[1,17]} = 8.08$, $p = 0.01$). We found significantly more native bees on native plants than exotic plants ($t_{[17]} = -3.32$, $p = 0.004$; Fig. 1) and $p < 0.05$ for all floral cover values greater than 15. At new hedgerow sites, there was no difference in native bee species richness and diversity between native and exotic plants (richness: $F_{[1,18]} = 0.83$, $p = 0.37$, diversity: $F_{[1,18]} = 0.17$, $p = 0.68$; Fig. 2).

At mature hedgerow sites, there was greater abundance (Fig. 1), richness, and diversity (Fig. 2) of native bees on native plants than exotic plants (abundance: $F_{[1,25]} = 19.22$, $p = 0.0002$, richness: $F_{[1,25]} = 13.07$, $p = 0.001$, diversity: $F_{[1,25]} = 10.00$, $p = 0.004$). Honey bee abundance was the same on native and exotic plants at new hedgerow sites

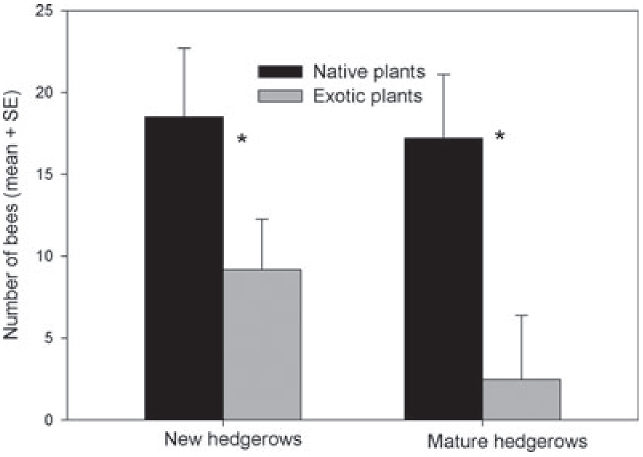

Figure 1. Mean number of native bees on exotic versus native plants from each site at each sample round. *Above bars indicates the response variable is different between native and exotic plants at $p < 0.05$.

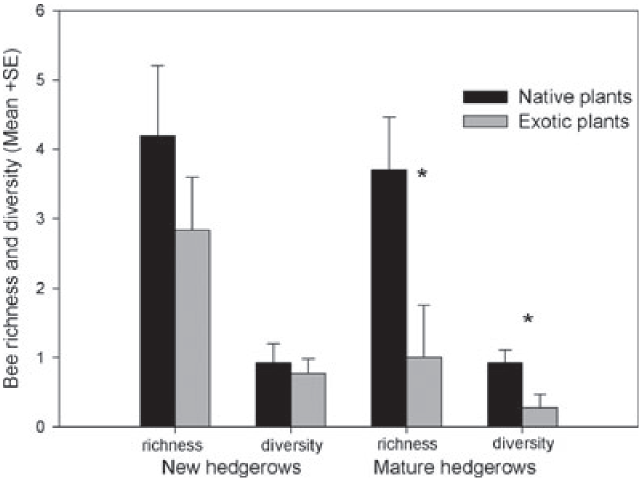

Figure 2. Mean native bee species richness and diversity (Shannon's diversity index) from each site and sample round at new hedgerow sites and mature hedgerow sites. * Above bars indicates the response variable is different between native and exotic plants at $p < 0.05$.

($F_{[1,17]} = 0.38$, $p = 0.55$). At mature sites, there was an interaction between floral cover and plant type on honey bee abundance ($F_{[1,24]} = 105.2$, $p < 0.0001$). Closer inspection of the region of significance revealed that honey bee abundance was greater on native plants at all cover levels and that the magnitude of difference between honey bee abundance on native versus exotic plants increased with increasing cover score.

Preference

At new hedgerow sites, regression slopes were significantly different for native bee abundance on native versus exotic plants (floral cover by plant type interaction: $F_{[1,11]} = 10.64$, $p = 0.008$). Mean bee abundance on native plants was greater than abundance on exotic plants ($t_{[11]} = -5.44$, $p = 0.0002$). At floral cover scores greater than 10, native bees showed a preference for native plants. As floral cover score increased, the difference between bee abundance on native and exotic plants increased (Fig. 3). Native bees preferred native plants over exotic plants at mature hedgerow sites at all cover amounts ($F_{[1,13]} = 39.08$, $p < 0.0001$) (Fig. 3).

Honey bees exhibited no preference for exotic or native plants in new hedgerow sites ($F_{[1,16]} = 0.01$, $p = 0.93$). In mature hedgerow sites, however, honey bees preferentially selected native plant species ($F_{[1,12]} = 102.81$, $p < 0.0001$) (Fig. 4).

Native Species Ranking

Semi-quantitative ranking of preference among native plant species showed that when present, *Eriogonum fasciculatum* and *Salvia* spp. were the most preferred native plant species (Table 1). Other species within the top preferred native plants for bee forage were *Eschscholzia californica*, *Rhamnus californica*, and *Grindelia camporum*. *Heteromeles arbutifolia*, *Achillea millefolium*, and *Atriplex lentiformis* had mixed results in terms of preference. *Sambucus mexicana* and *Rosa californica* were consistently less preferred by native bees when other native species were available. However, large numbers of syrphid flies (Family Syrphidae), which also can be important native pollinators of agricultural crops (Jauker & Wolters 2008), were caught on elderberry (L. Morandin & C. Kremen, unpublished data). Of the native bee species that were represented by greater than two individuals (17 species), four bee species were found on only one species of native plant in this subset of samples.

Discussion

These data indicate that native bees prefer to forage on native plants in both new and mature hedgerow sites. In addition, we found that bee abundance was greater on native plants in both new and mature hedgerows and bee richness and diversity were greater on native plants than exotic plants in mature hedgerows. Strikingly, 77% of bee species at mature hedgerows were only found on native plant species. These results indicate that in intense agricultural landscapes native plants are important for sustaining both abundance and diversity of native bee species.

Our finding of greater preference by native bees for native plants is contrary to some bee preference studies in natural or semi-natural areas that found greater or equal preference for exotic plants (Vila et al. 2009; Williams et al. 2011). At our new hedgerow sites, native shrubs were less than 3 years, and cover of exotic plants was greater at most sites; yet, we found that native bees preferentially chose native plants even when relative abundance of native plants was low.

Despite preference for native plants, at new hedgerow sites where native plants were sparse, substantial proportions of native bee (45%) and honey bee (66%) collections were on exotic plants. In contrast, at mature hedgerow sites, where native flowers were as abundant as exotic flowers, exotic plants

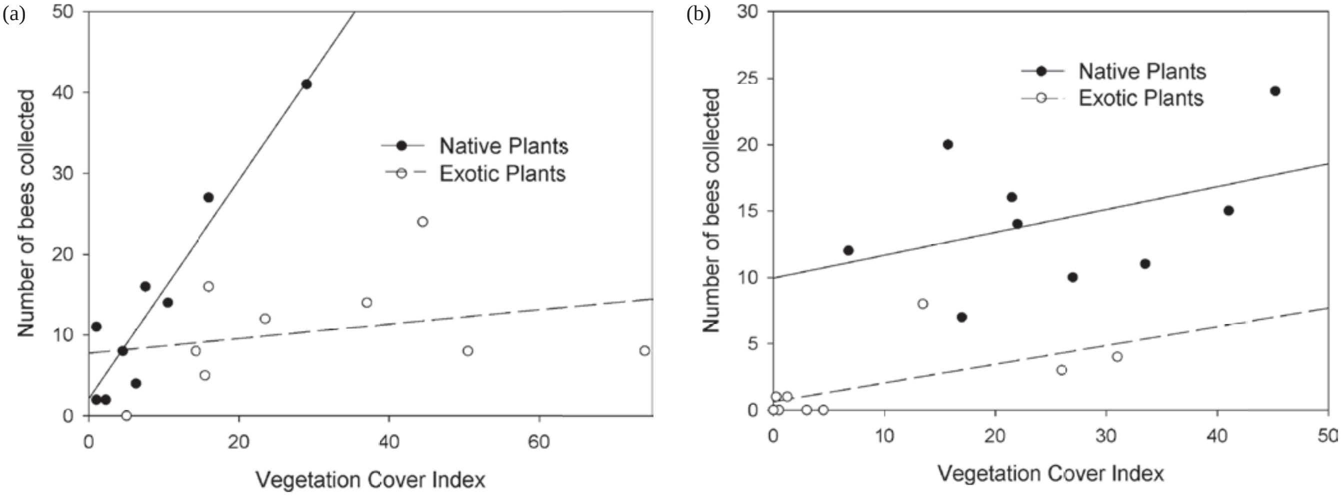

Figure 3. Native bee abundance on exotic and native plants at (a) new hedgerow sites and (b) mature hedgerow sites. Cover of exotic and native plants at each site, sample round combination was included as a covariate in the model in order to assess bee preference.

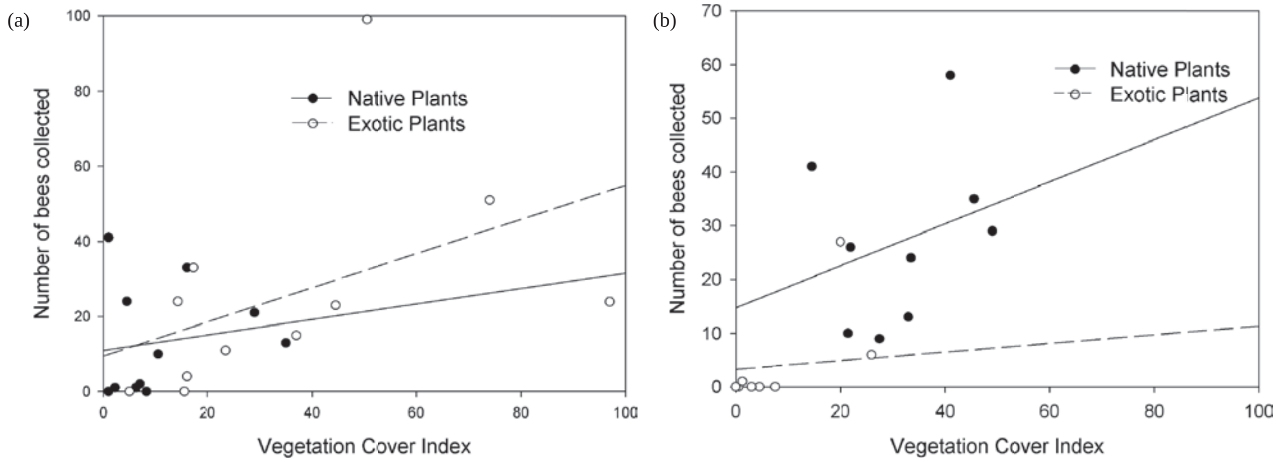

Figure 4. Honey bee abundance on exotic and native plants at (a) new hedgerow sites and (b) mature hedgerow sites. Cover of exotic and native plants at each site, sample round combination was included as a covariate in the model in order to assess bee preference.

were a less important resource for native or honey bees (12 and 16% of collections, respectively). This suggests that in regions where exotic plants dominate, they can be an important resource for native and managed bees. Williams et al. (2011) proposed that the greater reliance of native bees on alien species found in their study was driven by a subset of "super-generalist" plants that form links with a large proportion of native bees. Some of the alien species that were highly abundant and visited in the Williams et al. (2011) study were also found in relatively high density in our new and mature hedgerow sites (e.g. *Brassica nigra* and *Convolvulus arvensis*); yet we did not find these species to be preferred over co-occurring native plants.

Honey bees in new hedgerow sites did not prefer native plants but rather used native and exotic plants in proportion to their abundance. Honey bees are eusocial and recruit foragers to rewarding patches (Winston 1987). Returning honey bee foragers communicate information regarding location and floral odor of rewarding patches to the hive (Arenas et al. 2007). As native plants generally had low amounts of floral display at new hedgerow sites, there likely would be little recruitment to these plant species. Interestingly, at mature hedgerow sites where native floral cover was similar to the exotic floral cover, honey bees were found to prefer native plants. This suggests that given roughly equal floral display, honey bees were recruiting more bees to native plants in the mature hedgerow sites. In light of the recent serious declines of honey bees and suspected role of poor nutrition in agricultural settings (vanEngelsdorp et al. 2009), creation of native plant hedgerows in intense agricultural areas may benefit honey bee colony health.

At mature hedgerow sites bee species richness and diversity on native plants were greater than richness and diversity of native bees on exotic plant species. Recent studies suggest that habitats with greater bee diversity can result in greater or more stabilized crop production (Klein et al. 2007; Klein

Table 1. Semi-quantitative ranking of bee preference for native plant species in four hedgerow restoration sites in 2009.

Site	*SR*	*1*	*2*	*3*	*4*	*Co-occurring native plants with no bee visits during our sample*
1	1	ERFA2	SALVI	ACMI2		CEGR2
1	2	SALVI				HEAR5, ACMI2,S
1	3	SALVI	ACMI2	ERFA2		HEAR5,EPCA4
1	4	ERFA2	SALVI	EPCA4		ACMI2
2	3	ERFA2	ASFA			HEAR5
2	4	HEAR5	RHCA	SAME5	ERFA2	
3	2	ERFA2	GRCA	HEAR5		SAME5
3	3	ASFA				SAME5, ATLE
4	1	ESCA2	PHCA			
4	2	ESCA2	GRCA			ROCA2, HEAR5, FRCA6,S
4	3	GRCA	RHCA	ATLE		ROCA2,SAME5

ACMI2, *Achillea millefolium*; ASFA, *Asclepias fascicularis*; ATLE, *Atriplex lentiformis*; CEGR2, *Ceanothus griseus*; EPCA4, *Epilobium californicum*; ERFA2, *Eriogonum fasciculatum*; ESCA2, *Eschscholzia californica*; FRCA6, *Fremontodendron californicum*; GRCA, *Grindelia camporum*; HEAR5, *Heteromeles arbutifolia*; PHCA, *Phacelia californica*; RHCA, *Rhamnus californica*; ROCA2, *Rosa californica*; SALVI, *Salvia* spp.; SAME5, *Sambucus mexicana*.

Preference rank (1–4) was assigned by calculating the number of bees collected off of each flower type (at a site and sample round [SR]) divided by the cover proportion of flowers of each plant species. Plants with the highest value relative to other plants at each site and sample round were ranked as "1," the next highest value was ranked as "2," etc.

et al. 2009; Garibaldi et al. 2011). While few studies have examined mechanisms underlying the relationship between bee diversity and stability of pollination services, there is evidence that functional complementarity among bee groups may be an important factor leading to greater crop production (Hoehn et al. 2008; Winfree & Kremen 2009). Thus, native plant hedgerows, by enhancing bee diversity over exotic weedy edges, may help to stabilize or enhance crop production.

Recommendations for hedgerow plantings to promote pollinators often stress the use of a range of plant species in order to provide diverse and continuous resources throughout the season (Menz et al. 2011). Yet, in a review of restoration for bees, Winfree (2010) found that most studies showed that only a few plant species provided the majority of resources for bees, suggesting that restoration could be made more cost effective by focusing on the highly attractive subset of plant species. However, most of the reviewed studies were conducted in the EU on *Bombus* species. In contrast, we found wild bees on all native plant species in bloom in our hedgerows, except *Rosa californica* on which we have observed and netted native bees in other studies. Native plants with the highest visitation rates per unit of cover (preference score) changed among sample rounds within sites. This changing preference likely reflects differences in availability of flower species throughout the season as well as temporal turnover in bee community composition. Because a quarter of native bee species that had greater than two individuals collected at these sites were found on only one native plant species, and each on a different native plant species, our data suggest that a diversity of native plants is essential to maintaining native bee diversity. Our data support planting a wide range of native plants that are attractive to bees in order to provide spatially and temporally diverse resources.

Our study focuses on habitat enhancement using native perennial plants, whereas most studies on agricultural habitat enhancement in agroecosystems have examined non-native annual plants (Fiedler et al. 2008). Enhancement with native perennial plants can create long-term bee habitat that requires little input from the landowner after the first few years of maintenance (Long & Anderson 2010), and can provide other benefits such as conservation of native plants and associated fauna (Fiedler et al. 2008). Although the mature hedgerows were designed for natural enemy enhancement and pest control, the native plants were an important resource for bees. Previous research in the mature hedgerows examined in this study showed that natural enemy to pest ratios were greater in hedgerows relative to weedy areas (Morandin et al. 2011). Similar to our findings, Tuell et al. (2008) observed overlap in use of native plant species by pollinator and natural enemy insects suggesting that they may provide multiple ecosystem services (Fiedler et al. 2008).

The combination of low-maintenance and enhancement of multiple guilds of beneficial insects may provide incentives for growers to adopt hedgerow restoration with native plants. Our study provides promising first evidence that native bees preferentially choose native plants as forage resources in hedgerows. In addition, these data indicate that hedgerows of mature native plants will attract or promote a more species rich and diverse community of native bees than field edges where exotic plants dominate, possibly aiding stability of pollination function.

Implications for Practice

- In intense agricultural landscapes hedgerow restoration using native shrubs and forbs provide valuable resources for native bees.
- Native plants within these small, linear habitat elements are the most important resource for enhancing native bee abundance and diversity in degraded landscapes.
- Native and honey bee preference for native plants over co-occurring exotic plants supports the use of native plants in hedgerow restoration for pollination.
- A diversity of native plants is required to enhance native bee diversity.

Acknowledgments

We thank the growers and land owners in Yolo County, CA, that allowed us to work on their property. C. Locke, H. Wallis, S. Ambercrombie, C. Valiente, and G. Panlasigui, and J. Brennan assisted with the data collection. The research was funded by an NSERC Postdoctoral Fellowship to L.A.M., a Conservation Innovation Grant, a National Science Foundation grant, and a National Geographic Society Research and

Exploration grant. Members of the Kremen Laboratory, UC Berkeley, provided valuable comments on manuscript drafts.

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Ecological Applications, 23(4), 2013, pp. 829–839

Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields

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Abstract. In intensive agricultural landscapes, restoration within farms could enhance biodiversity and ecosystem services such as pollination by native pollinators. Although governments and conservation groups are promoting small-scale restoration on working farms, there are few studies that assess whether these practices enhance pollinator communities in restored areas. Further, there is no information on whether floral enhancements will deplete pollinators in adjacent fields by concentrating ambient populations or whether they result in a net increase in abundance in adjacent farm fields. We investigated whether field edges restored with native perennial plants in California's Central Valley agricultural region increased floral abundance and potential bee nesting sites, and native bee and syrphid fly abundance and diversity, in comparison to relatively unmanaged edges. Native bees and syrphid flies collected from flowers were more abundant, species-rich, and diverse at hedgerow sites than in weedy, unmanaged edges. Abundance of bees collected passively in pan traps was negatively correlated with floral abundance, was significantly different from communities captured by net sampling from flowers, and did not distinguish between site types; we therefore focused on the results of net samples and visual observations. Uncommon species of native bees were sevenfold more abundant on hedgerow flowers than on flowers at weedy, unmanaged edges. Of the species on flowers at hedgerows, 40% were exclusive to hedgerow sites, but there were no species exclusively found on flowers at control sites. Hedgerows were especially important for supporting less-common species of native bees in our intensive agricultural landscape. Hedgerows did not concentrate ambient native bee, honey bee, or syphid fly populations, and they acted as net exporters of native bees into adjacent fields. Within-farm habitat restoration such as hedgerow creation may be essential for enhancing native pollinator abundance and diversity, and for pollination services to adjacent crops.

Key words: biodiversity; Central Valley of California, USA; crop; ecosystem services; hedgerows; intensive agricultural landscape; native bees; pollination; restoration; syrphid flies.

INTRODUCTION

Habitat enhancement within farms is thought to be an important component for restoring ecosystem services in intensive agricultural landscapes. Growers have little or no control over the surrounding landscape, but can implement within-farm enhancements. However, whether restoration on a field scale can provide benefits to agricultural production, and thereby to growers, is largely unknown. This lack of information is hindering widespread adoption of within-farm habitat enhancement (see Griffiths et al. 2008, Brodt et al. 2009).

Loss of biodiversity in intensive agricultural landscapes has led to a reduction in ecosystem services that are essential for ensuring sustainable food production (Millennium Ecosystem Assessment 2005, Zhang et al. 2007). Managed honey bees now provide pollination services for the majority of global food crops that require insect-mediated pollen transfer (Klein et al. 2007). However, reliance on honey bees is becoming increasingly expensive and risky as managed honey bee colonies continue to decline in numbers in both North America and Europe (see Potts et al. 2010), coinciding with an increase in the proportion of crops that rely on insect pollination (Aizen and Harder 2009). Increasingly, growers and scientists are recognizing the value of conserving and/or restoring native bee populations as an alternative to such heavy reliance on honey bees for global crop pollination (Winfree 2010, Menz et al. 2011).

Numerous studies have shown that when crops are grown within a matrix of natural or uncultivated land, native bees are more abundant and diverse than in more homogenous crop areas (Morandin et al. 2007, Ricketts et al. 2008, Garibaldi et al. 2011). Further, in such situations, native bees can often provide adequate pollination services to crops without the aid of managed honey bees (Kremen et al. 2004, Winfree et al. 2008). However, intensive agricultural landscapes (for example, those with >80% of land devoted to rotational crops)

Manuscript received 20 June 2012; revised 25 October 2012; accepted 1 November 2012; final version received 26 November 2012. Corresponding Editor: A. K. Brody.

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dominate many parts of the world (e.g., National Agricultural Statistics Service, CropScape 2010, *available online*).[2] Restoring healthy communities of native pollinators in these intensive agricultural environments may prove problematic because large areas of natural and seminatural land are not available and are not likely to be created. Restoration of small areas on farms could counter the lack of large natural habitat areas in intensive agricultural landscapes.

With this goal of bringing biodiversity and ecosystem services into intensive agricultural areas, some growers and landowners are utilizing government incentive programs, which compensate farmers for enhancing environments on their land. Small-scale restorations, such as hedgerows, can use little or no arable land and are relatively easy for landowners to install, offering exciting potential as a means of integrating agricultural production with conservation of biodiversity and ecosystem services. However, there is a surprising lack of information on how hedgerow and other within-farm enhancements impact biodiversity and ecosystem services, especially considering the large amounts of money spent annually on habitat restoration in the European Union and United States (Kleijn et al. 2006, Winfree 2010).

Field edge enhancements with flowering plants may support a greater abundance and diversity of bumble bees (Carvell et al. 2007, Pywell et al. 2011) and other native bee species (Hopwood 2008, Batary et al. 2011). Flowering hedgerows can attract bees that are uncommon in the landscape (Hannon and Sisk 2009) and potentially increase biodiversity and native bee abundance in depauperate agricultural landscapes. Yet, little is known about how restoration of field edges will impact entire pollinator communities and how restored areas will impact biodiversity and abundance of pollinators in adjacent crop fields (Winfree 2010).

If restored areas increase only forage resources, these areas could act as concentrators of ambient pollinator populations, potentially diminishing or adding no net diversity or abundance of pollinators to adjacent crops. Few studies have examined whether enhancing floral resources on crop edges concentrates or exports pollinating insects to adjacent fields, a crucial question for population restoration and long-term ecosystem service delivery.

We assessed pollinator communities (native bees, native syrphid flies, managed honey bees) in hedgerows of native flowering shrubs in the Central Valley of California over two years (see Plate 1). We compared floral and nesting characteristics and populations of pollinators between restored native perennial plant hedgerows and weedy, relatively unmanaged field margins. We assessed abundance, diversity, and community composition of pollinators both in edges of hedgerow and control sites, and at designated distances into crop fields. We hypothesized that: (1) hedgerow sites would provide more nesting opportunities for native bees and more abundant, diverse, and continuous floral resources for pollinators than control margins; (2) native pollinators would be more diverse and abundant in hedgerows, and differ in composition between hedgerows and control edges; (3) hedgerows would enhance both common and less-common pollinator species; and (4) perennial hedgerows would act as net exporters of pollinators to adjacent crop fields rather than concentrating ambient populations from the surrounding landscape.

MATERIALS AND METHODS

Study design

The study was conducted in California's Central Valley in the summers of 2009 and 2010. The study area was primarily comprised of rotational field crops with regions of seminatural oak woodland, grassland, and riparian gallery forests to the west of some sites (Fig. 1). All sites were surrounded by at least 85% intensively managed cropland in a 1500 m radius. Four native plant hedgerow sites were selected each year, with two of them being the same in 2009 and 2010. Hedgerows were at least 10 years of age and had a row of perennial shrubs bordered by a stand of perennial grasses and ranged in length from 305 m to 550 m (for species composition, see Bugg et al. 1998, Long et al. 1998). Hedgerow plants were chosen so that there was successive and overlapping bloom from early spring to late fall.

Within each year we chose hedgerows that were adjacent to processing tomato fields, one of the most common crops in the region, in order to ensure that sites shared similar crop backgrounds. For each hedgerow site, we selected a matching control site with a weedy, relatively unmanaged edge. We chose to compare the hedgerows to weedy field edges because it is the most prevalent edge type for crops in our region. Control sites were located a minimum of 1 km and a maximum of 3 km from corresponding hedgerow sites (Fig. 1). Our design insured independence of bee communities at hedgerow and control sites, while allowing both treatments to span the same environmental conditions across the region.

Pollinators were assessed in hedgerow and control sites ("sites" herein refers to edges and adjacent fields) four times (sample rounds) during each summer, with approximately one month between sample rounds, from early May until early August. This time frame spans the summer crop bloom in our region. Samples were only done on days when the temperature was at least 18°C, the wind below 2.5 m/s, and the conditions partly cloudy to sunny for the duration of the sampling time. Because pollinator activity is very sensitive to weather conditions, collections were made at a hedgerow site and its corresponding control site on the same day.

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[2] http://nassgeodata.gmu.edu/CropScape

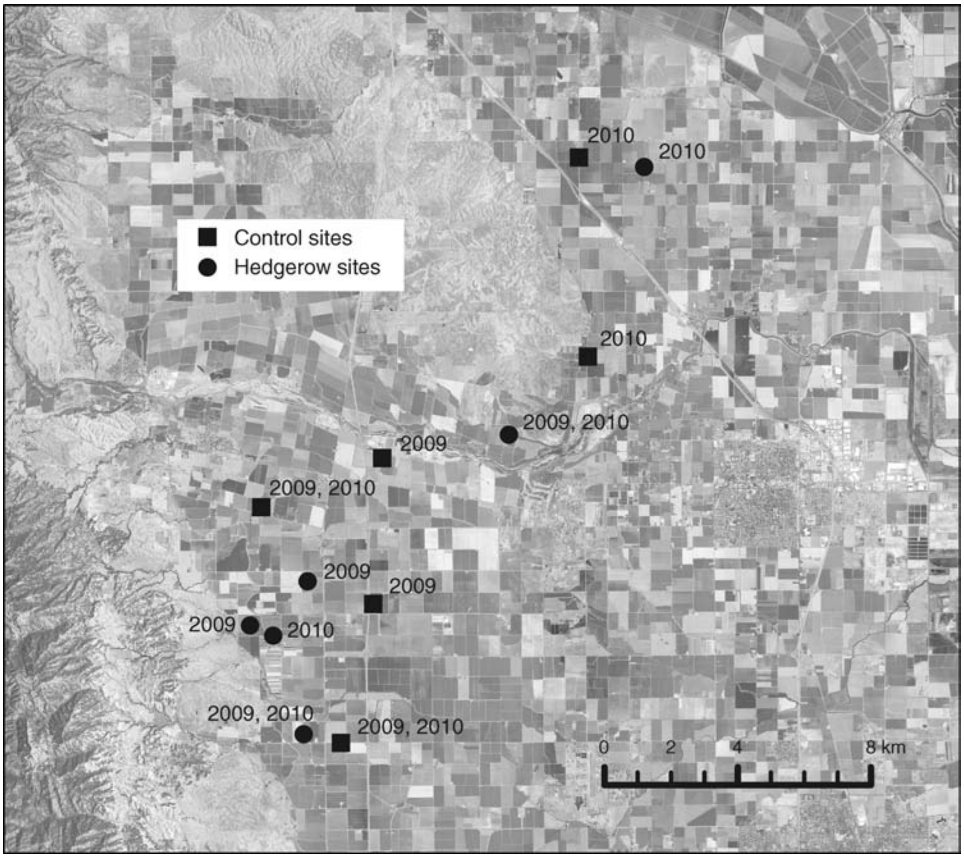

FIG. 1. Hedgerow and control sites from 2009 and 2010 in Yolo County, California, USA. Four hedgerows were matched with four control sites each year. Two hedgerow edges and two control edges were the same in 2009 and 2010, but due to rotation of tomato crops, the other sites were different between years.

Floral, nesting, and pollinator assessment

At each sample round, floral cover was assessed by placing 50 1-m^2 quadrats along the hedgerow or control edge, ~8 m apart. Plants in bloom were identified and floral cover per species was estimated using seven bins for percent cover scores. During the final sample round each year, bee nesting habitat was assessed in each of the 50 quadrats, following Potts et al. (2005). We quantified potential nesting resources as the percentage of quadrats with dead wood, hollow stems, bare ground, cracked ground, land slope, and soil hardness (using three measurements with a penetrometer per quadrat, at the two closest corners and the quadrat center). In addition, we counted small (<2 cm) and large (>2 cm) cavities in the ground, which could indicate ground-nesting bee tunnels.

In each sampling round, pollinators were assessed using three methods in edges and two methods in fields. In edges, we placed a total of 21 pan traps consisting of seven each of yellow, blue, and white traps made from spray painted bowls (6-ounce [~177 mL] Solo plastic bowls painted with fluorescent yellow and blue paint or left white) containing water and a small amount of detergent to reduce surface tension (Westphal et al. 2008). Pans were placed out in the morning, ~18 m apart on the ground along the hedgerow or control edge, in an alternating color pattern. Within fields, we placed three pan traps (one of each color) at each of three distances (10, 100, and 200 m from edges) along each of two transects into fields. Pans were left out for five to six hours before being collected.

We conducted timed aerial netting, capturing bees (Apoidea) and syrphid flies (Syrphidae) visiting flowers in edges. The collector checked every flower for the presence of a bee or syrphid fly. If a bee or syrphid fly was observed touching the reproductive parts of a flower, then it was collected in the net and put into a labeled vial specific to that plant species. The timer was stopped after the insect was captured in the net, until the collector was ready to recommence flower observations, so that total observation time was standardized among collections. Net collections were not done in fields because of the potential damage the net could cause to tomato flowers.

To further quantify abundance and diversity of flower visitors at our sites, we conducted visual observations in 1-m^3 areas. At three locations along edges, bees and syrphid flies were recorded as either landing on reproductive parts of flowers or flying through quadrat areas. Two 4-min visual observations of flower-visiting insects were made at each of the edge locations and one 4-min visual observation was conducted at each of the six in-field locations previously described. Bees were identified as either honey bees or within categories for native bees, as defined in Kremen et al. (2011). We did not attempt to categorize syrphid flies during visual observations and only recorded their numbers.

Data Analysis

Site characteristics

Floral cover bin scores were translated into percent cover by selecting the midpoint of each bin. Cover and flower species richness were compared between hedgerow and control sites using a mixed-model ANOVA (SAS 1999) with site type as a main effect, sample round as a repeated factor, and site nested within site type and year, and year as random effects. We used the same model, but excluded sample round, to compare nesting variables between control and hedgerow edges.

Pollinator communities, abundance, and diversity

We analyzed edge and field pollinator data separately. Throughout, native bee and syrphid fly data were analyzed separately due to fundamental ecological differences in their nesting and foraging strategies. Female bees are central-place foragers, with nest sites that they return to between foraging trips. Conversely, syrphid flies are ubiquitous foragers and do not return to nest sites.

We first conducted analyses of similarities between communities collected using pans vs. nets in order to assess whether data collected using these methods should be analyzed separately. We used a multi-response permutation procedure (MRPP) PC-ORD (McCune and Mefford 2006) and found that pan and net collections captured significantly different communities of native bees, regardless of site type ($P < 0.0001$). We therefore analyzed net and pan data separately when comparing communities of native bees. Another reason for analyzing pan and net data separately is the likelihood that floral resources were competing with pan traps for pollinating insects. Syrphid fly communities were not distinguishable by collection method; however, to keep analyses consistent between syrphid flies and native bees, we also analyzed syrphid fly community composition separately for pan- and net-collected specimens. Because visual data were resolved to category for bees and to abundance only for syrphid flies, they were analyzed separately from other data.

Bee and syrphid communities were compared statistically between site types using MRPP, with nonmetric multidimensional scaling for visual representation (McCune and Mefford 2006). MRPP is a nonparametric test of the null hypothesis of no difference between species composition between two or more groups. To compare pollinator abundance, richness, and diversity (Shannon index) between site types, we used mixed-model ANOVAs (SAS 1999) with site type as a fixed effect, sample round as a repeated factor, and site nested within year and treatment, and year as random effects. We also examined the influence of hedgerow vs. control on the abundance of pollinators, controlling for total abundance of each species, using an ANCOVA analysis for net and pan data. Site type and species were categorical main factors, and total abundance of each species (total collected in either net or pan from all sites) was the continuous variable, with a negative binomial distribution for over-dispersion and a log link function.

Kleijn et al. (2006) examined biodiversity benefits of agri-environment schemes in the European Union and assessed their benefit to uncommon species by specifically analyzing abundance of species (within species groups) that were found at <5% of sites in each country. We did not have enough sites to model our data in that way; hence, we first calculated species that made up <5% of total abundance and found that 81 of the 83 species of native bees were present at <5%. This was because of the large predominance of two species of native bees, *Lasioglossum incompletum* (Crawford) and *Halictus tripartitus* (Cockerelle), which made up 83% of our samples (64% and 19%, respectively). Syrphid flies samples were also dominated by a small number of species, *Toxomerus marginatus* (Meigen), *Eupeodes fumipennis* (Thomson), and *Syrphus opinator* (Osten Sacken) (60%, 10%, and 7%, respectively). We therefore adjusted our criteria for "uncommon" to species that made up <1% of the total individuals collected. We conducted ANOVA analyses of abundance of uncommon species of native bees and syrphid flies in hedgerow and control sites, using the same model outlined previously for abundance.

For analyses into fields (pan and visual data only), we added distance from edge (herein "distance"; 0, 10, 100, 200 m) and distance × site type interaction as fixed effects. Abundance and richness data were over-dispersed and we used a log link function with a Poisson, negative binomial, or gamma distribution, whichever normalized the over-dispersion best for that response variable.

We assessed whether there were "indicator" species and genera of hedgerow or control sites (McCune and Mefford 2006). The analysis contrasts individual species performance across two or more treatments (in our case, hedgerow and control sites). A perfect indicator species (or genus) is both always present and exclusive to that treatment. Based on these criteria, indicator values were generated and tested for significance using a randomization (Monte Carlo) technique.

Collection method

We hypothesized that pollinators might be more attracted to floral resources than they were to pan traps. If so, abundance in pan traps should be negatively correlated with floral cover (Baum and Wallen 2011).

We found a significant, negative relationship between native bee abundance in pan traps and floral cover ($F_{1,46} = 5.07$, $P = 0.029$), and negative (but not significant) relationships between syrphid fly and honey bee abundance in pans and floral cover. We therefore briefly summarize data from pan collections, but focus our results and discussion on net samples and visual observations, which reflect pollinator use of resources.

Concentrator vs. exporter.—We examined whether hedgerow plantings acted to concentrate ambient pollinators from the surrounding environment or whether hedgerow restorations can promote greater pollinator abundance in adjacent areas. We compared abundances in fields adjacent to hedgerows with those adjacent to control edges and assessed patterns that would be found under two alternate and one null hypothesis, as follows. H_0 (Null): there is no difference in pollinator abundances along distance transects in fields adjacent to hedgerow vs. control edges. H_1 (Concentrator): pollinator abundances are lower along distance transects located in fields adjacent to hedgerow edges compared to distance transects adjacent to control edges. H_2 (Exporter): pollinator abundances are higher along distance transects located in fields adjacent to hedgerows compared to distance transects adjacent to control edges.

The total abundance of pollinating insects in fields adjacent to hedgerow and control edges probably would depend on the attractiveness of the crop. Tomato is a relatively unattractive crop to many pollinating species and, therefore, hedgerow and other edge flowering vegetation might be more concentrating than if a more attractive crop were present. However, because we test the null and alternate hypotheses by comparing relative abundances of pollinating insects between fields adjacent to control and hedgerow sites, the relationship of abundance between field types (i.e., whether fields adjacent to hedgerows have an equal, lower, or greater abundance of pollinators than corresponding fields of the same crop adjacent to control edges) will support the null or alternate hypotheses regardless of the attractiveness of the crop.

RESULTS

Site characteristics

As expected, there was significantly greater floral cover in hedgerow than in control edges ($F_{1,14} = 9.46$, $P = 0.008$). Examining differences by sample round, however, revealed some unexpected findings. Mainly, although hedgerows had significantly greater floral cover in the first sample round, cover declined sharply by the second sample round to levels that were similar to control sites. In mid- and late summer, floral cover at control sites declined, but cover at hedgerow sites remained constant. Floral richness was marginally greater at hedgerow than control sites throughout the summer ($F_{1,14} = 3.88$, $P = 0.069$), with richness of 3.97 ± 0.36 (mean ± SE) and 5.84 ± 0.63 at control and hedgerow sites, respectively. There was significantly more dead wood (a potential nesting resource for tunnel and cavity nesters) at hedgerow sites than at control sites ($F_{1,14} = 10.40$, $P = 0.006$). There was a trend toward more bare ground (a potential nesting resource for ground nesting bees) at control sites, and more small cavities at hedgerow sites ($P < 0.10$).

Field edge pollinators

Native bees.—For pan-trapped specimens, there were no detectable differences in native bee abundance, richness, diversity, or community structure between hedgerow and control edges (Table 1).

For net-collected specimens, there was no difference in total abundance of net-collected native bee specimens between the site types. However, controlling for overall abundance of each species as a covariate, native bee abundance was greater at hedgerow than control sites ($F_{1,107} = 26.64$, $P < 0.0001$; Fig. 2a). Further, we found that abundance of uncommon species was greater at hedgerow than at control sites (5.7 ± 1.1 individuals (mean ± SE) and 0.8 ± 0.2 individuals at hedgerow and control sites, respectively; $F_{1,14} = 16.53$, $P = 0.001$). There was greater richness ($F_{1,14} = 7.07$, $P = 0.019$) and alpha diversity ($F_{1,14} = 9.03$, $P = 0.009$) of bees net-collected at hedgerow than at control edges (Fig. 3).

Community analyses (MRPP) indicated significantly different native bee communities at hedgerow and control edges ($t = -3.4$, $P = 0.005$). Bee communities were also more dissimilar from one another among hedgerow than among control sites (mean Sorenson (Bray-Curtis) distance measure = 0.76 and 0.41 at hedgerow and control sites, respectively, indicating higher beta diversity among hedgerows; $F_{1,54} = 158.8$, $P < 0.0001$). We compared the set of species known to be using floral resources at one site type (net-collected) vs. the species collected by both sample methods at the opposite site type, because net-collected specimens are known to be utilizing resources present at the site, whereas pan-collected individuals may simply be traversing through the area (Appendix: Table A1). This gives an indication of the number and proportion of species that are unique to the floral resources at hedgerow and control sites compared to species that are present at both site types. Of the 50 native bee species using floral resources at hedgerow sites, 20 species were absent from control sites (net or pan collections), whereas all of the 20 species net-collected at control sites were found in net and/or pan collections at hedgerow sites.

There were two marginally significant indicator species of hedgerows: *Megachile coquilletti* ($P = 0.07$) and *Bombus vosnesenskii* ($P = 0.07$). Indicator analyses by genera showed the genus *Megachile* ($P = 0.03$) as a significant indicator and the genera *Bombus* ($P = 0.075$), *Hylaeus* ($P = 0.076$), and *Osmia* ($P = 0.087$) as marginally significant indicator species of hedgerow restoration.

TABLE 1. Results (F values) of GLMM analyses of native bees, syrphid flies, and honey bees in four hedgerow and four control sites, in California's Central Valley, over two years.

Location and collection method	Species group	Abundance	Adjusted abundance	Uncommon species	Richness	Diversity
Edge						
Net	native bees	0.23	26.64***	16.53***	7.07*	9.03**
	syrphid flies	6.81*	4.45*	2.2	7.75*	5.57*
	honey bees	16.91***				
Pan	native bees	1.36	0.78	2.33	1.03	0.51
	syrphid flies	1.24	0.83	5.73*	0.01	0.35
	honey bees	0.11				
Visual	native bees	10.14**			5.39*	10.2**
	syrphid flies	2.16				
	honey bees	3.87				
Field						
Pan	native bees	0.57	1.43		1.2	2.74
	syrphid flies	0.11	0.12		0.39	0.59
	honey bees	1.8				
Visual	native bees	13.31**			10.23**	
	syrphid flies	0.37				
	honey bees	8.83**				

Notes: For F values, df = 1, 14 for all analyses except adjusted abundance, which was an ANCOVA controlling for total species abundance, with denominator df reflecting the number of species. In all cases where there is significance, values at hedgerows are greater than values at control sites.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Honey bees and syrphid flies.—For pan collections, there was no difference in honey bee or syrphid fly abundance between hedgerow and control field margins. Syrphid richness and diversity did not differ between the two site types, but there were more uncommon syrphid species in pans at hedgerow than at control sites ($F_{1,14} = 5.73$, $P = 0.03$). There were no significant differences in syrphid community composition between the two site types.

For net collections, there were significantly more honey bees ($F_{1,14} = 16.91$, $P = 0.001$) and syrphid flies ($F_{1,14} = 6.81$, $P = 0.02$) net-collected off of flowers in hedgerows than in control margins. Analysis of covariance, controlling for overall abundance of each species, showed that there were significantly more of each syrphid species in hedgerow than control sites ($F_{1,39} = 4.45$, $P = 0.04$; Fig. 2b). There was no difference between control and hedgerows in abundance of uncommon syrphid species. Syrphid fly richness ($F_{1,14} = 7.75$, $P = 0.015$) and diversity ($F_{1,14} = 5.57$, $P = 0.033$) were greater at hedgerow than control field margins (Fig. 3). Syrphid fly communities

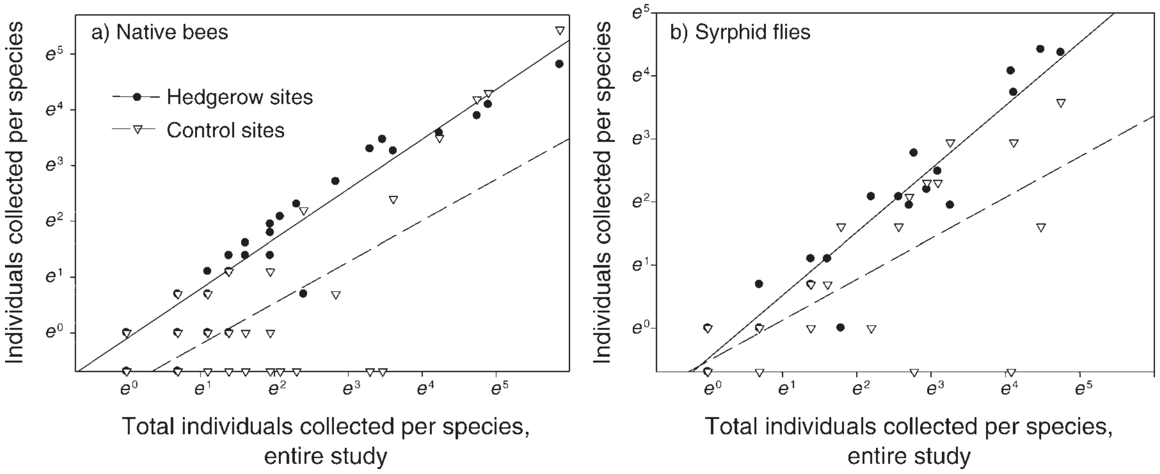

FIG. 2. For (a) native bees and (b) syrphid flies, the number of individuals of each species collected from flowers at either hedgerow or control sites in relation to the total number of individuals collected for that species in both site types. The axes are on a natural logarithm scale ($e = 2.7182818$). In both panels, the hedgerow regression is above the control; all regressions are significant at $P < 0.0001$. For native bees, $r^2 = 0.96$ for hedgerow and 0.99 for control; for syrphid flies, $r^2 = 0.94$ for hedgerow and 0.64 for control.

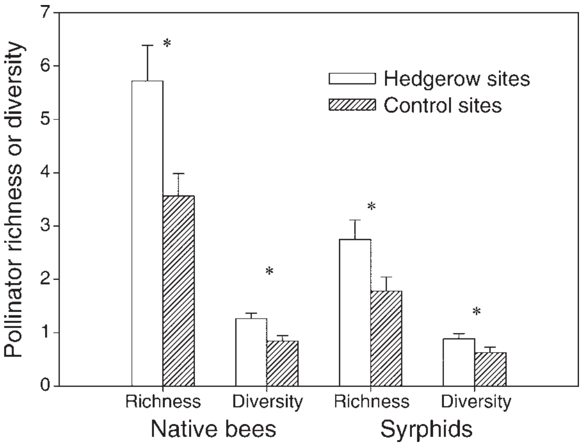

FIG. 3. Native bee and syrphid richness (number of species) and Shannon's diversity index (values are shown as mean + SE) on flowers in hedgerow and control edges in 2009 and 2010. Asterisks indicate a significant difference between hedgerow and control sites.
* $P < 0.05$.

were not different among treatments (MRPP), and showed a high dissimilarity among sites within treatment types (0.82 and 0.81 for control and hedgerow sites, respectively).

Visual observations

More native bees ($F_{1,14} = 10.14$, $P = 0.007$) and marginally more honey bees ($F_{1,14} = 3.87$, $P = 0.069$) were observed at hedgerow than control sites. Visual observations of native bees showed greater categorical richness ($F_{1,14} = 5.39$, $P = 0.036$) and diversity ($F = 10.2$, $P = 0.006$) at hedgerow sites. Syrphid fly abundance did not differ between the two site types.

In-field pollinators

Native bees.—For pan-collected specimens, there was no interaction between distance and treatment, and no difference in abundance of native bees in pan traps at hedgerow and control sites, but there was a significant decrease with distance into fields at both site types ($F_{1,125} = 12.42$, $P = 0.001$). Further examination of differences among distances revealed that there were significantly more bees at 10 m than at 100 and 200 m ($P < 0.05$) into the field, and no difference in abundance between 100 and 200 m.

Pan-collected bees did not differ in richness or diversity between site types, but there was a significant difference between bee communities in fields adjacent to hedgerows and those adjacent to control edges (MRPP; $t = -1.9$, $P = 0.048$).

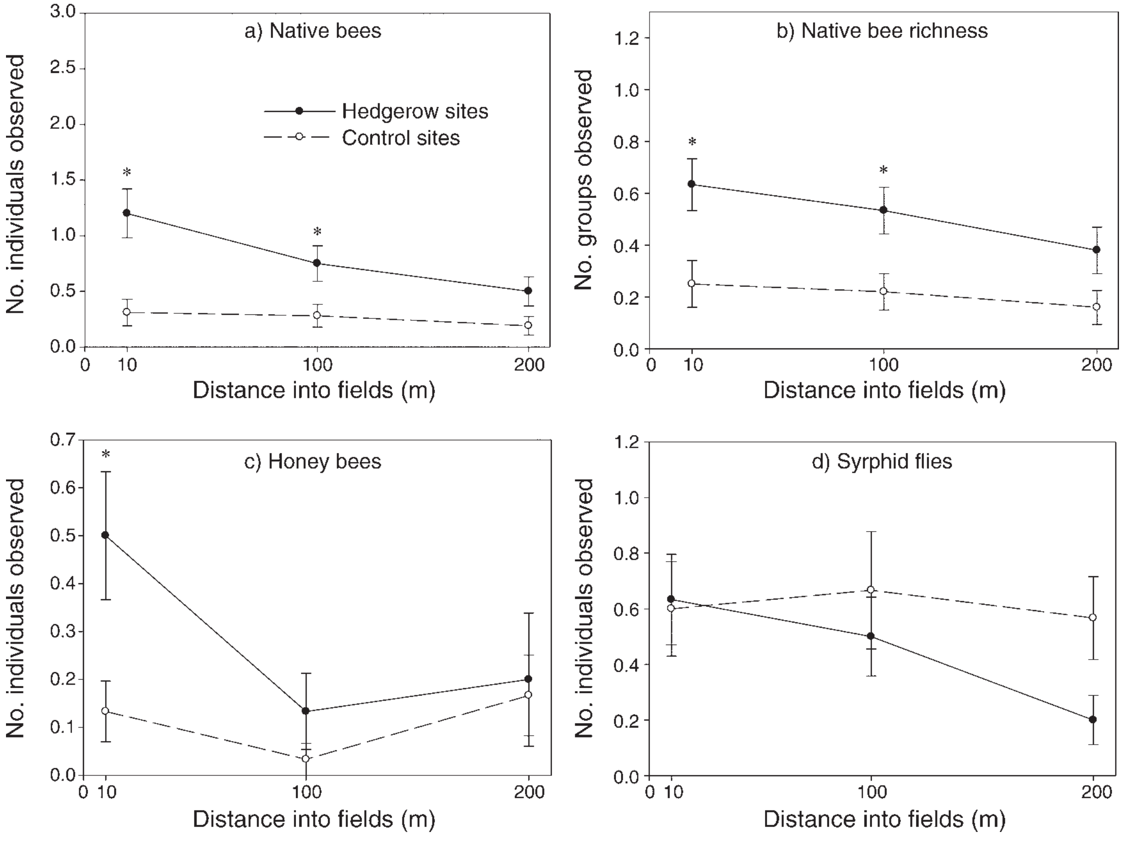

FIG. 4. Observed numbers (mean ± SE) of (a) individuals of native bees, (b) species of native bees, (c) individuals of honey bees, and (d) individuals of syrphid flies at three distances into fields that were adjacent to hedgerow or control edges, in 2009 and 2010.

For visual observations, there were significantly more native bees observed in fields adjacent to hedgerows than in fields adjacent to control edges ($F_{1,14} = 13.31$, $P = 0.002$), and a significant decrease with distance into fields ($F_{1,175} = 10.45$, $P = 0.002$; Fig. 4a). We observed significantly more native bees in fields at hedgerow than at control sites at 10 m and 100 m ($P < 0.05$), and marginally more native bees at hedgerow than at control sites at 200 m ($P = 0.08$). Native bee categorical richness was greater in hedgerow than control sites ($F_{1,14} = 10.23$, $P = 0.006$) and there was a significant decrease in categorical richness with distance into fields ($F_{1,175} = 5.17$, $P = 0.024$; Fig. 4b).

Honey bee and syrphid flies in fields.—For pan-collected specimens, there was no difference in honey bee abundance, in syrphid abundance and richness between site types, or effect of distance.

For visual observations, there was a marginally significant interaction effect between field treatment and distance into the field on honey bee abundance ($F_{1,174} = 3.72$, $P = 0.056$; Fig. 4c); we therefore left the interaction in the model. We observed significantly more honey bees in fields adjacent to hedgerows than in fields at control sites ($F_{1,14} = 8.83$, $P = 0.01$). Pairwise examination showed that there was a greater abundance of honey bees at hedgerow than at control sites only at the 10-m distance. There were no significant differences observed in syrphid abundance in fields, or in decrease with distance into fields (Fig. 4d).

Discussion

Abundance, richness, and diversity of native bees and syrphid flower-visitors were enhanced in field edges by the presence of mature hedgerows, supporting our hypothesis that small, field-scale hedgerow restoration in intensively managed agricultural landscapes can benefit pollinator populations. In addition, we found greater abundances of native bees up to at least 100 m into fields (visual observations), suggesting that the hedgerows were net exporters, rather than neutral or concentrators, of ambient native bees. Greater floral abundance, floral diversity, and nesting opportunities (greater amounts of dead wood) were found at hedgerows compared to control sites and may have lead to the more diverse and abundant pollinator communities in edges, and more diverse and abundant native bees into fields, at hedgerow sites.

These results add to other recent findings in agricultural settings indicating that small, florally enhanced strips or patches can increase the abundance and diversity of bumble bees (Carvell et al. 2011, Pywell et al. 2011) and other pollinators (Kohler et al. 2008, Batary et al. 2011). Interestingly, we found no differences in abundance, richness, and diversity of native bees and syrphid flies collected in pan traps. These individuals may be simply traversing the area; alternatively, because we found a negative correlation between the numbers of individuals trapped in pans and floral cover, the relative lack of floral resources at control sites may make pan traps more enticing, enhancing the apparent abundance of native bees and syrphids there and obscuring true differences between hedgerow and control sites (see Baum and Wallen 2011). We suggest that pan traps may not be an accurate way of assessing differences in pollinator communities among areas that differ in floral display.

For flower-visiting (net-collected) individuals, we found that all species of native bees at control sites were also found at hedgerow sites (in nets, pans, or both), but the converse was not true. At hedgerow sites, 40% of flower-visiting native bee species (20 of 50 species) were not present in either of our collection methods at control sites. In addition, significantly greater abundance of uncommon bee species on flowers at hedgerow sites than at control sites indicates that the native perennial hedgerows in our landscape were particularly supporting species that were less common in the region. Our results differed from the review by Kleijn et al. (2006) of biodiversity benefits of agri-environment schemes in the European Union. The schemes that they examined primarily benefited common species and had limited usefulness for conservation of uncommon species. Kleijn et al. (2006) point out other studies showing that agri-environment schemes can promote endangered species on farmland, but only when the schemes are tailored to the needs of a single species or are in the direct vicinity of nature reserves. Although our restored hedgerows were designed to enhance natural enemy communities of insects (Bugg et al. 1998), they significantly promoted uncommon native bee (but not syrphid fly) species. Similar to our findings for native bees, Hannon and Sisk (2009) found that flowering shrubs in hedgerows were able to support native bee species that were otherwise uncommon in their agricultural landscape.

In addition to increasing diversity, abundance, and uncommon species of native bees, hedgerow sites showed greater diversity among sites in native bee species composition (beta diversity), and also differed significantly in species composition compared to control sites. Native plant hedgerows in our study area are therefore a unique resource, at least in comparison to the most common untilled land of weedy plants, for supporting uncommon native bee species and promoting high turnover among communities, both locally and at the landscape scale.

Yet, whether florally enhanced areas act as exporters of pollinators to adjacent crops, or as concentrators of ambient populations, has received little attention in the literature. This is a vital area of research because many growers are concerned that addition of floral resources may draw pollinators, both managed and native, away from crop plants, thus reducing pollination services to agriculture. Although no previous studies have directly addressed whether enhancements concentrate or export pollinators, there has been discussion related to polli-

PLATE 1. A mature, perennial hedgerow adjacent to a tomato field at Rominger Brothers Farms, Yolo County, California, USA. Photo credit: L. A. Morandin.

nator movement in landscapes. The Circe Principle, first proposed by Lander et al. (2011) and further discussed by Bartomeus and Winfree (2011), contends that attractive, flower-rich areas, rather than encouraging pollinator movement through landscapes, may cause pollinators to be waylaid.

We propose that whether florally enhanced areas act as net exporters or concentrator of pollinators may be dependent on the permanence and nesting opportunities in the enhancement. Kohler et al. (2008) assessed native bees and syrphid flies along 1500-m transects in farmland adjacent to newly established flower-rich patches. They found that both richness and abundance of bees and syrphid flies were greater in the flower-rich patches than in the control patches. But, they noted that the flower-rich patches had a negative effect on bee abundance in the direct vicinity of the patches, possibly due to their young age and lack of nesting resources. In contrast, Samnegard et al. (2011), examining bee abundance, diversity, and seed set proximally and distant from established domestic gardens in an intensively managed agricultural landscape, found that bee populations were enhanced closer to the gardens. The perennial, established nature of our hedgerows and the gardens in the Samnegard et al. (2011) study may have resulted in these habitats being net exporters of pollinators to adjacent crops, rather than concentrators.

Established or mature, floral-rich enhanced areas may aid the reproductive success of native bees by jointly providing not only greater and more consistent foraging resources, but also more nesting opportunities, that result in increasing populations over years. In contrast, although newly established floral-rich areas of annual plants may aid pollinator populations by providing additional resources and/or continuity of resources in agricultural landscapes, they may not *generate* pollinators. Thus, at times during the season, they may concentrate, rather than export, pollinators. Given the few existing studies that directly assess whether annual and perennial enhancements export or concentrate pollinators, further investigation is merited.

Although hedgerows in our study were net exporters of native bees, syrphid fly abundance did not differ between fields adjacent to hedgerow and those adjacent to control margins, indicating that edge differences had little effect (i.e., neutral hypothesis) on populations in fields. The difference between the pattern seen for syrphid flies and native bees could be due to life history differences between the groups. Although native bees in crop fields mainly are searching for forage (nectar and/or pollen), syrphid flies were more likely moving into tomato fields in our study to search for aphids for oviposition sites (Almohamad et al. 2009).

We found that *Bombus* (bumble bees), *Megachile* (leaf-cutter bees), *Hylaeus*, and *Osmia* (orchard mason bees) were indicators of hedgerow sites. *Bombus* species are cavity nesters, often using old rodent burrows or hollows in ground debris. The other three genera nest in existing tunnels and holes in old wood and stems. In addition to the enhanced floral abundance and consistency at hedgerow sites, the greater amounts of dead wood and woody vegetation at the hedgerow sites, as well as undisturbed ground suitable for rodent nesting, may have provided more nesting opportunities for these groups.

Honey bee abundance was greater in hedgerow than control edges. However, similar to that of syrphid flies, the greater abundance did not extend far into fields (only to 10 m for honey bees). Honey bees in our region are managed, and therefore hedgerows would not act to increase populations as they could with free-living species. Honey bees, however, may benefit from native plants in hedgerows, which provide a greater abundance, diversity, and consistency of nectar and pollen than do plants at control sites. This may aid managed honey bee colonies by providing extra resources normally absent in intensively managed agricultural landscapes (Decourtye et al. 2010). Perhaps just as importantly, our data indicate no reduction in honey bees in fields adjacent to hedgerows. Some growers have concern that the abundance of attractive floral resources in enhanced hedgerows may draw honey bees from rented colonies away from crop plants needing pollination (Jessa Guise, Xerces Society for Insect Conservation, *personal communication*). The hedgerows in this study were designed to have successive and overlapping bloom, from early spring to late fall, and therefore there were always some hedgerow flowers in bloom. However, growers could choose to design hedgerows using plant species that did not have co-occurring bloom with major crop species. Whether greater abundance and diversity of native bees in hedgerows and adjacent fields results in greater service provision to the crop will, in part, rest on the dependence of the crop on insect pollination, the type of native bees enhanced in the edges, and the presence of other pollinators such as managed honey bees.

Conclusions

The native perennial hedgerows had more abundant, diverse, and sustained floral resources than control edges, and showed some evidence of greater nesting resources for native bees. Both native bee and syrphid fly flower-visitors were more abundant and diverse on flowers in hedgerows than in control edges. Hedgerows resulted in higher alpha and beta diversity of pollinator species and supported native bee species that were uncommon in the landscape. Managed honey bees were more abundant in hedgerow than control edges. Hedgerows appeared to act as net exporters of native bees to adjacent crops and appeared to be neutral for syrphid flies in adjacent crops. Our findings suggest that native perennial plant restorations are essential for maintaining local and landscape pollinator alpha and beta diversity, especially for maintaining less-common pollinator species. The semipermanent nature of the perennial plant hedgerows, with continuous floral resources in proximity to nesting habitat, probably resulted in the enhanced pollinator populations over multiple seasons.

Acknowledgments

We thank the growers and land owners in Yolo County, California, who allowed us to work on their property. S. Kaiser, H. Wallis, S. Ambercrombie, and L. Swain assisted with the data collection, specimen processing, and data entry. The research was funded by an NSERC Postdoctoral Fellowship to L. A. Morandin, a Conservation Innovation Grant, a National Science Foundation grant, and a National Geographic Society Research and Exploration grant. Members of the Kremen Laboratory (UC–Berkeley) provided valuable comments on manuscript drafts. Pan and net collected pollinators were identified by R. W. Thorp (Henry B. Laidlaw Bee Biology Center; bee specimens) and M. Hauser (California Department of Food and Agriculture; syrphid fly specimens).

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SUPPLEMENTAL MATERIAL

Appendix

Native bee species collected off of flowers at control and hedgerow sites (aerial net collections) (*Ecological Archives* A023-041-A1).

Title:
Pest Control and Pollination Cost-Benefit Analysis of Hedgerow Restoration in a Simplified Agricultural Landscape

Journal Issue:
JOURNAL OF ECONOMIC ENTOMOLOGY, 109(3)

Author:
Morandin, LA
Long, RF
Kremen, C

Publication Date:
06-01-2016

Series:
UC Berkeley Previously Published Works

Permalink:
http://escholarship.org/uc/item/30r8x89m

DOI:
https://doi.org/10.1093/jee/tow086

Keywords:
hedgerow, pest control, pollination, economics

Local Identifier:
1604576

Journal of Economic Entomology Advance Access published May 11, 2016

Journal of Economic Entomology, 2016, 1–8
doi: 10.1093/jee/tow086
Research article

Apiculture & Social Insects

Pest Control and Pollination Cost–Benefit Analysis of Hedgerow Restoration in a Simplified Agricultural Landscape

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Received 23 November 2015; Accepted 30 March 2016

Abstract

Field edge habitat in homogeneous agricultural landscapes can serve multiple purposes including enhanced biodiversity, water quality protection, and habitat for beneficial insects, such as native bees and natural enemies. Despite this ecosystem service value, adoption of field border plantings, such as hedgerows, on large-scale mono-cropped farms is minimal. With profits primarily driving agricultural production, a major challenge affecting hedgerow plantings is linked to establishment costs and the lack of clear economic benefits on the restoration investment. Our study documented that hedgerows are economically viable to growers by enhancing beneficial insects and natural pest control and pollination on farms. With pest control alone, our model shows that it would take 16 yr to break even from insecticide savings on the US$4,000 cost of a typical 300-m hedgerow field edge planting. By adding in pollination benefits by native bees, where honey bees (*Apis mellifera* L.) may be limiting, the return time is reduced to 7 yr. USDA cost share programs allow for a quicker return on a hedgerow investment. Our study shows that over time, small-scale restoration can be profitable, helping to overcome the barrier of cost associated with field edge habitat restoration on farms.

Key words: hedgerow, pest control, pollination, economics

Simplified agricultural landscapes are highly productive, but have low biodiversity due to the large-scale monoculture cropping systems having limited surrounding natural habitat. This lack of natural habitat leads to a loss of ecosystem service benefits such as water filtration, natural pest control, and pollination. Potentially, this deficit also causes costly water quality impairments, greater pesticide use, and a higher demand for a limited supply of managed honey bee hives for pollination on farms (Zhang et al. 2007, Rusch et al. 2016). As a result, there is wide-spread concern that simplified agricultural systems are not sustainable (Tilman 1999, Millennium Ecosystem Assessment [MEA] 2005, Hobbs 2007, Jonsson et al. 2015).

Farmers are the primary land-use decision makers for agricultural landscapes, and their land-use practices are mostly based on direct economic returns rather than environmental and social concerns such as biodiversity enhancement and ecosystem service benefits (Jackson et al. 2007, Pascual and Perrings 2007). Resultantly, there has been poor adoption of agri-environment and biodiversity enhancement incentives by landowners and farmers (Burton et al. 2008, Griffiths et al. 2008, Brodt et al. 2009, Carvalheiro et al. 2011). To overcome this barrier and increase the likelihood that farmers will adopt on farm conservation practices, direct economic benefits of habitat plantings need to be shown (Pascual and Perrings 2007).

Research shows that biodiversity and other ecosystem services can contribute to economic benefits to farming systems, particularly in pollination and pest control, that are quantifiable (Morandin and Winston 2006, Dale and Polasky 2007, Chaplin-Kramer et al. 2011, Winfree et al. 2011, Blaauw and Isaacs 2014, Morandin et al. 2014). However, studies on the impact of restoration projects on crop yield and profit are rare, and there are no studies that integrate multiple economic benefits of pest control and pollination in cropping systems (Griffiths et al. 2008, Garibaldi et al. 2014). With economic benefits differing between ecosystems, crops, and type of habitat planted, this information is needed to help growers make informed decisions on costs and direct economic returns of specific restoration practices to minimize risks on their investments.

Our study focused on restored California native, perennial plantings on field crop edges (herein referred to as hedgerows) in California's Sacramento Valley. We assessed the combined economic benefits of pest control and pollination ecosystem services in adjacent crops, at sites with and without hedgerows on field edges. We included the cost of installation of a standard hedgerow planting in this region, benefits from the potential reduction in pesticide applications from natural pest suppression, and potential crop seed set increases from native bee enhancement due to farm-habitat restoration practices. These economic estimates were used to determine the net benefit of hedgerow plantings over time and how long it would take for the farmer to make a return on the investment.

Materials and Methods

The impact of field edge management on annual pollination and pest control services in adjacent crops was studied through a comparison of four hedgerow sites and four conventionally managed sites from 2009 to 2011. The study was in Yolo County, CA, an intensively farmed area with large-scale monoculture orchards and rotational field crops such as processing tomatoes and seed crops. The conventionally managed edges (herein referred to as controls) were mowed, disced, or sprayed with herbicides, but always had some residual vegetation with weeds germinating following the different management practices. The control edges represent the most common type of field edge in our study area, and during the cropping season, they generally are full of vegetation composed of mainly of nonnative grasses and nonnative flowering herbaceous plants. The hedgerows were planted about 10 yr prior to the study and consisted of mature California native, perennial shrubs and grasses including California buckwheat (*Eriogonum fasciculatum foliolosum*), California lilac (*Ceanothus griseus*), California coffeeberry (*Rhamnus californica tomentella*), Coyote brush (*Baccharis pilularis*), Elderberry (*Sambucus nigra*), and Toyon (*Heteromeles arbutifolia*) (Morandin et al. 2014). Each hedgerow field site was paired with a control site 1–3 km away, promoting independence of pollinator, pest, and natural enemy communities among sites, while maintaining treatments in similar landscapes and spanning the entire study area in all project years.

Hedgerow and control edges were ∼300–350 m long (or if longer, we used 350 m) that bordered 16 ha to 32 ha processing tomato fields each year. We choose tomatoes as our adjacent crop because they are one of the most common, high-value crops in the region (Yolo County Crop Report 2014), permitting us to obtain sufficient replication of mature hedgerows adjacent to the same crop each year. To control for differences in field management practices, paired hedgerow and control fields were managed primarily by the same farmer. The processing tomato crops were conventionally managed, with the exception of one organic farm, and all sites were monitored and treated with insecticides for pest control when needed.

Pest control studies were conducted in 2009 and 2010 and reported in Morandin et al. (2014). Pollination studies were conducted on sentinel canola (*Brassica rapa* L. v. Eclipse) plants placed in tomato fields in 2010 and 2011. This methodology was used because processing tomatoes do not need pollinators for fruit set and we could not find fields of pollinator-dependent crops adjacent to a sufficient number of hedgerows. Canola was selected because this plant increases fruit set in response to pollinator visits, shows minimal self-pollination, and is easy to work with for pollination studies (Morandin and Winston 2006).

Hedgerow Cost

The one-time fixed cost of installing a hedgerow and maintaining it for the first three years was estimated by Long and Anderson (2010) using data from the establishment of the same hedgerows examined in this study. Their cost estimate was based on a 305-m-long hedgerow with a single row of shrubs, forbs, and perennial grasses planted along a field crop edge. The estimate included materials and labor for site design, field preparation, plants, weed control, irrigation, and vertebrate pest control. The total cost estimate for establishment of a hedgerow including labor was US$3,847, which we rounded up to US$4,000 for our model. Some of the hedgerows in our study were part of the Environmental Quality Incentives Program (EQIP), a United States Department of Agriculture (USDA) federal government cost share program, which usually covers 50% of habitat establishment costs (http://www.nrcs.usda.gov/wps/portal/nrcs/main/wi/programs/financial/eqip/). We therefore included models that account for a 50% establishment cost reduction to the grower. The establishment cost for the conventionally managed field edge was considered to be zero.

Long and Anderson (2010) noted minimal additional upkeep costs for hedgerows beyond the first three years of establishment that included mowing and herbicide use for weed control. As conventionally managed control field edges require similar yearly maintenance, in calculating differences between costs and benefits of the two edge types, we did not include a yearly upkeep cost in our model. We did not include crop losses due to a reduction in crop acreage as in our study area, hedgerows are planted on field edges and do not take land out of production. In addition, hedgerows of shrubs and grasses generally do not get big enough to cause adjacent crop losses due to competition for resources, so there was no need to include potential losses from factors such as shading.

Valuation of Pest Control Services

In 2009 and 2010 growing seasons, we monitored key pest species of processing tomatoes using University of California Integrated Pest Management guidelines (http://www.ipm.ucdavis.edu/PMG/C783/m783yi01.html). Pests included potato aphids (*Macrosiphum euphorbiae* (Thomas)), stink bugs (*Euschistus conspersus* (Uhler) and *Thyanta pallidovirens* (Stål)), tomato fruitworm (*Helicoverpa zea* (Boddie)), western flower thrips (*Frankliniella occidentalis* (Pergande)), and armyworms (*Spodoptera* spp.). Three times each season, from tomato bloom until shortly before harvest, we examined populations of pests, pest damage on leaves, and their economic control threshold levels. During the second and third crop assessments, we also quantified damage to fruit and pests on fruit. We conducted assessments at 10, 100, and 200 m along two transects into fields from field edges for a total of six sample locations in each field.

To estimate the economic benefit of hedgerows for natural pest control, we evaluated the difference between pest control costs with and without hedgerows in the proportion of fields that reached threshold pest or damage levels requiring control by insecticides as follows:

$$P_{PC} = \sum_{S=1}^{n} (W_S - H_S) C_S \qquad (1)$$

Where P_{PC} is the average profit increase, in dollars, attributed to having a hedgerow adjacent to the field, W_S is the proportion of fields with conventionally managed edges, and H_S is the proportion of fields with hedgerow plantings that had pest populations or damage for species S at or above the recommended treatment threshold. C_S is the average cost for insect pest control for a typical processing tomato field in our study area, for pest species S (Miyao et al. 2008). In our model, revenues were considered the same between fields, with growers having set contracts and prices paid per ton of tomatoes by the industry.

Valuation of Pollination Services

Measurements of pollination limitation (herein referred to as seed deficit) can be used to estimate profits resulting from differences in ambient pollinator populations among sites (Morandin and Winston 2006). To determine the impact of field edge management on crop pollination, we calculated proportional seed set deficit due to pollen limitation at four hedgerow and four control sites in 2010 and 2011 using sentinel canola plants in adjacent tomato fields. This approach isolated the effect of pollinators on seed yield by field edge treatment, which otherwise would vary due to factors such as crop type and field management practices.

We used 32 potted canola plants per site, in clusters of four placed along the two transects, as described in the pest control services section, at 0, 10, 100, and 200 m into the field for both hedgerow and control sites. We manually cross-pollinated two–three flowers on each plant to achieve maximum pollination and left three–four flowers on each plant open for pollination from ambient pollinator populations (Morandin and Winston 2006). In 2010, canola plants were placed in tomato fields for 5 h, and we conducted one, 4-min pollinator observation on each cluster of plants. In 2011, plants were in fields for 2.5 d and we conducted four, 4-min observations on each cluster (two on each of 2 d). During visual observations, we recorded all flower visitors that touched the reproductive parts (anther and stigma) of any mature flower in the cluster. The different types of flower visitors were recorded in citizen scientist monitoring (CSM) categories described in Kremen et al. (2011).

To measure pollination limitation, seed deficit was calculated at each location (location was defined as one set of four plants at each distance into each field) as the mean number of seeds per fruit from manually cross-pollinated fruit minus mean seeds per fruit from open-pollinated flowers, divided by full potential seed set at each location. Full potential seed set at each location was the mean of either seeds from manually cross-pollinated or open-pollinated flowers, whichever was greater (maximum seed set at that location). A greater difference in seed number between open and manually pollinated flowers indicated a greater degree of pollen limitation. If open-pollinated flowers resulted in pods with at least the number of seeds as fruit from manually cross-pollinated flowers, a zero pollination deficit was recorded, as a negative proportional seed deficit value is not meaningful.

Because native bees are the most important unmanaged crop pollinator (Klein et al. 2007, Garibaldi et al. 2013), and can be enhanced in adjacent fields by the presence of farm habitat restoration (Morandin and Kremen 2013, Garibaldi et al. 2014), we first calculated pollination differentials with all floral visitors. We then calculated pollination deficit differences due only to differences in native bee abundance, removing the contribution of honey bees and syrphid flies to discern the impact of native bee pollinators between our hedgerow and control field edge management practices. Bees considered native in our study, may not all have been native. In a previous study in the same region (Morandin and Kremen 2013) where we identified bees to species, ~2% of the non*Apis* bees were nonnative, naturalized species. In this study, the percent of nonnative, naturalized species in our native bee category likely was similarly low, and we therefore use the term native bee throughout.

In 2010, canola plants were in fields for only 5 h. By contrast, in 2011, plants were in fields for the life of the flower, allowing us to measure visitor abundance and seed deficit when most flowers were fully pollinated. To calculate the relationship between observed pollinator visitation and pollination deficit, we used the 2010 and 2011 data. We determined the relationship between floral visitor abundance and seed deficit using nonlinear regression of proportional seed deficit (bound at zero) on total number of pollinators observed at each location.

Using the estimated total floral visitor abundance and the relationship between visitor abundance and seed deficit (nonlinear regression), we then calculated an estimated seed deficit for the 2010 data, if the plants had been left out for the total flower life. We calculated regressions between the number of flower visitors observed in the first 4-min observation in 2011 to the total observed in 2011, over all four 4-min observations (one regression for each of the six CSM categories, at each site type) and used the regression equations to calculate estimated total floral visitor abundance, from each CSM category, for the 2010 data.

In order to observe the contribution of seed set from native bee pollinators, independent of honey bees and syrphid flies, we first determined pollination efficiency of each pollinator group. Contribution to seed set from one visit of each floral visitor group was experimentally determined in 2012 using methods outlined in Kremen et al. (2002). We set out potted canola (*B. rapa* v. Eclipse) plants at sites known to have high bee abundance and diversity. The evening prior to bringing plants out to the site, flower buds that were ready to open the next day were bagged with mesh bags. At the site the next day, observers removed bags on two–three flowers at a time, and observed these flowers until a pollinator had contacted the reproductive parts of the flower. Immediately after the pollinator left the flower, the flower pedicel was marked with acrylic paint in a color unique to that pollinator group (CSM group), and the baggie was carefully placed over the flower so that the flower was disrupted as little as possible and no parts of the baggie touched the flower. Plants were left undisturbed (other than periodic watering) for 2 d, so as to not move plants while experimental flowers were still in bloom. Approximately 20 d later, pods were harvested and seeds counted.

We compared these seed set values and if any were significantly different from average seed set, we used these seed set values to weigh relative contribution of each group when we removed a group from the pollinator deficit model. Because seed set contribution of each group did not differ ($F_{5,288} = 0.11$, $P = 0.99$), we did not include a pollinator efficiency in the model. We factored out estimated contribution of honey bees and syrphid flies to seed set at each location by subtracting their observed (2011 data) or estimated (2010 data) visits.

We used R Core (Team 2013) and lme4 (Bates et al. 2012) to perform a linear mixed effects analysis of the relationship between proportional seed deficit (arcsine-square-root transformed) and field type (control or hedgerow). Field type and distance were entered as fixed effects, and site and year as random effects. *P*-values were obtained by likelihood ratio tests of the full model with field treatment (hedgerow or control edge) against the model without field treatment. Proportional differences in seeds were used rather than absolute differences in seed number between open and manually pollinated flowers because maximal seed set may have varied among fields due to factors other than pollination, such as differences in microclimate and field conditions. If mean proportional seed deficit (calculated using 1. all floral visitors and 2. only native bees) was significantly different between site types, we then calculated the difference between the mean proportional increase in seed set (*PI*) due to the presence of a hedgerow, as average PI at control sites minus PI at hedgerow sites. We expected hedgerow sites to have lower proportional seed deficit values than control sites, leading to $PI > 0$.

Assuming costs were held constant between the two treatments, we translated PI into profit change per unit area:

$$P_P = MV \times Y \times PI \qquad (2)$$

Where P_p is the estimated change in profit ($) with a 305-m hedgerow, resulting from a change in seed set, MV is the market value per ton of the crop, and Y is the average yield per unit area (tons).

Economic Cost–Benefit Model Synthesis for Pest Control and Pollination

Using the insecticide treatment reduction and pollination increase data, we created a cost–benefit model for a hedgerow installation bordering two typical, 16-ha crop fields (one on each side). We have observed that it takes ~3 yr before plants are mature with floral resources, and therefore, net benefits were calculated starting at $Y > 3$. Estimated economic benefit to growers for establishing hedgerows, for each year (Y) after the third year of establishment was calculated as:

$$B_Y = \left\{\sum_{Y=4}^{Y}\left[\frac{(P_P + P_{PC})}{1.05^Y}\right]\right\} - C \qquad (3)$$

Where B_Y is the estimated net economic benefit in dollars per field at Y years, starting at $Y = 4$, from the time of initial restoration, P_p is the mean profit increase resulting from differential pollination deficit, between control and hedgerow sites, P_{PC} is the average profit change attributed to having a restored hedgerow adjacent to the field for pest control, and C is the cost of establishing and maintaining a 305-m hedgerow for the first three years. We took into account the time value of money (i.e., that money available now is worth more than the same amount in the future), and the uncertainty of future returns by applying a discount rate of 5%, such that profit each year was divided by 1.05^Y.

Results

Valuation of Pest Control Services

In 2009, one tomato field in the control group was treated for aphids. In 2010, three control fields and one hedgerow field reached the threshold for aphid treatment in our assessments. In total therefore, four of the eight control tomato fields and one of the eight hedgerow tomato fields reached thresholds and were treated for aphids. Using an average cost of one treatment for aphids of US$43.24/ha (Miyao et al. 2008), it would cost ~US$692 to treat a 16-ha field for aphids. With 4/8 or half of control fields needing treatment, that equals an average cost of US$346 per control field. When only 1/8 hedgerow fields require treatment for aphids, average costs for aphid control on hedgerow fields is US$86, 75% less per field than control fields. Although we sampled 200 m into fields from hedgerows, we calculated potential savings to a 16-ha field (400 by 400 m^2), as there was no decline in pest suppression of aphids up to the distance we measured (200 m from hedgerows; Morandin et al. 2014).

Few pests, other than aphids, were observed in our tomato fields at economic treatment threshold levels in the years of this study. Some fields were treated with sulfur for tomato russet mites (*Aculops lycopersici* (Massee)); however, we did not include this in our model because these mites are not effectively controlled by natural enemies and therefore their populations would not be impacted by the presence of hedgerows (University of California Integrated Pest Management [UC IPM] 2013).

Valuation of Pollination Services

The number of replicated pollinator visits for the canola pollination efficiency study was between 31 and 83 for all groups except the CSM group, "small dark bees" which only had 12 replicate visits. Pollination efficiency of each group, based on seed set from one visit from an individual of that group (number in brackets is average seeds per pod from one visit), was honey bees (3.0), syrphid flies (3.1), striped sweat bees (3.0), tiny dark bees (2.6), small dark bees (2.8), and hairy legged bees (2.9), with no significant differences between any group ($F_{5,288} = 0.11$, $P = 0.99$; Table 1).

In the studies with sentinel canola plants in the crop fields, there was no difference in total abundance of visitors on *B. rapa* flowers between hedgerow and control sites (Fig. 1). However, there was a greater abundance of native bees observed on *B. rapa* plants at hedgerow than control sites ($F_{1,14} = 26.06$, $P = 0.0002$). Because overall floral visitor abundance was not different between field types, we did not see differences in seed set between fields with and without hedgerows. We used the relationship between floral visitors and seed set to estimate seed set differences due to differences in native bee abundance differences. The best-fit relationship between observed floral

Table 1. Mean seeds per pod (±SE) from one floral visit by each pollinator group on canola, *B. rapa*

Pollinator group[a]	Average seeds per pod from one floral visit (±SE)	No. of replicates
Honey bees	3.0 ± 0.39	60
Syrphid flies	3.1 ± 0.43	54
Striped sweat bees	3.0 ± 0.41	54
Tiny dark bees	2.6 ± 0.28	83
Small dark bees	2.8 ± 0.82	12
Hairy legged bees	2.9 ± 0.52	31

Pollinator efficiency was not significantly different among groups, $P = 0.99$.

[a] The different types of flower visitors were recorded in CSM categories described in Kremen et al. (2011).

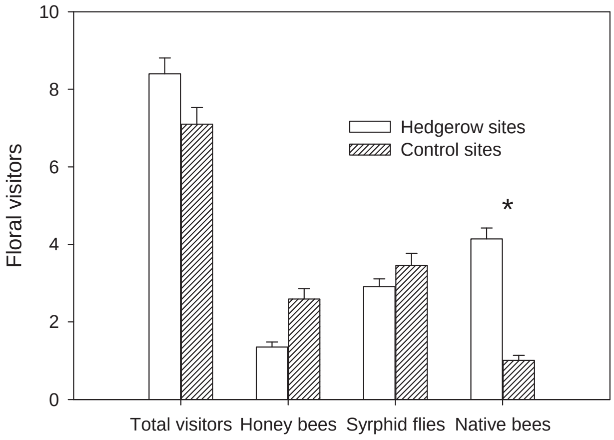

Fig. 1. Mean floral visitors (+SE) observed during 4-min visual observations on *B. rapa* sentinel canola plants in processing tomato fields adjacent to hedgerows or control (conventionally managed) field edges. Stars above a pair of bars indicate a difference in abundance for that group between treatments ($P < 0.05$).

visitors and seed deficit was an exponential decay equation: $y = 0.45\exp(-0.128x)$ ($R^2_{adj} = 0.42$, $F_{1,118} = 77.1$, $P < 0.0001$; Fig. 2).

Crop yields vary widely based on agronomic conditions; however, we used an average yield of 1,200 kg/ha and the 2011–2012 average value of canola seed at US\$600/ton (US\$0.60/kg) to calculate an average value from canola production of US\$720 per hectare (http://www.canolacouncil.org/markets-stats/statistics/). Input costs for non-GM canola were ~US\$300/ha resulting in a net profit of ~US\$420/ha.

When we removed the estimated seed set resulting from honey bee and syrphid fly visits, field treatment (hedgerow or control edge) affected proportional seed deficit ($\chi^{2(1)} = 10.5$, $P = 0.001$). Using the mean values for seed deficit considering only native bees ($PI = 0.21$), there was a 21 ± 4.9% (standard error) seed increase at hedgerow sites due to enhanced native bee populations. Therefore, if a hedgerow were present, greater pollination from enhanced native pollinator populations would increase yields 21% to 1,452 kg/ha and a net profit of US\$571/ha, which represents a US\$151 profit increase, per hectare, over no hedgerows. As in Morandin and Winston (2006), we acknowledge that harvest and transport costs could increase slightly with greater yield; however, this likely would be a small amount and we do not factor it in.

Using the above values, profit from a 16-ha canola field with a conventional edge would be US\$6,720. With the pollination increase from native bee enhancement by hedgerows (in an area with no managed honey bees or other effective pollinators), profit would be increased on a field by US\$151/ha (from US\$420/ha to US\$571/ha, or 36% increase) resulting in a profit increase of US\$2,416 per 16-ha field.

Overall profit therefore, from the combined benefits of increased pollination and fewer pest control treatments over time will help offset the costs of a 305-m hedgerow plantings as shown in Fig. 3. Scenario 1 shows the benefits from reduction in insecticide treatments alone each year (either no pollinator-dependent crops in the rotation or managed honey bees in the system provide all pollination needs). Scenario 2 is identical to scenario 1 but includes a 50% USDA EQIP cost share program. Scenario 3 depicts benefits from reduction in insecticide treatments each year and enhanced pollination in a pollinator-dependent crop every 3 yr. Like Scenario 2, Scenario 4 is identical to Scenario 3, but includes a 50% USDA EQIP cost share program.

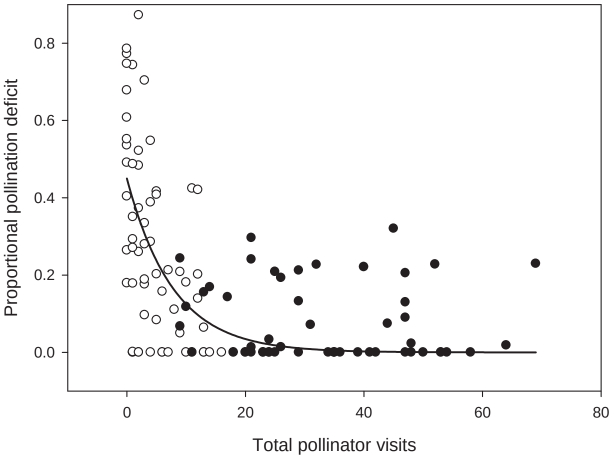

Fig. 2. Relationship between pollination deficit (maximal seed set minus open seed set, divided by maximal seed set at each grouping of four canola plants) and the observed abundance of floral visitors (honey bees, native bees, and syrphid flies) on *B. rapa* at four fields with hedgerows and four fields with conventionally managed edges (control) in each of two years, 2010 (open circles) and 2011 (closed circles).

Discussion

All of our hedgerows or control edges had crops on either side of them, usually with both fields owned by the same grower, and therefore we modeled benefits to two, 16-ha fields on either side of the hedgerow. Due to crop rotations, we modeled a situation in which the adjacent crops would benefit from natural pest control services and a reduction in insecticide use every year (at the rate calculated for a processing tomato field although the benefit could be greater or less depending on the actual crop present). The enhanced profit from native bee enhancement would only be realized if pollination was deficient prior to native hedgerow installation, unlikely if managed honey bees or other pollinators such as syrphid flies were abundant in the area and efficient pollinators of the crop (such as in our case where there were abundant managed honey bees and syrphid flies, both efficient pollinators of *B. rapa*). Therefore, Scenarios 1–2 (Fig. 3) account for hedgerow installation cost return from reduced pest control costs only, and assume either crops that do not benefit from pollination or a situation where pollination is saturated already from wild and or managed pollinators.

However, as has often been shown to be the case in simplified agricultural landscapes, pollination is a limiting factor to seed set (Kremen et al. 2002, Long and Morandin 2011, Klein et al. 2012), and seed set is increased in the presence of enhanced native bee populations (Klein et al. 2003, Kremen et al. 2004, Morandin and Winston 2006). In addition, with current uncertainty in managed honey bee supply, it is important to understand input of native bees and ways to

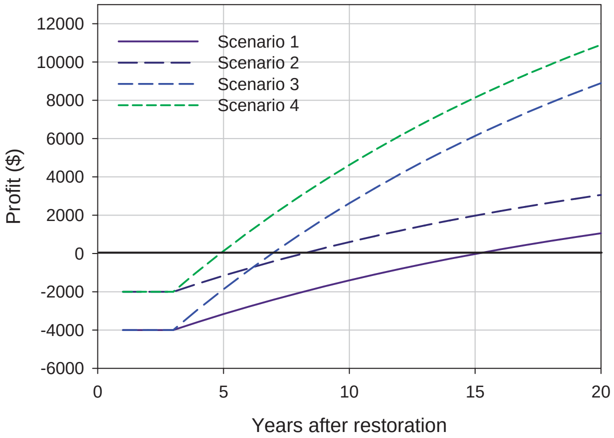

Fig. 3. Discounted profit (US\$ 1.05% discounted rate per annum) from installation of a 305-m hedgerow of native California flowering plants on a field crop edge, calculated from the cost of installation and potential cost savings incurred from hedgerows from reduction in insecticide application and pollination benefits from natural enemies and pollinators. Scenario 1: benefits from reduction in insecticide treatments alone each year (either no pollinator-dependent crops in the rotation or managed honey bees in the system provide all pollination needs). Scenario 2: same as Scenario 1 but with a 50% USDA EQIP cost share program. Scenario 3: benefits from reduction in insecticide treatments each year and enhanced pollination in a pollinator-dependent crop every 3 yr. Scenario 4: same as Scenario 3 but with a 50% USDA EQIP cost share program. We do not show a potential for cost benefit from reducing the number of honey bee hives needed for pollination. However, a grower could also gain from the enhancement of native bees if they needed to rent fewer honey bee hives. Hedgerows were planted on field borders, so there was no loss in crop production. (Online figure in color.)

enhance their populations and pollination contribution to add resilience in cropping systems (Garibaldi et al. 2011, Winfree 2013, M'Gonigle et al. 2015). This information is vital because recent overwintering losses of managed honey bee colonies in many parts of the world (vanEngelsdorp et al. 2009, Neumann and Carreck 2010) and a 300% increase in the proportion of crops requiring pollination (Aizen and Harder 2009) has resulted in uncertainty as to whether managed honey bees can meet future global crop pollination requirements. Furthermore, a recent data synthesis found that crop yields around the world are responsive to increases in native pollinator visitation rates but not to increases in honey bee visitation rates (Garibaldi et al. 2013). Syrphid flies were also efficient pollinators of the canola plants in our study, but we did not include them in our cost–benefit model because their numbers are highly variable from year to year in California, so cannot be relied on for crop pollination (N. M. Williams, personal communication). In addition, abundances in fields are not affected by the presence of hedgerows (Morandin and Kremen 2013). Their somewhat greater abundance in control fields than in fields adjacent to hedgerows in our study was likely due to greater aphid abundance in control fields (Morandin et al. 2014).

In Scenarios 3–4, we show economic benefit of hedgerows if crop rotations include pollinator-dependent crops and managed honey bees in the system do not provide all pollination needs. We factored in the pollination benefit only once every third year, to account for crop rotation of nonpollinator-dependent crops two out of three years, by reducing the pollination enhancement benefit by 1/3rd each year on both sides of the hedgerow. Although not significant, visual inspection of a boxplot of the interaction between distance and treatment on seed deficit showed a slight increase in seed deficit at hedgerow sites at the 100 and 200 m distances (still significantly lower than at control sites that had constant seed deficit at all distances). To keep our cost return estimates conservative, we therefore only applied the pollination benefit to the first 200 m of the field (8 ha).

We did not include potential reduction in cost of honey bee hive rental in our profit equations for the scenarios where managed honey bees are abundant in the landscape because of the inability from our data to make accurate predictions in the amount of reduction in hive rental that would be possible from enhancement of native bees with hedgerow restoration. However, hive rental reduction could greatly increase profit from hedgerows.

Cost return, using a 5% discount rate per year, to the grower in this case would take about 16 yr if the grower paid for the full amount of the hedgerow with only the savings that we observed from reduced insecticide application (Fig. 3). However, with a 50% cost share such as EQIP, a grower would break even in costs and return at ~9 yr postinstallation, less than the age of the hedgerows in this study. Thus, in situations where pollinator-dependent crops are not within the rotation, based on insecticide application savings calculated for processing tomato, growers likely will recuperate their initial investment in hedgerow restoration, especially when a cost-share program is used. When we modeled a situation in which we exclude pollinators other than native bees, simulating an environment with no managed pollinators or efficient pollinators other than native bees, cost return times decrease substantially to 5 yr and 7 yr (with and without cost-share programs, respectively).

This cost–benefit model is a starting point for valuing the economic benefit of multiple ecosystem services resulting from on-farm restoration in highly simplified agricultural landscapes. The value could be an over or under estimate for multiple reasons. These values could be underestimates of benefits of hedgerows to growers because costs can be comprehensively estimated, while total benefits are multifaceted and comprehensive estimation is beyond the scope of any one study (Olson and Wackers 2007). Specifically, we have not valued the impact of natural enemies on multiple pests in tomatoes. For example, we conducted a sentinel stink bug egg parasitism experiment in order to assess differences in parasitism between control and hedgerow sites (Morandin et al. 2014). We found greater parasitism up to 100 m into hedgerow sites than control sites. However, from this experiment, it was not possible to extrapolate to direct economic impact and cost savings from reduced pesticide use because stink bug levels remained below economic treatment thresholds during the years of this study. Also, there is the potential that enhancement of native bee populations may reduce the need for honey bee hive rental, a possible important savings with high rental costs and supply uncertain due to honey bee health issues. Further, some crops, in some areas, may benefit more from pollination enhancement by native bees and pest control than the crops and location that we used to create this model. And finally, other ecosystem services potentially provided by hedgerows, such as water quality enhancement through filtration of sediments and other pollutants, are not part of this study.

Our economic analysis could also be an overestimate in agroecosystems with crops where pest control protocols are preemptive rather than dictated by pest levels in individual fields, such as when insecticides are applied prophylactically as in neonicotinoid seed treatments (Douglas and Tooker 2015). This problem could be mitigated if more growers and pest advisers used IPM protocols and pest threshold levels when making pesticide use decisions on crops. Overestimates may also occur in agroecosystems with few crops that require or benefit from pollination services or have their pollination needs met with managed honey bees.

We may also be overestimating the pollination impacts by using sentinel canola plants and scaling up to whole field crop systems. In using sentinel canola plants within a pollinator independent tomato crop, the canola may have concentrated available pollinators, which could lead to overestimation of the pollination service when scaled up to the field scale. The same number of pollinators, spread over a much larger field of canola, might have a much smaller effect on pollination. In addition, manual pollination can result in a greater number of seed and seed size, requiring a greater allocation of plant resources, resulting in an overestimate of pollination limitation (Zimmerman and Pyke 1988, Knight et al. 2006). However, Morandin and Winston (2005) found there was no decline in seeds per fruit in open-pollinated canola (*B. rapa* and *B. napus*) compared with manually cross-pollinated flowers, so we do not believe this was the case for our study.

Our research demonstrated that small-scale restorations can be cost effective, and provide profit to land owners in simplified agricultural landscapes. Using this, or similar models, data on pollination and pest control service enhancement from hedgerow or other habitat augmentation on multiple crops can be used to calculate cost return times and profit in a variety of situations for growers. In addition, other ecosystem service benefits could be added to these cost–return calculations. While the data derived from our study area in Yolo County, CA, show revenue after 5 to 16 yr, the cost–benefit model can vary depending on local conditions, including farm management and crop rotations (Sardiñas and Kremen 2015). As a result, more long-term monitoring of crop yield, pollination levels, and pest populations on farms with and without hedgerows are needed. This model is a starting point for evaluating multiple ecosystem service benefits and economic return of within farm habitat enhancement to help minimize risks of investments. It can be applied to any agroecosystem where pest, natural enemy, and pollinator abundances are impacted by farmland habitat restoration.

Acknowledgments

We thank our grower cooperators for allowing us to work on their farms. We thank S. Kaiser, H. Wallis, S. Ambercrombie, L. Swain, and R. Hanifin for assistance with data collection, specimen processing, and data entry, and K. Steinmann for advice on the manuscript. The research was funded by an NSERC Postdoctoral Fellowship to L.A.M., a Conservation Innovation Grant to C.K. and the Xerces Society, National Science Foundation grant (DEB 0919128) and a National Geographic Society Research and Exploration grant to L.A.M. and C.K.

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Global Change Biology

Global Change Biology (2015), doi: 10.1111/gcb.13117

On-farm habitat restoration counters biotic homogenization in intensively managed agriculture

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Abstract

To slow the rate of global species loss, it is imperative to understand how to restore and maintain native biodiversity in agricultural landscapes. Currently, agriculture is associated with lower spatial heterogeneity and turnover in community composition (β-diversity). While some techniques are known to enhance α-diversity, it is unclear whether habitat restoration can re-establish β-diversity. Using a long-term pollinator dataset, comprising ~9,800 specimens collected from the intensively managed agricultural landscape of the Central Valley of California, we show that on-farm habitat restoration in the form of native plant 'hedgerows', when replicated across a landscape, can boost β-diversity by approximately 14% relative to unrestored field margins, to levels similar to some natural communities. Hedgerows restore β-diversity by promoting the assembly of phenotypically diverse communities. Intensively managed agriculture imposes a strong ecological filter that negatively affects several important dimensions of community trait diversity, distribution, and uniqueness. However, by helping to restore phenotypically diverse pollinator communities, small-scale restorations such as hedgerows provide a valuable tool for conserving biodiversity and promoting ecosystem services.

Keywords: β-diversity, bees (Hymenoptera: Apoidea), community assembly, ecological filter, pollinators, trait diversity

Received 22 June 2015; revised version received 30 August 2015 and accepted 24 September 2015

Introduction

Widespread conversion of natural ecosystems to agriculture, combined with intensification of farming practices, is causing major declines in biodiversity globally (Tilman et al., 2001; Green et al., 2005; Tscharntke et al., 2005). Agriculture is particularly associated with the homogenization of biological communities (Gabriel et al., 2006; Clough et al., 2007; Hendrickx et al., 2007; Vellend et al., 2007; Ekroos et al., 2010; Flohre et al., 2011). The turnover of species through space and subsequent heterogeneity of community composition (β-diversity) is a primary determinant of the total species diversity present in a landscape (Flohre et al., 2011). Thus, by homogenizing communities, agriculture can act to reduce biodiversity on both local and regional scales (Hendrickx et al., 2007; Ekroos et al., 2010; Flohre et al., 2011).

Spatial heterogeneity in community composition can be influenced by a variety of deterministic (niche-based) and stochastic (neutral) processes. Species are thought to 'deterministically' track the biotic and abiotic conditions to which they are adapted and, in a heterogeneous environment, this will contribute to the spatial structuring of communities (Whittaker, 1960; Condit et al., 2002; Chase, 2007; Püttker et al., 2014). Stochastic processes, such as priority effects or rare long distance dispersal events, can then amplify or weaken these signals (Condit et al., 2002; Chase, 2003; Püttker et al., 2014).

Ecological filters are one deterministic process that can shape community assembly because only species with particular sets of physical, functional, and life-history traits are able to persist (Chase, 2007; Püttker et al., 2014). The diversity and distribution of ecological filters in a landscape contributes to spatial heterogeneity. By reducing the diversity of filters, habitat homogenization (e.g., the conversion of complex landscapes into simplified landscapes such as monocultures) can reduce β-diversity and species' trait diversity (Chase, 2007; Püttker et al., 2014).

The loss of species and/or species trait diversity that can result from conventional monoculture agriculture may also compromise the provisioning of important ecosystem services such as pollination, pest control, and nutrient cycling (Tscharntke et al., 2005; Kremen & Miles, 2012). Currently, our agricultural system compensates for these lost ecosystem services by increasing external inputs (Kremen et al., 2012), which can have unwanted negative consequences on both humans and wildlife (Eskenazi et al., 2007; Gill et al., 2012). The negative ramifications of high-input agricultural systems have fostered the development and refinement of

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agricultural techniques that minimize external inputs by utilizing and regenerating ecosystem services (Kremen & Miles, 2012; Kremen et al., 2012). Through local and landscape-scale diversification of crops and habitat, these techniques seek to promote biological interactions that lead to better provisioning of ecosystem services. Such systems also support higher local biodiversity (Hole et al., 2005; Gabriel et al., 2013; Gonthier et al., 2014; Tuck et al., 2014) and spatial heterogeneity in community composition (Gabriel et al., 2006; Clough et al., 2007) than conventional monoculture agriculture. Particularly, techniques that foster landscape-level diversification by maintaining or restoring fragments of natural habitat have been shown to be effective in supporting greater numbers of species and the ecosystem services that they provide (Ricketts et al., 2008; Garibaldi et al., 2011; Kennedy et al., 2013) while also increasing community level β-diversity (Kehinde & Samways, 2014). However, if landscape diversification reduces yields, it may lead to further extensification, harming biodiversity (land-sparing argument Ref. Phalan et al., 2011). Recent work suggests that land-sparing arguments promoting intensive, simplified agriculture are over-simplified (Kremen, 2015), because such forms of agriculture often also lead to extensification (Meyfroidt et al., 2014).

In the most simplified agricultural areas, natural habitat is nearly nonexistent. In some cases, farmers have adopted the habitat restoration technique by planting strips of native plants along farm edges (hedgerows) to help diversify the landscape, without removing arable land from production. Hedgerows have been shown to support higher diversity and abundance of various ecosystem service providers, including beneficial insects, and birds (Hinsley & Bellamy, 2000; Bianchi et al., 2006; Hannon & Sisk, 2009; Morandin & Kremen, 2013; Morandin et al., 2014). It remains unclear, however, whether they mimic natural habitat by re-creating spatially structured communities, by leading to higher β-diversity. In addition, communities with diverse traits can provide higher quality and more stable ecosystem services (Klein et al., 2009). Thus, if hedgerows maintain the spatial heterogeneity of communities at different hedgerows by supporting species with a diversity of traits, they may promote the provisioning of ecosystem services such as pollination in agricultural areas (Klein et al., 2009). Understanding whether simple restoration interventions such as hedgerows can counter biotic homogenization when replicated across a landscape will be critical in assessing their value for ecosystem service provision and biodiversity conservation.

Focusing on pollinators, key ecosystem service providers (Klein et al., 2007), here we ask whether hedgerows support more spatially rich communities with more diverse suites of species traits. We do so using a long-term dataset from the highly simplified and intensively managed agricultural landscape of California's Central Valley. We also identify which mechanisms are likely responsible for driving the spatial trends we find. Specifically, we uncover the processes leading to the observed patterns in pollinator β-diversity and, further, investigate whether there is evidence that pollinator species track biotic and abiotic resources. Lastly, we test whether simplified agriculture imposes an ecological filter on insect pollinators by favoring species with particular set of traits. In our study landscape, hedgerows augment the richness and abundance of pollinators (Morandin & Kremen, 2013) and the occurrence, persistence, and colonization of both resource generalists and specialists (Kremen & M'Gonigle, 2015; M'Gonigle et al., 2015), while also exporting pollinators into agricultural fields (Morandin & Kremen, 2013). Understanding whether hedgerows support spatial heterogeneity of communities is the next step toward understanding whether they can conserve biodiversity and promote the provisioning of ecosystem services in agricultural areas.

Materials and methods

Study sites and collection methods

We surveyed pollinators from 21 hedgerow sites and 24 unrestored control sites, located in the Central Valley of California in Yolo, Colusa, and Solano Counties (Fig. 1). This is an intensively managed agricultural area dominated by monocultures of conventional row crops, vineyards, and orchards. The monitoring sites represent a sample of field margin conditions across the northern Central Valley. Hedgerows, which consist of native, perennial, shrub, and tree plantings (Morandin & Kremen, 2013), are ca. 3–6 m wide and approximately 350 m long and border large (ca. 30-hectare) crop fields. They are typically planted along field margins where they do not remove valuable land from production. Hedgerows differ in age from newly established, 'maturing' (1–10 years postplanting) to 'mature' (established >10 years ago). By investigating hedgerows at different stages of maturity, we can determine whether the effects of hedgerows on β-diversity accumulate with hedgerow maturation. We also monitored unrestored control sites which are weedy edges that represent a variety of relatively unmanaged field edges found in the region. Control sites were selected to match conditions surrounding the hedgerow sites. For each hedgerow, we selected 1–2 unrestored controls adjacent to the same crop type (row, orchard, pasture, or vineyard), within the same landscape context. The crop fields adjacent to hedgerows and controls were similarly managed as intensive, high-input monocultures. The mean distance between monitoring sites was 15 km, and

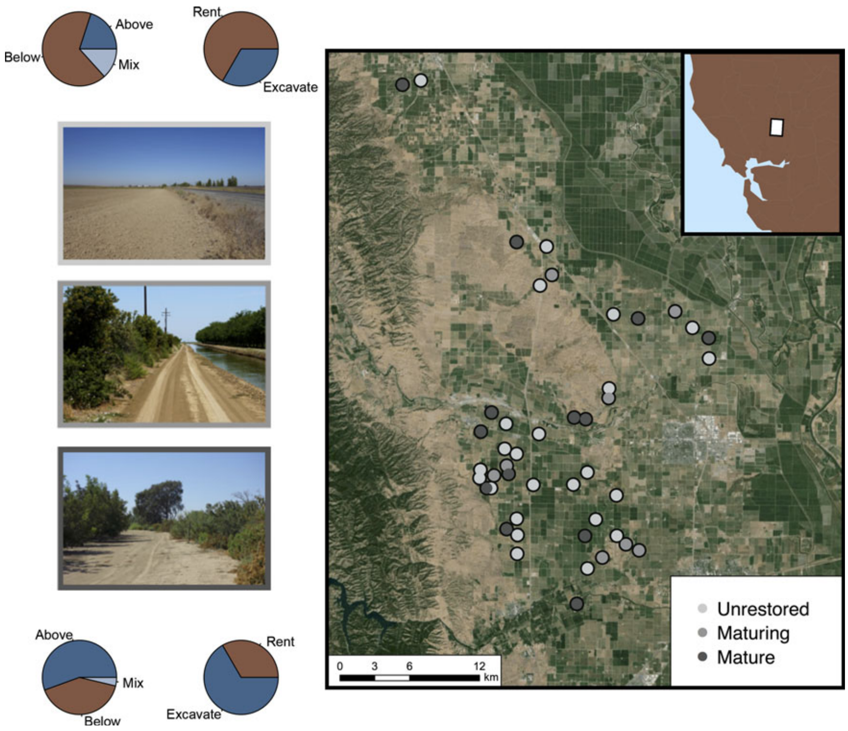

Fig. 1 Location of hedgerow and unrestored control sites in California (inset) and surrounding landcover. Pie charts represent the selected trait makeup of species found only at controls (top) or hedgerows (bottom). The left pie charts represent the nest location of the species, and the right charts depict the nest construction behavior.

the minimum distance between sites of the same type sampled in the same year was 2 km. The entire area surveyed spanned almost 300 km^2.

We sampled pollinator communities between April and August each year from 2007 through 2013 (Tables S1 and S2). Sites were sampled between two and five times per year (Tables S1 and S2).

In each round of sampling, the order in which sites were sampled was randomized. Surveys were conducted under sunny conditions when the temperature was above 21 °C and wind speed was below 2.5 m s^{-1}. Flower visitors to plants in hedgerows and unrestored controls were netted for 1 h of active search time (the timer was paused when handling specimens). All insect flower visitors that touched the reproductive parts of the flower were collected; however, here we focus only on wild bees, the most abundant and effective pollinators in the system (C. Kremen, A. Klein, and L. Morandin, unpublished data). Bee specimens were identified to species (or morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*) by expert taxonomists.

Surveys of the biotic and abiotic conditions were also conducted at each site throughout the flight seasons of the pollinators. At each site, each flowering plant in 50, one meter quadrats along the length of the hedgerow or control site was identified to species or morpho-species. The abundance of each plant species was estimated as the mean number of quadrats a species was present in, each year. In addition, in 2011 and 2012, we used the same quadrats to evaluate the physical characteristics of the site including the amount of vegetative cover and uncultivated, bare ground.

Diversity estimates and statistical analysis

To estimate the species turnover between sites of the same type (i.e., unrestored controls, maturing hedgerows, or mature hedgerows), we used the variance in community composition as a measure of β-diversity (i.e., multivariate dispersion, see Section for details, 2,3). To calculate this metric, we first calculated the pairwise dissimilarity between sites within each year of the dataset using a dissimilarity estimator that incorporates species abundances, while also accounting for unobserved species (Chao et al., 2005).

Dissimilarity estimates can be affected by the total number of species and individuals sampled at a site (Chase et al., 2011; Kraft et al., 2011). For example, sampling from a fixed species pool, the probability that two sites do not share any species is higher when there are few individuals at those sites. Confounding sampling effects and species turnover can yield misleading results (Chase et al., 2011; Kraft et al., 2011). By extending the method described by (Chase et al., 2011) to include estimates of species' abundances, we used null models to estimate the deviation of the observed dissimilarity from that which would be expected under a completely random community assembly process (see Section for details). With the corrected dissimilarity values, we then calculated the multivariate dispersion of communities as the variability in species composition within a site type (see Section for details, Anderson et al., 2011).

To investigate effects of site type, the β-diversity estimates were used as the response variable in a linear mixed model with site type (unrestored control, maturing hedgerow, mature hedgerow) as an explanatory variable along with random effects for both year and site (Bates et al., 2014; Kuznetsova et al., 2014). All analyses were conducted in R, version 3.1.1 (R Core Team, 2014).

Sources of β-diversity

We next assessed which spatial pattern was most responsible for maintaining β-diversity within each site type in our landscape. Communities that turnover in species composition across space (i.e., those that exhibit β-diversity) are thought to arise via two processes: (i) species replacement and (ii) predictable species loss/gain (Gaston & Blackburn, 2000; Baselga, 2012). In the latter case, species-poor sites will often be subsets of species-rich sites, and thus, communities should exhibit some degree of nestedness. Such a pattern might occur when, for example, species assemble along a resource gradient (Baselga, 2012). In contrast, species replacement should lead to communities that turnover in composition via substitution of species. This pattern could result when species track their preferred resource or, somewhat randomly *via* colonization and priority effects. Unlike species loss/gain, these communities would not be expected to exhibit any patterns in nestedness. Thus, to identify which of these two scenarios best describes the patterns in the landscape within each year, we determined whether our communities were significantly nested (Almeida-Neto et al., 2012). We used the index NODF to measure nestedness (Ulrich & Gotelli, 2007; Almeida-Neto et al., 2012).

To further uncover the processes contributing to spatial heterogeneity, we asked whether the dissimilarity between pollinator communities within and between site types was related to the geographic distance between sites. To do this, we compared the pollinator community dissimilarity matrix to the geographic distance between sites using Mantel tests. To assess the significance of the correlation, we permuted dissimilarity values among sites within each year to maintain the hierarchy of the data.

We also looked for evidence that pollinator communities track resources across the landscape. One important such resource is floral hosts; if the majority of the pollinators track specific floral resources, differences in floral community composition between sites should generate corresponding differences in pollinator communities. To test this, we used Mantel tests to compare the pollinator community dissimilarity matrix to an analogous dissimilarity matrix for flowering plant species within and between site types. As we did for the bee community, we used an abundance-based measure to estimate the dissimilarity of the floral communities (Chao et al., 2005).

Rather than tracking particular flowering plant species, bees may track floral resources generally. Therefore, we also characterized floral communities according to their species richness, diversity, and total floral abundance, all proxies for floral resource availability. We then used a Gower dissimilarity measure to characterize the changes in the floral resources between sites and then compared that to the pollinator community, again using Mantel tests to look for associations between and within site types.

Lastly, both abiotic conditions and resources may affect which pollinator species are present. Bee species vary considerably in their nesting habits, and therefore, the availability of specific nesting materials may influence which species are able to occupy an area (Potts et al., 2005; Sardinas & Kremen, 2014). To examine this, we characterized the nesting resources at each site. Specifically, we measured the mean and variability of the amount bare ground, dead wood, hollow stems, cracks in the soil, and vegetation cover (Potts et al., 2005). We used Mantel tests to correlate pollinator community turnover with differences in the physical characteristics of sites, between and within site types, estimated using Gower dissimilarity.

Community traits

We determined whether agricultural areas act as an ecological filter on pollinator groups by comparing the trait distributions of pollinators found at unrestored controls to those found at hedgerows. Our unrestored control sites comprise a variety of unmanaged crop field edges and, therefore, represent the dominant conditions in our landscape. Consequently, the species visiting these sites are those that are likely present in the landscape prior to any restoration.

To characterize the trait diversity of the bee communities, we computed three metrics that capture diversity, uniqueness, and distribution of trait values in the community: trait dispersion, divergence, and evenness (Villéger et al., 2008; Schleuter et al., 2010). Trait dispersion is a measure of trait diversity, corrected for species richness (Schleuter et al., 2010); trait divergence measures how species abundances are distributed within the trait space (i.e., a measure of trait uniqueness, Villéger et al., 2008); trait evenness measures the regularity with which traits are distributed across trait space, accounting for abundance (Villéger et al., 2008). In combination, these metrics provide a relatively complete overview of the different aspects of species trait diversity (Villéger et al., 2008; Schleuter et al., 2010).

Selection of appropriate characters is essential to the characterization of the community's distribution and diversity of traits (Villéger et al., 2008). We selected resource capture and use traits that collectively influence the distribution of bee species as pollinators over space and time (Kremen & M'Gonigle, 2015) including resource specialization (quantitative, d'; Blüthgen et al., 2006), body size (quantitative, inter-tegular span, mm, Cane, 1987) sociality (categorical: eusocial, solitary, cleptoparasitic), nest location (categorical: aboveground, belowground or mix), and nest construction (categorical: excavate or rent; Williams et al., 2010) as described in more detail in Kremen & M'Gonigle (2015). Each trait has the same weight in trait diversity metric estimation (Villéger et al., 2008; Schleuter et al., 2010). Pollinator specialization was calculated using plant–pollinator interaction observations from a more extensive dataset from Yolo County (18 000 interaction records) that included both the data included in this study and additional data from sites where we collected flower visitors using the same methods (M'Gonigle et al., 2015). The specialization metric measures the deviation of the observed interaction frequency between a plant and pollinator from a null expectation where all partners interact in proportion to their abundances (Blüthgen et al., 2006). It ranges from 0 for generalist species to 1 for specialist species. To determine whether trait evenness, dispersion, and divergence differed between controls and hedgerows at different stages of maturation, we used the trait diversity metrics as response variables in linear mixed models with site type as a fixed effect and year and site as random effects (Bates et al., 2014; Kuznetsova et al., 2014).

If agriculture creates an ecological filter, the trait composition of agricultural bee communities should differ from that of a community that was randomly assembled from a shared meta-community. To test whether agriculture constitutes an ecological filter, we compared the observed trait values with the distribution of traits of randomly assembled communities. Because species richness differs between hedgerow and control sites (Morandin & Kremen, 2013) and furthermore, because differences in species richness may constrain the observed trait values and trait diversity (e.g., if only one species was observed, the trait diversity will always be zero), we randomly assembled communities of the same species richness as the observed communities. For quantitative traits, we focused on the mean trait value at a site weighted by abundance, and for categorical traits, we calculated the mean Simpson's diversity of traits (finite sample formulation). To generate the randomized communities, we shuffled the species between sites while maintaining the species richness and the number of occurrences of a species within each year. We then re-calculated the mean trait value and Simpson's diversity of traits for 9999 randomly assembled communities (Schleuter et al., 2010). Lastly, to calculate the probability of the observed trait value given a random assembly process, we computed the fraction of randomly assembled communities that had trait values greater than or equal to that of our observed community. For a given trait, if that probability was <0.025% (two-tailed test), we concluded that site type exerted an ecological filter on that trait.

To complement the previous analysis, we also asked whether the trait diversity and Simpson's diversity of traits was significantly different between hedgerows and unrestored controls. We compared the mean trait value or Simpson's diversity across site types using linear mixed models, with site status as an explanatory variable and site and year as random effects, as before (Bates et al., 2014; Kuznetsova et al., 2014).

Lastly, we asked whether the pollinator composition of communities supported by between hedgerows and unrestored controls differed using a permutational multivariate analysis of variance (PERMANOVA) (Anderson & Walsh, 2013). When comparing community composition, PERMANOVAs can be too liberal when the experimental design is unbalanced and the multivariate dispersions are heterogeneous because it is testing multiple hypotheses simultaneously (Anderson & Walsh, 2013). As the number of sites was nearly equal for hedgerows and controls within but not between years, we compared the community composition within each year.

Results

Over seven years and 545 samples, we collected and identified 9898 wild bees comprising 114 species. The species came from five families and 30 bee genera. Most species occurred infrequently in the landscape: nearly 20% of species were observed two or fewer times.

We found that β-diversity was higher in mature hedgerows than unrestored controls (estimate for the difference between mature hedgerows and controls, ± standard error of the estimate, 0.134 ± 0.045, P-value = 0.005, Fig. 2). β-diversity across maturing hedgerow sites was not, however, significantly different from that for control sites. These findings were robust to our use of different methods when generating the randomly assembled communities that we used to account for the expected β-diversity given the observed differences in the number of individuals and species (compare Fig. 2 and Fig. S3). We found that pollinator communities were not significantly nested, except for a single year and site type (Table 1), suggesting that species replacement, rather than species loss/gain, was the primary determinant of spatial heterogeneity in species composition for each site type.

Dissimilarity of pollinator communities at unrestored sites and between all site types was significantly correlated with the geographic distance (Fig. S1, Table 2). In addition, we found that the bee community dissimilarity was significantly correlated with the floral community dissimilarity between site types (Fig. S1, Table 2). The bee community was also significantly correlated

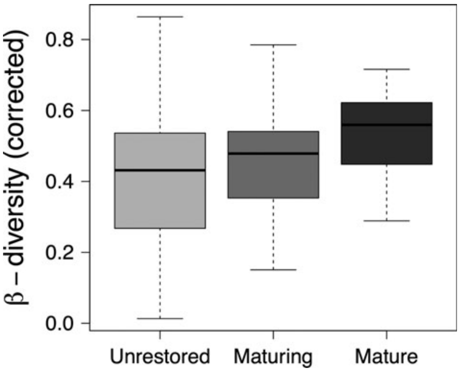

Fig. 2 Mature hedgerows support significantly higher corrected β-diversity than maturing hedgerows and unrestored controls. Corrected β-diversity values represent the dispersion of site community composition to the centroid of each site type. Boxplots represent medians (black horizontal line) first and third quartiles (box perimeter) and extremes (whiskers).

Table 1 The nestedness of pollinator communities, by year, for each site type. The *z*-scores were calculated by generating 9999 null communities, subtracting the mean of the calculated nestedness from the observed nestedness, and dividing by the standard deviation of the nestedness (Ulrich & Gotelli, 2007). Empirical *P*-values were calculated as the probability that the nestedness of the null communities was equal to or greater than the observed community nestedness. Pollinator communities were significantly nested only in 2013 for the unrestored site type

	Year	*z*-Score	*P*-value
Unrestored control	2007	−2.357	0.971
	2008	0.403	0.369
	2009	0.766	0.23
	2010	2.864	0.019
	2011	−0.787	0.78
	2012	−0.314	0.607
	2013	3.634	0.001***
Maturing hedgerow	2009	−0.391	0.644
	2011	1.617	0.059
	2012	1.062	0.153
	2013	−1.55	0.957
Mature hedgerow	2009	−1.15	0.892
	2010	−0.788	0.769
	2011	−0.785	0.781
	2012	0.524	0.287
	2013	−0.786	0.79

Symbols denote significance, with *** indicating 0.001.

with the floral community at mature hedgerows and controls, although the strength of the association at controls was weak (Table 2). Thus, the dissimilarity of floral communities between sites predicts the dissimilarity of the pollinator communities within mature hedgerows, while geographic distance more strongly structures the compositional turnover in controls. Maturing hedgerows may still be undergoing community assembly, and therefore, pollinator communities do not significantly respond to floral communities. The bee community was not correlated with floral or nesting resources, however (Fig. S1, Table 2).

Mature hedgerows positively affected each of the three trait diversity metrics compared to unrestored controls (estimate for the difference between mature hedgerows and controls, evenness: 0.100 ± 0.0366, $P = 0.009$; dispersion: 0.0759 ± 0.023, $P = 0.002$; divergence: 0.100 ± 0.0367, $P = 0.009$, Fig. 3). Compared to control sites, mature hedgerows therefore better support individuals with unique traits, as well as a greater diversity of trait values that are more evenly distributed across trait space. The trait diversity supported by maturing hedgerows, however, was not significantly different from controls.

Table 2 The correlation between the dissimilarity of pollinators communities and floral communities, nesting and floral resources, and geographic distance within and between site types

	Geographic distance		Floral community		Floral resources		Nesting resources	
	Mantel statistic *r*	*P*-value	Mantel statistic *r*	*P*-value	Mantel statistic *r*	*P*-value	Mantel statistic *r*	*P*-value
Across all site types	0.029	0.02*	0.134	0.0003***	−0.002	0.588	0.139	0.159
Unrestored controls	0.076	0.003**	0.085	0.019*	0.024	0.156	0.063	0.286
Maturing hedgerows	0.03	0.205	0.011	0.373	−0.061	0.697	−0.042	0.517
Mature hedgerows	−0.011	0.298	0.187	0.004**	−0.035	0.738	−0.619	0.979

Symbols denote significance, with *, **, and *** indicating 0.05, 0.01 and 0.001, respectively.

Examining each trait individually, we also found evidence that only species characterized by particular trait values are found in unrestored, agricultural areas. We found that, compared to randomly assembled communities, control sites exhibited significantly lower trait values for floral specialization and body size, and lower diversity than expected for each categorical trait except sociality (Fig. 4) suggesting that the species that visit or inhabit unrestored controls comprise only a subset of the available species pool. Mature and maturing sites had trait values expected by randomly assembled communities. Similarly, the linear mixed models indicated that, compared to bee communities occupying unrestored controls, bee communities at both mature and maturing hedgerow sites were comprised of species that are significantly larger (estimate for the difference between controls and mature 0.278 ± 0.080, $P = 0.001$; controls and maturing: 0.223 ± 0.092, $P = 0.02$) and more specialized (controls and mature: 0.048 ± 0.013, $P = 0.0004$; controls and maturing: 0.058 ± 0.015 $P = 0.0003$, Figs 4 and S4). Bees at hedgerows also exhibited more diversity in nesting locations and nest construction behaviors (nest location diversity, estimate for the difference between controls and mature: 0.137 ± 0.057, $P = 0.022$, controls and maturing: 0.172 ± 0.067, $P = 0.014$; nest construction trait diversity, controls and mature: 0.121 ± 0.051, $P = 0.02$, controls and maturing: 0.158 ± 0.060, $P = 0.012$, Figs 4 and S4). Sociality diversity was not significantly different between site types.

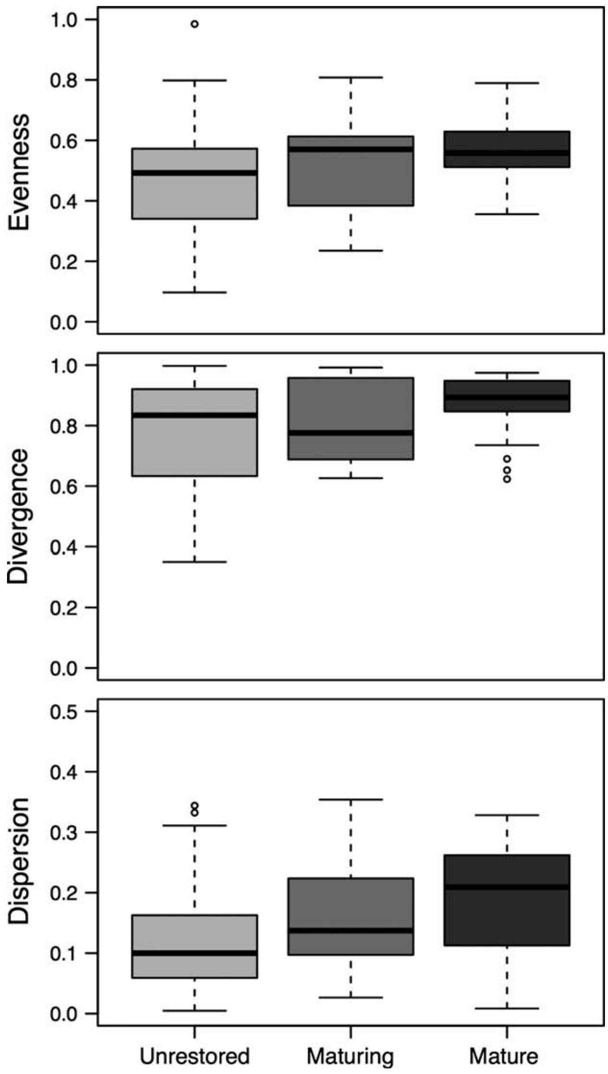

Fig. 3 The evenness, divergence, and dispersion of the pollinator traits for communities at control sites, maturing hedgerows, and mature hedgerows. Pollinator communities at mature hedgerows had significantly higher values for all metrics. Relative to the range of trait values in the landscape, mature hedgerows had 12% higher evenness, 15% higher divergence, and 21% higher dispersion than unrestored controls.

Although the trait diversity at hedgerows and unrestored controls differed significantly, the composition of communities did not significantly differ between controls and hedgerows (Table S4, Fig. S2).

Discussion

We have shown that on-farm restorations in the form of hedgerows, when replicated across a landscape, can promote the assembly of spatially heterogeneous and phenotypically diverse pollinator communities in intensively managed and simplified agriculture. Such restorations may thus help to slow or even reverse the biotic homogenization that is characteristic of such landscapes. Without hedgerows, intensive and simplified agriculture imposed a strong ecological filter that eroded patterns of spatial structuring between communities and diminished almost every aspect of community trait diversity and distribution that we investigated. This ecological filter affected a variety of phenotypic traits including nesting habits and also selected for smaller, less specialized bees. In concordance with a number of other studies conducted across a wide variety of taxa, we found that, by homogenizing communities, agriculture has the potential to affect the distribution of species over large scales (Gabriel et al., 2006; Hendrickx et al., 2007; Ekroos et al., 2010; Flohre et al., 2011).

Loss of such diversity may impact the functioning and resilience of natural systems which could have profound implications for humans and wildlife. The provisioning of ecosystem services, such as pollination, requires a stable and diverse community of wild bees (Kremen, 2005; Klein et al., 2009). These pollination services are critical both in natural communities and economically: 87% of all flowering plant species and 75%

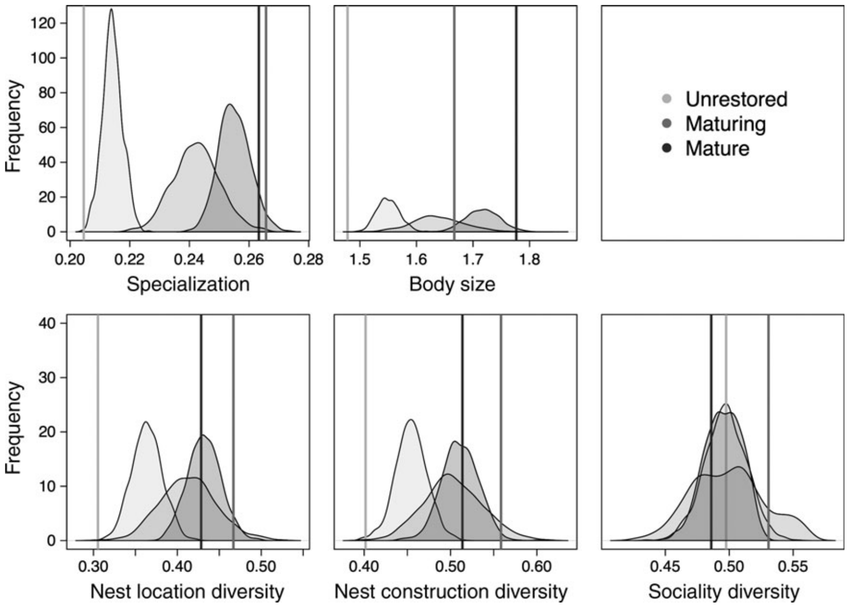

Fig. 4 The mean trait value (top panel) and trait diversity (bottom panel) of pollinator communities at different site types. The solid lines are the observed trait values, and the shaded curves are trait distributions for randomly assembled communities with the same species richness as the observed communities for each site type. The unrestored controls had significantly lower ($P < 0.025$) trait values and diversity than expected for a randomly assembled community for all trait groups except sociality diversity. In the context of the range of trait values observed in the study landscape, mature hedgerows had 21% higher specialization than controls, 16% larger bees, 12% more nest location diversity, and 11% more nest construction diversity.

of crop species depend to some extent on animal pollinators in order to produce fruits or seeds (Klein et al., 2007; Ollerton et al., 2011). Animal-pollinated crops also supply a large proportion of essential nutrients to the human diet (Eilers et al., 2011; Smith et al., 2015).

Based on findings in other cropping systems, lower functional diversity, combined with the loss of key service providers, will likely negatively affect levels of pollination in both crops and wild plant populations (Hoehn et al., 2008; Klein et al., 2009; Brittain et al., 2013). In addition, by reducing the size of the species pool, simplified agriculture may impact the stability of services (Winfree & Kremen, 2009) and thus the reliability and predictability of plant reproduction and crop yields (Garibaldi et al., 2011; Garibaldi et al., 2013). Encouragingly, however, relatively small-scale restorations such as hedgerows can mitigate the homogenization caused by simplified agriculture, when replicated across landscapes. Hedgerows have also been shown to support other ecosystem services (Hinsley & Bellamy, 2000; Bianchi et al., 2006; Hannon & Sisk, 2009), so these small-scale, on-farm restoration measures may also provide an economic benefit to growers (Blaauw & Isaacs, 2014), although this is likely to be context dependent (Sardiñas & Kremen, 2015).

We have shown that, in addition to supporting a higher diversity and abundance of pollinators (Morandin & Kremen, 2013), hedgerows also support approximately 14% higher β-diversity and approximately 10% more trait diversity, uniqueness, and evenness than unrestored field margins. In addition, because the trait diversity of the communities differed significantly between hedgerows and unrestored controls but community composition did not, the communities at controls are likely a subset of those at hedgerows. For example, 28% of the total species pool was found only at hedgerows, whereas only 13% of species were unique to unrestored controls (Table S3). Of the species only at controls, 80% were represented by a single individual. The species only at hedgerows tended to have more specialized nesting requirements (above-ground renters), whereas those only at controls were primarily generalists (below-ground excavators, Fig. 1). Also, although the majority of the species (68%) were found at both hedgerows and unrestored controls (Table S3), species ranging from relatively rare (<10 individuals) to common (between 10 and 100 individuals) were infrequent at controls and more abundant in hedgerows (Fig. S5). Interestingly, the three species observed over 100 times, *Lasioglossum incompletum*, *Halictus tripartitus* and *Halictus ligatus*, all small-bodied floral and nesting resource generalists, were at similar abundances in hedgerows and unrestored controls, if not slightly more abundant in controls (Fig. S5).

Although hedgerows may help counter homogenization of pollinator communities in simplified agricultural landscapes, comparing the spatial heterogeneity they support to that which is observed in natural communities is important in assessing their overall conservation value. In remnant chaparral/oak woodland communities in the same ecoregion and adjacent to our study landscapes (Forrest et al., 2015), an average of 30% of species were not shared across sites located within 3.5–50 km of each other. The Central Valley, which was once described as 'one vast, level, even flower-bed' (Muir, 1916), has been extensively converted to agriculture, likely limiting the species pool due to local extinctions. Even so, at hedgerows an average of 15 km apart, we found between 36% and 67% of species were not shared between sites, depending on the year. Both the spatial scale and biota of our study and that of (Forrest et al., 2015) are comparable, suggesting that hedgerows are, in fact, restoring spatial heterogeneity to approximately the same range as might occur in adjacent natural systems. In addition, in the disparate landscape of the southwestern United States, a diversity hot spot for bees (Minckley et al., 1999), 61% of species were not shared across sites within 1–5 km of each other (Minckley et al., 1999). Although the species pool is richer in the southwest, the amount of species turnover at hedgerows is not unlike what is observed in that highly heterogeneous region (Minckley et al., 1999). Thus, across many aspects of biodiversity, hedgerows might provide a valuable measure for conserving biodiversity (Hinsley & Bellamy, 2000; Bianchi et al., 2006; Klein et al., 2009; Morandin & Kremen, 2013; Garibaldi et al., 2014; Kremen & M'Gonigle, 2015).

Only mature hedgerows (and not young, recently planted hedgerows) in this study supported higher trait and β-diversity when compared to nonrestored farm edges. Thus, the processes that lead to a buildup of spatial turnover in pollinator communities are slow and may take considerable time before observably affecting pollinator communities. However, we have recently shown that hedgerow restoration leads to increased rates of colonization and persistence of pollinators in maturing hedgerows and that this effect becomes stronger over time (M'Gonigle et al., 2015). Further, we found that maturing hedgerows differentially support more specialized species over time (Kremen & M'Gonigle, 2015). These two temporal studies on the early phases of hedgerow maturation (0–8 years post restoration) show that hedgerows begin to impact pollinator communities much earlier than 10 years. Combined, these findings suggest a possible mechanism whereby restoration might lead to increases in species turnover; as a hedgerow matures, species with a wider variety of life-history traits are better able to colonize and persist there, thus leading to the accumulation of differences in community composition between sites over time. This then leads to greater spatial heterogeneity in pollinator communities at hedgerows. Conversely, in unrestored areas, the rate of colonization and persistence is lower, particularly for species with more specialized habitat requirements, thereby creating an ecological filter that limits the total diversity and, thus, turnover that is possible.

This above-described process can be, in part, deterministic; restored and nonrestored farm edges differ fundamentally in which pollinator species are able to colonize and/or persist in them (Kremen & M'Gonigle, 2015; M'Gonigle et al., 2015). Thus, pollinators respond to the differences in the plant communities between hedgerows and controls, and the pollinator community at mature hedgerows tracks floral hosts. Interestingly, however, the pollinator communities at hedgerows that were closer to one another were not necessarily more similar than sites that were further apart. In addition, hedgerows maintain β-diversity in the landscape by supporting unique combinations of species, and we did not find evidence that communities at hedgerows were nested subsets of one another (Baselga, 2012). Because hedgerows are planted, the floral communities the pollinators are tracking will not necessarily be spatially structured like natural communities. In addition, bees are known to be highly spatially and temporally variable (Minckley et al., 1999; Williams et al., 2001) and thus, stochastic processes that do not result in spatial structuring are likely operating as communities assemble.

In contrast to within hedgerows, the dissimilarity of pollinators at unrestored controls responded positively to geographic distance. Because the conditions at controls are relatively uniform across space, this suggests a role for dispersal limitation in determining pollinator community composition at unrestored controls (Chase et al., 2005). In addition, the number of shared species between hedgerows and controls was also positively related to distance (Table 2), suggesting the communities at controls may be influenced by landscape context such as the presence of nearby hedgerows. Hedgerows may therefore represent a source of bee diversity in the landscape.

Here we focus on the effects of hedgerows on β-diversity, but there are likely other contributions to spatial heterogeneity in our landscape. There are a number of crops that provide floral resources to pollinators in our area, including mass-flowering sunflower, melons, and almonds (Kremen et al., 2002; Greenleaf & Kremen, 2006; Klein et al., 2012). Different crops attract different pollinators (Winfree et al., 2008) and thus may affect the spatial heterogeneity of communities. In addition, some crops might also pull resident species from the hedgerows (Sardiñas & Kremen, 2015), while others may attract species that may subsequently colonize hedgerows (Kovács-Hostyánszki et al., 2013). Differences in adjacent crops between hedgerows and unrestored controls thus may add noise to the underlying signal of β-diversity. However, because hedgerows and controls are matched for crop type, while there may be a contribution of crop type on β-diversity, it should be a random one affecting hedgerows and controls simultaneously.

To achieve sustainable food production while protecting biodiversity, we need to grow food in a manner that protects, utilizes, and regenerates ecosystem services, rather than replacing them (Kremen & Miles, 2012; Kremen et al., 2012; Kremen, 2015). Diversification practices such as installing hedgerows, when replicated across a landscape, may provide a promising mechanism for conserving and restoring ecosystem services and biodiversity in working landscapes while potentially improving pollination and crop yields (Blaauw & Isaacs, 2014; Garibaldi et al., 2014).

Acknowledgements

We would like to thank Marti Anderson, Perry de Valpine, David Ackerley, and two anonymous reviewers for their invaluable discussions and comments. We thank the growers and land owners that allowed us to work on their property. We also appreciate the identification assistance of expert taxonomists Robbin Thorp and Jason Gibbs. This work was supported by funding from the Army Research Office (W911NF-11-1-0361 to CK), the Natural Resources Conservation Service (CIG-69-3A75-12-253, CIG-69-3A75-9-142, CIG-68-9104-6-101, and WLF-69-7482-6-277 to The Xerces Society), the National Science Foundation (DEB-0919128 to CK), The U.S. Department of Agriculture (USDA-NIFA 2012-51181-20105 to Michigan State University). Funding for LCP was provided by an NSF Graduate Research Fellowship and the USDA NIFA Graduate Fellowship and for LKM by an NSERC Postdoctoral Fellowship.

Author contributions

CK designed the study; LKM, LCP, and CK collected data; LCP analyzed output data. LCP wrote the first draft of the manuscript; and all authors contributed substantially to revisions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Supporting Methods.
Table S1. The number of sampling rounds conducted at each control site in each year of the study.
Table S2. The number of sampling rounds conducted at each hedgerow site in each year of the study.
Table S3. Bee species found at hedgerows and controls.
Table S4. The test statistics for the permutation anovas comparing pollinator community composition between mature hedgerows, maturing hedgerows and unrestored controls within each year.
Figure S1. The dissimilarity of pollinator communities as a function of the dissimilarity of the floral communities, floral resources, nesting resources, and geographic distance at each site type across all years of the study.
Figure S2. The dissimilarity of communities in multivariate space using a principal coordinate analysis.
Figure S3. The beta-diversity (corrected using random communities that have the same number of individual as observed communities) at unrestored controls, maturing hedgerows and mature hedgerows.
Figure S4. The mean trait value and trait diversity of pollinator communities at different site types.
Figure S5. The frequency of observing specific abundances at a site across years of a sample of species found in both hedgerows and controls.

Agriculture, Ecosystems and Environment 207 (2015) 17–25

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Pollination services from field-scale agricultural diversification may be context-dependent

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ARTICLE INFO

Article history:
Received 10 November 2014
Received in revised form 18 March 2015
Accepted 19 March 2015
Available online xxx

Keywords:
Apoidea
Ecosystem services
Hedgerows
Mass-flowering crop
Restoration
Sunflower
Wild bees

ABSTRACT

Diversification of field edges is widely used as a strategy to augment pollinator populations and, in turn, supplement crop pollination needs. Hedgerow plantings, a commonly applied field-scale diversification technique, have been shown to increase wild bee richness within edges and into crop fields; however, their effects on pollination services in mass-flowering, pollinator-dependent crops typical of large-scale commercial monocultures are less well-known. We evaluated the indirect contribution of hedgerows to sunflower (*Helianthus annuus*) seed set vis-á-vis wild bee abundance and the interaction between wild bees and managed honey bee pollinators. Although wild bee species richness and the interaction between wild and managed pollinators were significantly associated with augmented seed set, these factors were unrelated to whether a hedgerow was present. The pollinator species foraging within crop fields differed significantly from those found within adjacent hedgerows and bare or weedy field edges, with hedgerows supporting higher species richness than crop fields or unenhanced edges. However, in an independent data set, greater numbers of sunflower-pollinating bees were found in hedgerows than in control edges. Hedgerows may therefore help these crop-pollinating species persist in the landscape. Our findings suggest that hedgerows may not always simultaneously achieve crop pollination and wild bee conservation goals; instead, the benefits of hedgerows may be crop- and region-specific. We recommend evaluation of hedgerow benefits in a variety of crop and landscape contexts to improve their ability to meet ecosystem-service provisioning needs.

1. Introduction

Global production of pollinator dependent crops has increased by 300% in the past 50 years (Aizen and Harder, 2009). At the same time, managed honey bee (*Apis mellifera* L.) populations are declining due to a complex of factors including novel diseases, pesticides and habitat change (Ellis et al., 2010; Potts et al., 2010; Smith et al., 2013). Pollinator deficiencies may precipitate significant yield reductions and increased food prices, ultimately jeopardizing food security (Meffe, 1998; Kevan and Phillips, 2001; Steffan-Dewenter et al., 2005; Klein et al., 2007; Gallai et al., 2009). Unmanaged bees (hereafter “wild bees”) are highly effective pollinators of a variety of crops and act as insurance against loss of pollination function due to honey bee deficits (Winfree et al., 2007; Garibaldi et al., 2013). While proximity to natural habitat increases populations of such alternate pollinators (Kremen et al., 2002; Ricketts et al., 2008; Kennedy et al., 2013), intensive agricultural landscapes often contain little remnant habitat. As a result, re-diversification of agricultural areas has been proposed as a means of bolstering pollination services from these alternate pollinators (Steffan-Dewenter and Leschke, 2003; Kremen et al., 2007; Tscharntke et al., 2005; Brosi et al., 2008; Holzschuh et al., 2008; Winfree, 2010; Garibaldi et al., 2014).

Diversification of agricultural landscapes can take place at many scales, including within fields (e.g., polyculture), along field edges (e.g., hedgerows and wildflower plantings), or bordering landscape features (e.g., riparian corridors such as irrigation canals or natural water features; Kremen and Miles, 2012). One benefit of field edge techniques is that they create habitat without sacrificing arable land (Menz et al., 2011; Morandin and Kremen, 2013), and comprise a large portion of non-cropped area in farming regions globally (Decourtye et al., 2010). Farm bill conservation programs in the United States and agri-environmental schemes in the European Union prioritize on-farm habitat creation projects that target pollinators, providing incentives through cost-share programs (Vaughan and Skinner, 2008). Despite the prominence of these programs, there is little information as to the effectiveness of field-margin diversification techniques, and specifically, whether they can bolster pollinator services and affect yields to the same

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http://dx.doi.org/10.1016/j.agee.2015.03.020
0167-8809/

levels documented in patches of natural habitats (but see Morandin and Kremen, 2013; Blaauw and Isaacs, 2014) while simultaneously conserving pollinator species (Garibaldi et al., 2014; Kremen and M'Gonigle, 2015).

One common field edge diversification technique, hedgerow restoration (linear plantings of native shrubs and forbs), has been found to increase pollinator richness within field edges (Hannon and Sisk, 2009; Carvell et al., 2011) and up to 100 m into nearby crop fields (Morandin and Kremen, 2013). Additionally, hedgerows show potential for increasing pollination function within adjacent fields. Using sentinel canola plants, Morandin, Long and Kremen (unpublished data) found that wild bees enhanced seed set, once the contribution from managed honey bees was accounted for. However, the canola plants provided a highly attractive resource within an unattractive crop matrix of processing tomato, which provides few nectar rewards and requires buzz-pollination to release pollen stores. These conditions are not reflective of the field conditions created by monoculture plantings of pollinator-dependent crops, which generate hundreds of thousands of synchronous, though short-lived, blooms within a single field (known as mass-flowering crops).

Mass-flowering crops (MFCs) can exert strong effects on pollinator populations. Pulses of highly attractive floral resources can create dilution effects, drawing species away from adjacent seminatural habitat and reducing pollination services there (Holzschuh et al., 2011). Yet in spite of the attractiveness of MFC fields, wild bee abundance and richness has been found to be higher in habitats, including hedgerows, in closer proximity to MFC fields (Hanley et al., 2011; Le Féon et al., 2013). The effects of MFCs may be species-specific, with some exhibiting higher preference for MFCs over other resources (Rollin et al., 2013). Specialist pollinators, such as the squash bee (*Peponapis pruinosa* S.), seek out fields of their host plant, cultivated squash, in the landscape (Ullmann and Williams, in review). While the influence of MFCs on pollinator populations and services has been well-studied, whether the presence of field-scale restorations can augment pollinator populations and pollination services within MFC fields remains an open question (but see Stanley and Stout, 2014).

We examine the ability of hedgerows to enhance pollination services in a simplified agricultural landscape when adjacent to a mass-flowering, pollinator-dependent crop, cultivated sunflower (*Helianthus annuus* L.). We ask whether the identity of the pollinator species found within hedgerows during the crop bloom period is the same as those found within adjacent sunflower fields. Then, using an independent data set, we determine whether the most abundant wild sunflower visitors, sunflower specialist bees, also utilize hedgerow plantings in our study landscape. We also determine whether hedgerow presence affects wild bee abundance and richness in sunflower fields, and if this, in turn, translates into increased sunflower seed set.

2. Material and methods

2.1. Study system

Field sites were located in Yolo County, an intensively-farmed agricultural region of California's Central Valley that contains a mixture of conventionally managed row and orchard crops. The majority of natural and semi-natural habitat in the county is concentrated around the borders of agricultural lands and not embedded within them (California Department of Water Resources, 2008). We sampled 18 sunflower fields between June and July (10 fields in 2012 and 8 fields in 2013). Half of the fields were adjacent to bare or weedy edges (hereafter called controls), and half were adjacent to hedgerows (Fig. S1a). Sites were paired based on the timing of the sunflower bloom, the sunflower variety (specific to company), and landscape context. Field pairs were a minimum of 900 m apart (range, 947–5409 m) to maintain independence (Greenleaf et al., 2007). To avoid contamination of varieties, sunflower fields are moved every year; therefore no field was sampled in multiple years although two fields were adjacent to the same hedgerow in different years.

2.2. Sunflower

In Yolo Co., acreage planted in sunflower has increased by over 55% during the past 5 years (Yolo County Weights and Measures, Crop Statistics). It is the 8th most-planted crop in the region, grossing nearly $28 million USD in 2013 (Yolo County Weights and Measures, Crop Statistics). It is produced mainly for hybrid seed, which is then grown for oilseed or confection. While sunflower is native to North America, the breeding system of sunflower grown for hybrid seed has been altered to be artificially gynodioecious, with separate male-fertile (nectar and pollen producing; 'male') plants and male-sterile (nectar-only producing; 'female') plants. For hybrid seed production, rows of male plants are interspersed with rows of female plants. Wild bees predominantly visit male plants to collect pollen for nest provisioning (Parker, 1981; Greenleaf and Kremen, 2006). Although honey bees visit both male and female plants, workers typically either collect nectar from female plants or pollen from male plants which limits cross-pollination events (Free, 1964). Honey bee movement between pollen and nectar producing rows of sunflower is often spurred by interference interactions with wild bees. When a wild bee and honey bee meet on a sunflower head, one or both fly to different sunflower heads or rows (Greenleaf and Kremen, 2006; Pisanty et al., 2014). These interactions that increase pollen flow between rows also increase honey bee per visit efficiency, therefore have great potential to heighten seed set (Greenleaf and Kremen, 2006; Carvalhiero et al., 2011). Honey bees were stocked at an average rate of approximately 100 hives per field, or 1.5 hives per acre (Greenleaf and Kremen, 2006).

We did not evaluate pest management (treated versus untreated fields) because sunflower fields managed by different companies (four main companies) used similar practices. For example, all companies used pre-emergent herbicides prior to planting and seeds were treated with insecticides (Cruiser®, active ingredient: thiamethoxam) and either a fungicide or nematicide. Other management practices, including fertilization, tillage, row width and ratio of male to female rows, are also similar between companies (Long et al., 2011), although irrigation practices vary by field, with the majority using furrow irrigation.

2.3. Hedgerows and control edges

Hedgerows were planted by growers to support beneficial insect populations, and include highly similar plant species composition (for more information on hedgerow plantings see Long et al., 1998). Hedgerows were 250–300 m long and 3–6 m wide. During the sunflower bloom period, only a portion of plants in the hedgerow were flowering (Tables S1 and S2). *Eriogonum fasciculatum var. fasciculatum*, *Heteromeles arbutifolia*, and *Sambucus nigra* ssp. *cerullea* were the only woody species in bloom. Forbs in bloom included *Achillea millefolium, Asclepias californica, Asclepias fascicularis, Aster chilensis* and *Grindelia camporum*. Weedy species were present in all hedgerows and most control sites; the dominant species were *Convolvulus arvensis*, *Brassica* sp., and *Polygonum arenastrum*. Control margins contained only non-native plant species, or were maintained as bare, weed-free areas. Bare/weedy field margins in our study region are managed by burning, herbicides, or scraping; no management actions took place during our study period. By design, hedgerows contained more plant species and more blooms than control weedy edges (Tables S1 and S2).

2.4. Landscape context

To quantify the landscape surrounding each site we created 18 land use categorizations (Table S3). We then hand digitized National Agriculture Imagery Program (NAIP) within a 1 km buffer around study sites in ArcGIS 10.1 (Farm Service Agency U.S. Department of Agriculture, 2006; ESRI, 2011). To determine landscape effects on wild bee populations in sunflower, we examined the proportion of habitat within each buffer that could provide resources to wild bees (hereafter "potential pollinator habitat"). This included both natural habitats (e.g., grasslands and riparian scrub) and altered habitats (e.g., weedy patches and hedgerow restoration). Potential pollinator habitat around our study sites varied from 1 to 40%, with a median of 5% (Table S4). Control and hedgerow sites were paired by landscape context to minimize differences.

2.5. Sampling methods

We established two 200 m transects within each field, perpendicular to the field edge or hedgerow and 100 m apart (Fig. S1b). We netted and observed pollinators at four distances along these transects: 10, 50, 100 and 200 m from the edge. We varied the starting sampling location within fields and edges at each study site (surveyors started at different starting distances on each transect) to reduce conflation of distance with temporal variation in bee foraging behavior, which peaks in the morning and late afternoon (Pisanty et al., 2014). Each site was sampled once, during peak bloom (>90% sunflower heads in bloom), on a clear day with wind speeds <2.5 m/s and temperatures >18 °C between 08:00 h and 14:00 h.

We visually observed visitation for 2 min each in two male-fertile and two male-sterile 2×1 m plots at each distance. Within hedgerows and edges we haphazardly sampled floral visitors for 2 min in eighth plots containing floral blooms. Only insects that contacted the anthers or stigmas were recorded as floral visitors. We also recorded non-bee visits; these accounted for <1% of all visits and were, for simplicity, excluded from analyses. We were unable to identify bees to species in visual observations; therefore we classified them to citizen science categories from Kremen et al. (2011.

After visual observations were completed, we netted bees visiting male-sterile and male-fertile plants for 8 min at each distance along each transect, and for 16 min along edges. We paused stopwatches during specimen handling. We did not collect *Apis* in netted samples. Specimens were identified by Dr. Robbin Thorp, except *Melissodes* spp., which were identified by H.S. Sardiñas. Wild bees include both native and non-native non-*Apis* bees. Non-native wild bees, including *Ceratina dallatorreana* and *Megachile apicalis*, make up a small portion (1%) of all records. We did not include feral *Apis* in our wild bee categorization because we were unable to distinguish them from managed *Apis*.

2.6. Seed set

To determine ambient pollination rates, we collected three sunflower heads at each distance/transect combination prior to harvest. In the first year of this study we bagged one male-sterile sunflower head at each distance along both transects to determine seed set levels without cross-pollination events. No seeds were produced in any bagged sunflower head, therefore we did not account for seeds set due to selfing in our models of seed set. Heads were dried, measured, and all mature seeds were removed, weighed and counted with a Syntron automatic seed counter. We tested for differences in head size (diameter) between companies using a generalized linear model, with site nested within pair as a random effect, in the R package lme4 (Bates et al., 2013; R version 3.1.2). Sunflower head size was similar between companies (estimated head area 25 cm^2; Table S5), although one company had a wider range of head sizes and was significantly different from the other three companies in the study ($t = -2.22$, $P < 0.05$; Table S5). All hedgerow and control sites were paired by company.

2.7. Field edge use by sunflower specialists

Sunflower specialists are more effective pollinators of sunflower than generalist species (Parker, 1981; Greenleaf and Kremen, 2006). We therefore also investigated whether sunflower specialists were more abundant in hedgerow or control field edges using an independent data set from 26 hedgerows and 21 control edges in Yolo Co. (see Supplement; Fig. S2). Floral visitors were netted for 1 h in hedgerows and control edges during 4–5 sample rounds between April and August in 2012–2013. We queried this specimen database for sunflower specialist bees, which we defined as primary oligoleges (Hurd et al., 1980). To assess whether the amount of nearby sunflower in the landscape impacted sunflower specialist presence in field edges in the independent dataset, we constructed 1 km buffers around sites in ArcGIS 10.4 and recorded the proportion of sunflower fields around each site using pesticide spray records (California Department of Pesticide Regulation), which identify which crop is grown on each parcel, and the California crop improvement sunflower isolation map (California Crop Improvement Association).

2.8. Statistical analyses

We used a chao estimator to evaluate species richness within sites in the R package vegan (Oksanen et al., 2013). To determine the impact of hedgerow presence, field location (field or edge), and surrounding pollinator habitat in the landscape on wild bee species richness and abundance (from aerial net data) we used general linear models with Poisson and negative binomial distributions respectively in the R package lme4 (Bates et al., 2013). Both models included an interaction between hedgerow presence and field location. We used raw species richness because we only sampled each site once and some sites contained too few individuals for estimation or rarefaction (Gotelli and Colwell, 2011). We also assessed factors influencing sunflower visitation rates by honey bees and wild bees. Hedgerow presence, distance from hedgerow, and their interaction, potential pollinator habitat and sunflower sex (male-fertile or male-sterile) were independent variables. In species richness, abundance and visitation models, site nested within pair was included as a random effect.

We evaluated the differences between the community of bees in control edges, hedgerows and crop fields using a perMANOVA on their Chao1 dissimilarities in the R package vegan (Oksanen et al., 2013). We then determined whether male and female sunflower specialist bees utilized hedgerows or control field edges using the independent data set (all other analyses were on the sunflower data). We modeled counts of bees as the dependent variable with a Poisson distribution in the R package lme4 (Bates et al., 2013). Hedgerow presence, proportion of sunflower and potential pollinator habitat within a 1 km radius, bee specialization on sunflower, bee sex and an interaction between specialization and hedgerow presence were the independent variables. Site nested within pair was included as a random effect.

To determine which factors impacted sunflower seed set, we used negative binomial generalized linear models in the R package lme4 that accounted for overdispersion in the seed data (Bates et al., 2013). We examined the effect of wild bee abundance and richness on seed set from net and visitation data separately. We used raw species richness because some site-distance combinations contained too few individuals for estimation or rarefaction (Gotelli and Colwell, 2011). In all models, sunflower seed set was the dependent variable. In the model for netted bees, independent variables were hedgerow presence, wild bee abundance, wild bee species richness, sunflower company, distance into the field from the edge, and an interaction between netted wild bee abundance and honey bee visitation (based on the observation that honey bees displayed greater per visit pollination efficiency as native bee abundance increased; Greenleaf and Kremen, 2006). For the model including visitation rates, additional explanatory variables included aggregate wild bee visitation to male-fertile and male-sterile flowers, honey bee visitation, and an interaction term between wild bee visitation and honey bee visitation. Site nested within pair was included as a random effect in both models.

All continuous variables were scaled ($(x-\text{mean})/\text{sd}$). We checked all variables for collinearity (variance inflation factor <3; Zuur et al., 2009), and no collinear variables were included in any model. For example, sunflower head size was correlated with variety. However, varieties were specific to sunflower company, so only sunflower company was retained in the model.

3. Results

3.1. Aerial netting

We collected 670 wild bees with aerial netting representing 30 species. Species richness within sites ranged from 0 to 3.71, with a mean chao estimated richness of 2. Rarefaction showed that collection of new species was still increasing at a rapid rate (Fig. S3). More species are likely present within the system, although Greenleaf and Kremen (2006) found a similar number of species visiting sunflower in the same study region in fields closer to natural habitat (33 species). We did not net any bees in three control edges that were devoid of floral resources (i.e., managed as bare edges with no weedy species present).

We collected more bees in hedgerow edges than in control edges (Table 1 and Fig. 1a). On average, hedgerow edges supported higher species richness (5.11 ± 0.89, mean ± standard error; Fig. 1b) than control edges (2.11 ± 0.48), hedgerow fields (1.41 ± 0.20) or control fields (2.06 ± 0.20; Table 1). We detected a significant interaction between hedgerow presence and location within fields (edge or field) for abundance ($t=-3.91$, $P<0.001$) and species richness ($t=-4.22$, $P<0.001$; Fig. S4). Proportion of potential pollinator habitat with a 1 km radius did not influence wild bee species richness ($t=-0.83$, $P=0.41$) or abundance ($t=-0.49$, $P=0.62$) within sunflower fields.

Table 1
Model results for abundance and species richness of netted wild bees, and visitation of wild and honey bees, in sunflower fields adjacent to hedgerows or unenhanced in field edges.

Variable	Estimate	SE
Species richness model		
Hedgerow presence	0.91^{**}	0.32
Edge of field (field)	−0.27	0.24
Hedgerow presence × location	-1.26^{***}	0.3
Abundance model		
Hedgerow presence (present)	1.04^{*}	0.48
Edge of field (field)	−0.37	0.30
Hedgerow presence × location	-1.80^{***}	0.41
Visitation model		
Hedgerow presence (present)	0.11	0.11
Distance into field	0.00	0.00
HB or WB (WB)	-1.11^{***}	0.08
Sunflower sex (male-fertile)	0.129^{*}	0.06
Hedgerow presence × distance	0.00	0.00

Note: WB, wild bee; HB, honey bee.
* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

3.2. Visitation rates

We recorded 2745 visits to sunflower from wild (339 visits) and honey bees (2406 visits). We detected 7 times more honey bees visits than wild bee visits ($t=-15.38$, $P<0.001$; Fig. S5). We did not find a main or interactive effect of hedgerow presence or distance from the edge on visitation rates (Table 1). The amount of pollinator habitat in the surrounding landscape did not affect visitation rates ($t=1.11$, $P=0.27$). Confirming past findings (e.g., Greenleaf and Kremen, 2006; Parker, 1981), we found that wild bees visited male-fertile plants at higher rates (91.4% of visits) than male-sterile plants. Similarly, both honey bees and wild bees

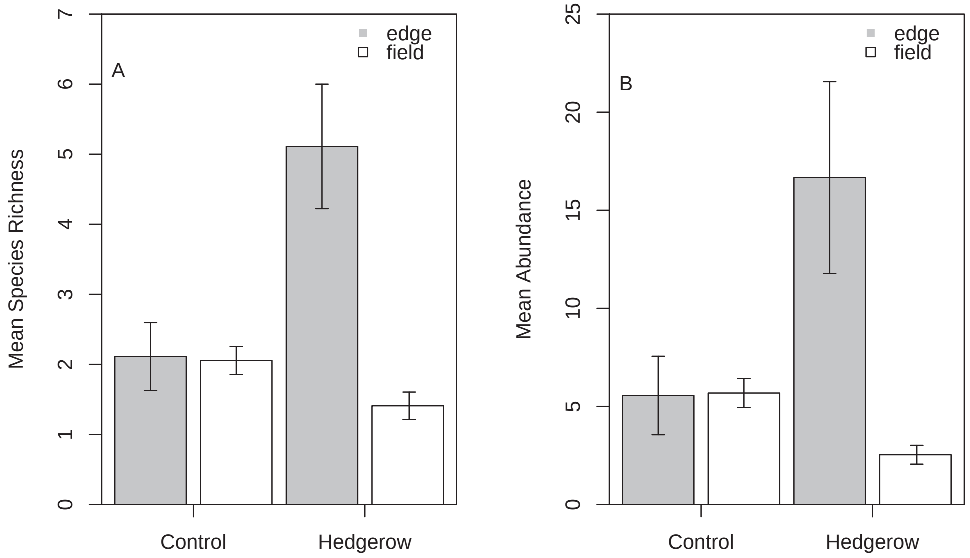

Fig. 1. Hedgerow edges supported higher species richness (a) and abundance (b) of wild bees than control edges and sunflower fields.

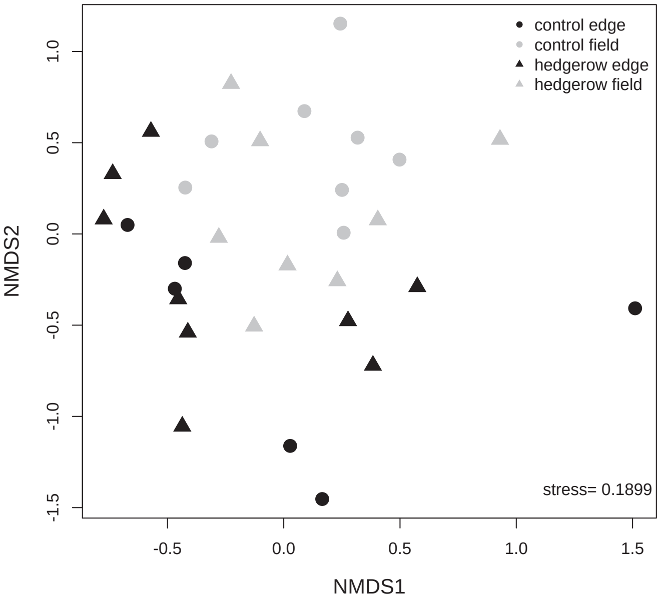

Fig. 2. Chao1 (abundance-based) dissimilarities between wild bee communities found in control edges, hedgerows, control fields and hedgerow fields; visualized using non-metric dimensional scaling. All sites with fewer than one specimen were excluded from this perMANOVA analysis.

visited male-fertile sunflower heads more frequently than male-sterile, seed-producing sunflower heads ($t = 2.56$, $P < 0.05$).

3.3. Wild bee habitat use

The communities of bees we found in fields versus edges with aerial netting were strongly differentiated ($F = 4.11$, $P = 0.001$), but the communities found at hedgerow or control edges were not distinct (Fig. 2), despite differences in floral blooms between the edge types (Tables S1 and S2). Bee communities in edges were dominated by generalists (e.g., *Halictus tripartitus*) whereas bee communities in fields contained higher numbers of sunflower specialists (e.g., *Melissodes agilis*; Table S6).

In the independent dataset, we found 627 records of sunflower specialists visiting control and hedgerows edges in 2012–2013 (Table S7). Proportion of sunflower within 1 km of study sites ranged from 0 to 0.34. We detected a significant interaction between sunflower specialists and hedgerow presence ($Z = 9.79$, $P < 0.001$; Table 2; Fig 3). The majority of sunflower specialists visiting edge habitat were males (87.7%; $Z = -26.85$, $P < 0.001$). Specialists visited 16 different plant species, 5 of which were hedgerow plants; the remaining were weedy species (Table S8). 48.8% of all visits were to buckwheat (*Eriogonum fasciculatum*; male bees – 285 visits, female bees – 36 visits).

Table 2
Model results for the independent analysis assessing the use of field edges by sunflower specialists, categorized as primary oligoleges (Hurd et al., 1980).

Variable	Estimate	SE
Hedgerow presence (absent)	−0.05	0.14
Proportion sunflower within 1 km	1.31***	0.32
Proportion potential pollination habitat within 1 km	−0.43	0.44
Specialization (generalists)	−0.77***	0.14
Wild bee sex (female)	−0.71***	0.03
Hedgerow presence × sunflower specialization	1.49***	0.15

*** $P < 0.001$.

Fourteen of these sites were adjacent to sunflower in both 2012 and 2013, and the majority of specialist bees were found there (90%), although these were concentrated in 2 hedgerows, which contained 79% of all specimens collected. Proportion of sunflower within a 1 km radius positively affected sunflower specialist presence in field edges ($Z = 4.15$, $P < 0.001$). 48 specimens were found in 6 edges that were not adjacent to sunflower, and only 2 of those sites were in close proximity to sunflower fields during previous years. Proportion of potential pollinator habitat in the surrounding landscape did not affect the number sunflower specialists in field edges ($Z = -0.98$, $P = 0.33$).

3.4. Sunflower seed set

Seed set was affected by netted wild bee species richness ($t = 2.05$, $P = 0.039$; Table 3), but not abundance ($t = -1.27$, $P = 0.20$). We did not detect an interaction effect between netted wild bee abundance and honey bee visitation rates (Table 3). In the visitation model, the interaction between wild bee and honey bee visitation influenced seed set ($t = 2.04$, $P = 0.041$). Neither hedgerow presence nor distance from the field edge impacted sunflower seed set in either the net or visitation models, whereas company strongly affected seed set (Fig. 4).

4. Discussion

Measuring the levels of ecosystem services derived from field-edge habitat management in a variety of contexts is critical to demonstrating their efficacy and flexibility. If services are highly variable over time or from site to site, costs may outweigh the benefits and limit the adoption of diversification practices (Ghazoul, 2007; Hanes et al., 2013). Although other studies have found that field-edge diversification increase pollinator populations both in edges and fields (Morandin and Kremen, 2013) and enhance pollination services to crops in adjacent fields (Blaauw and Isaacs 2014; Morandin, Long and Kremen, unpublished data), we did not detect any differences in rates of seed set in sunflower fields adjacent to hedgerow or control edges. Wild bee richness and an interaction between wild bee visitation and managed honey bee visitation, however, positively impacted seed set; yet these factors were not influenced by hedgerow presence. Proportion of pollinator habitat in the surrounding landscape did not influence the bee community visiting sunflower, despite a large body of evidence supporting strong positive landscape effects (e.g., Ricketts et al., 2008; Kremen et al., 2002). We did find higher numbers of sunflower specialist bees in hedgerows than in control sites. Based on these findings, we conclude that sunflower in not a good candidate crop for field edge enhancements, at least in our study region, although they exhibit potential for supporting populations of sunflower pollinating bees.

We detected distinct differences in community composition of wild bees present in edges versus fields. This difference was likely driven by the fact that the dominant bee species found within fields, sunflower specialists, were either rare visitors to or absent from both hedgerow and control edge habitats. We only sampled each site once, therefore increased sampling could lead to more convergence or divergence between bee communities in these habitats. There can be significant overlap between species found in MFC fields and adjacent hedgerows (Stanley and Stout, 2014), however species composition in hedgerows has also been shown to more closely resemble bee communities in forest habitat than adjacent crop fields (Hannon and Sisk, 2009). One factor likely driving the differences in species composition in our study region is the absence of sunflower planted within hedgerows due to concerns about genetic contamination of sunflower crop varieties. Because female sunflower specialists collect only sunflower pollen

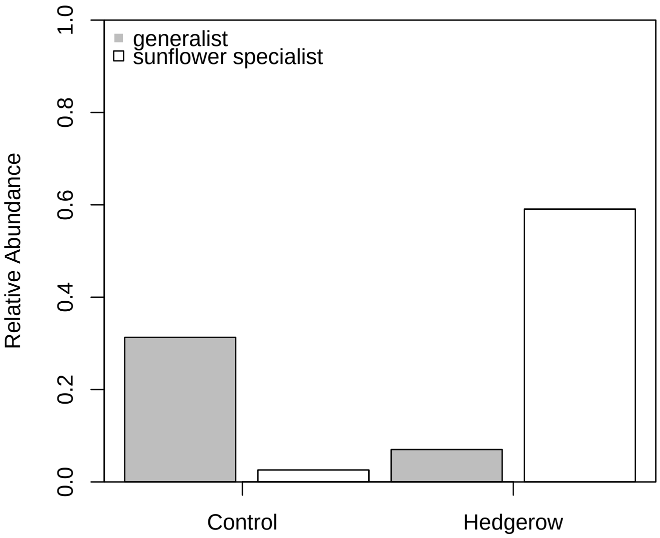

Fig. 3. In the independent data set, more sunflower specialists were found in sites with hedgerows, indicating a significant interaction between hedgerow presence and wild bee specialization on sunflower.

to provision their nests, they may not be attracted to the resources in hedgerows during the sunflower bloom period, instead being drawn into fields (Holzschuh et al., 2011). Nevertheless, assessment of the independent dataset indicated that hedgerows provide important floral resources to sunflower specialist bees, especially males. Male sunflower specialists have been observed investigating honey bees as potential mates, which increases honey bee movement from male-fertile to male-sterile sunflowers and increases their pollination efficacy (Greenleaf and Kremen, 2006). Male bees, therefore, likely contribute to the interactive effect between wild bee richness and honey bees on rates of seed set.

We found a slight positive effect of wild bee species richness on seed set rates, indicating that a higher number of bee species benefits pollination function in sunflower. Functional complementarity between species can enhance fruit and seed production in a variety of crops (Hoehn et al., 2008; Blüthgen and Klein, 2011). Bee foraging behavior and bee body size can influence within-inflorescence foraging, leading to more complete pollination in a single flower (e.g., strawberry, Chagnon et al., 1993). Bee foraging activity can also be affected by preferences for particular weather conditions (e.g., almond, Brittain et al., 2013), temperatures (e.g., radish, Albrecht et al., 2012), or preferences for floral phenology (Pisanty et al., 2014) leading to temporal complementarity. Interspecific interactions between bee species can also increase honey bee efficiency (Greenleaf and Kremen, 2006; Carvalheiro et al., 2011). In almonds, wild bee presence increases the likelihood that honey bees will move between different rows, which leads to higher pollen tube initiation and subsequent fruit set (Brittain et al., 2013). Both niche complementarity and interspecific interactions likely underlie the positive relationship we detected between richness and seed set (Klein et al., 2009).

In agreement with past findings (Greenleaf and Kremen, 2006; Carvalheiro et al., 2011), we detected an interactive effect between wild bee and honey bee visitation on sunflower seed set. We did not, however, detect any main effects of wild bee and honey bee visitation, despite strong evidence that wild bees positively increase seed set regardless of honey bee abundance (Garibaldi et al., 2013). In order to evaluate the direct contribution of wild bees, other studies have estimated the contribution of wild and honey bee visitation to seed set separately (Kremen et al., 2002; Isaacs and Kirk, 2010; Winfree et al., 2011; Morandin, Long and Kremen, unpublished data). We were unable to do this because of our study design, which did not examine seed set from single bee visits. Nevertheless, this is the first sunflower seed set study to detect an interspecific interactive effect at the community-level rather than at the individual-level. However, despite the importance of these interactive effects on sunflower yield, company was the factor that most strongly influenced seed set. Although there was little variation in head size between sunflower companies (Table S5), using company as a classification may mask other differences, such as genetic differences between varieties and variation in field management techniques. By pairing control and hedgerow sites by company, variety and landscape context, we sought to minimize these potential differences, and the few differences in management practice were noted between companies.

It is hypothesized that the effectiveness of field-edge vegetation re-diversification is maximized in landscapes that retain a small percentage of natural areas that can facilitate recolonization of restored habitats (Tscharntke et al., 2005). The added benefits of diversification efforts may be minimal in complex landscapes with high proportions of natural habitat since ecosystem service providers are often already supported. Diversification efforts may not support ecosystem providers in highly intensified (cleared) landscapes with no remaining natural habitat, either because there are no source areas to colonize the new habitats or because the new habitats alone cannot support populations of ecosystem service providers (Tscharntke et al., 2005). Although the landscape where we conducted our study constitutes a “cleared” landscape, and we did not detect landscape effects, other studies in the same location have found that hedgerows increase wild bee abundance, richness and population persistence and promote rare and/or more specialized species (Morandin and Kremen, 2013; M’Gonigle et al., 2015; Kremen and M’Gonigle, 2015). Nevertheless we did not find evidence that these biodiversity benefits translated into higher rates of pollination services in adjacent sunflower crop fields. Although both wild bee richness and abundance were important factors contributing to sunflower seed set, these contributions may be attributable to factors other than hedgerows. For example, wild bee visitors to sunflower were predominately sunflower specialists; the amount of sunflower maintained in the

Table 3
Model results for netted and visitation models where sunflower seed set was the dependent variable. Site was nested within pair, which was included as a random factor in both models.

Variable	Estimate	SE
Seed set-netted data		
Hedgerow presence (present)	–0.067	0.07
Company B	0.53^{*}	0.18
Company C	0.44	0.25
Company D	0.75^{***}	0.21
Distance into field	0.00	0.00
WB species richness	0.07^{*}	0.03
WB abundance	–0.04	0.03
HB visitation	–0.03	0.02
WB abundance × HB visitation	0.02	0.02
Seed set-visitation data		
Hedgerow presence (present)	–0.01	0.10
Company B	0.55^{***}	0.13
Company C	0.38^{*}	0.19
Company D	0.76^{***}	0.15
Distance into field	0.00	0.00
WB visitation	0.05	0.03
HB visitation	–0.04	0.02
WB visitation × HB visitation	0.33^{*}	0.01

Note: WB, wild bee; HB, honey bee. $^{**}P < 0.01$.
*** $P < 0.001$.

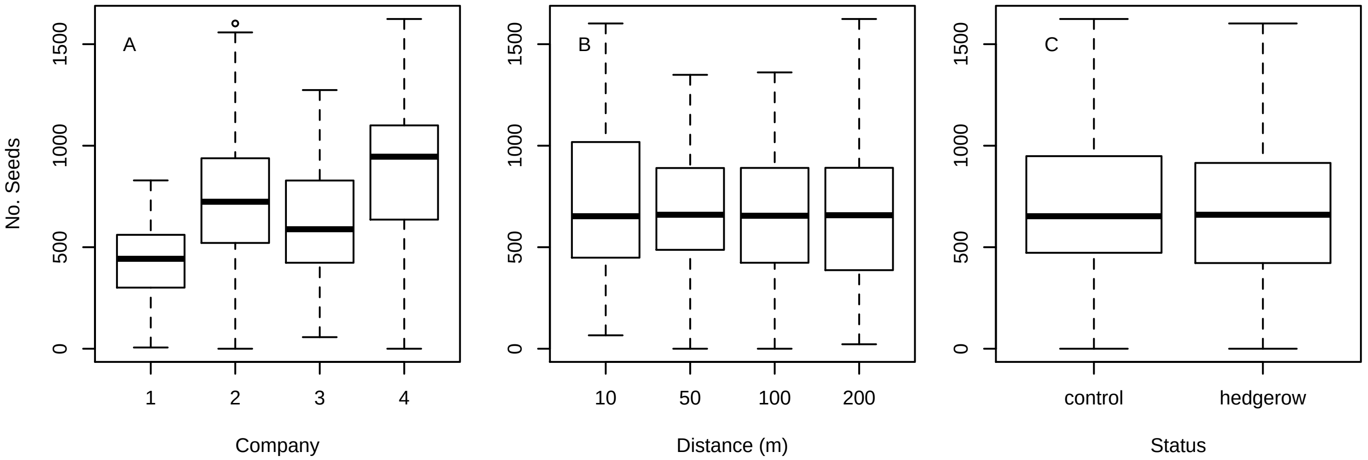

Fig. 4. Sunflower variety, which was associated with seed company (a), strongly influenced rates of sunflower seed set. Neither distance from the edge (b) nor hedgerow presence (status; (c)) impacted seed set. The dark line in each box shows the mean, the outer lines of the box denotes the 1st (lower) and 3rd (upper) quartiles, and the whiskers show the minimum and maximum values.

landscape over time could therefore influence sunflower pollinator populations more strongly than hedgerow plantings that do not contain floral resources suitable for the specialists' dietary requirements (Greenleaf and Kremen, 2006), as we found was true in the independent dataset.

It is important to balance the conservation value of field-edge plantings with ecosystem service delivery objectives. While conservation and ecosystem service outcomes can be synergistic, win–win scenarios are challenging to achieve (Naidoo et al., 2008; Tallis et al., 2008). Hedgerows augment pollinator populations, which can be important for achieving wild bee conservation goals (M'Gonigle et al., 2015; Kremen and M'Gonigle, 2015); however, they may not be a "silver bullet" strategy for increasing crop pollination. Both the scale of the re-diversification effort relative to the farming system and the adjacent crop type could limit the effectiveness of hedgerow plantings.

Hedgerows occupy <1% of our study landscape and contain 175 times less area than a typical average crop field in our study area. The intensity of bloom in hedgerows is also minimal in comparison to the hundreds of thousands of blooms in a single MFC field (Williams et al., 2012). Increasing the size of hedgerows relative to fields or introducing a suite of diversification techniques could increase the effectiveness of re-diversification efforts (Kremen and Miles, 2012). Patch size may influence a habitat's capacity to host different densities of pollinators (Carvell et al., 2011). Alternately, the configuration of habitat could impact pollinator populations. For example, when Morandin and Winston (2006) examined the optimal spatial distribution of a MFC, canola (*Brassica napus*), they found that both profits and pollination services would be maximized if a central field was left fallow or allowed to revert to semi-natural habitat. The size, configuration and quality of habitat may all interact to influence pollinator communities (Garibaldi et al., 2014).

The benefits of field-edge diversifications may also differ based on crop identity and landscape context (Garibaldi et al., 2014). For example, sunflower has easily accessible florets that attract both generalist and specialist pollinators. However, in systems where flowers have specific requirements, such as highbush blueberry (*Vaccinium corymbosum* L.) that requires buzz-pollination, the identity of pollinator species may be of more importance (Button and Elle, 2014). Further, species-specific responses to habitat features may differ. Carvell et al. (2011) found bumble bees had differential responses to wildflower patch size and landscape heterogeneity, indicating that local and landscape habitat factors can also interact with one another, and with crop-specific attributes, to affect crop pollination. In a tropical region, Carvalheiro et al. (2012) found that wildflower plantings worked in concert with natural habitat to heighten mango (*Mangifera indica*) production. There are a paucity of studies on the ecosystem service benefits from field-edge plantings, therefore the complex range of factors, including farming type, crop system, landscape context, and region (Holzschuh et al., 2007), influencing their performance is still relatively unknown (Garibaldi et al., 2014).

5. Conclusion

While hedgerow plantings show promise for augmenting pollinator populations in edge habitats and pollination services in some crop types, benefits from hedgerows likely vary in different cropping systems and landscapes. This context-dependency presents a challenge for promoting hedgerows as a "silver-bullet" strategy to enhance crop pollination. Different crops may require alternate diversification methods or changes in hedgerow design in order to attract pollinators and achieve pollination increases in adjacent crop fields. In intensively-managed ("cleared") landscapes, hedgerows alone may not be sufficient to promote pollinator populations, and other diversification techniques may be needed to complement hedgerows, such as reducing field size and increasing crop heterogeneity, using more varied crop rotations, etc. (Kennedy et al., 2013; Kremen and Miles, 2012). To maximize the efficacy of farm-scale re-diversification techniques, it is important to continue examining the levels of pollination services delivered from farm-scale re-diversification techniques to a variety of crops in a variety of regions. Field-scale interventions can then be targeted to crops and regions where they will have the highest impact.

Acknowledgements

We thank two anonymous reviewers for greatly enhancing this manuscript. We also thank the Kremen Lab for their insightful comments on earlier versions of this manuscript. We would like to acknowledge the contribution of our crew of field assistants, who made this work possible: Ashley Ellis, Tim Luttermoser, Kaysee Tom, Collette Yee, Brenden Sostak and Riley Waytes. Thank you to the farmers who collaborated with us and allowed us access to their fields, hedgerows and sunflower seeds. We sincerely appreciate the ongoing support of four anonymous sunflower companies that have contributed to this projects' success. This research was funded by a National Institute of Food and Agriculture graduate fellowship (to H.S.S), a Western Sustainable Agriculture and Education Graduate grant (to H.S.S.), and grants from the Army Research Office (W911NF-11-1-0361 to C.K.), the Natural Resources Conservation Service (WLF-69-7482-6-277 to The Xerces Society/C.K.), the National Science Foundation (DEB-0919128 to C.K.), and The U.S. Department of Agriculture (USDA-NIFA 2012-51181-20105 to Rufus Isaacs, Michigan State University).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2015.03.020.

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Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Hedgerow presence does not enhance indicators of nest-site habitat quality or nesting rates of ground-nesting bees

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A major challenge in habitat restoration is targeting the key aspects of a species' niche for enhancement, particularly for species that use a diverse set of habitat features. However, restoration that focuses on limited aspects of a species' niche may neglect other resources that are critical to population persistence. We evaluated the ability of native plant hedgerows, planted to increase pollen and nectar resources for wild bees in agricultural landscapes, to provide suitable nesting habitat and enhance nesting rates of ground-nesting bees. We found that, when compared to unmanaged field edges (controls), hedgerows did not augment most indicators of nest habitat quality (bare ground, soil surface irregularity, and soil hardness), although coarser soils were associated with higher incidence and richness of nesting bees. Hedgerows did not augment nesting rates when compared to control edges. Although all the bee species we detected nesting were also found foraging on floral resources, the foraging versus nesting assemblages found within a site were highly dissimilar. These results may reflect sampling error; or, species found foraging but not nesting in hedgerows could be utilizing hedgerows as "partial habitats," nesting outside hedgerow plantings but foraging on the floral resources they provide. We conclude that although hedgerows are known to provide critical floral resources to wild bees especially in resource-poor intensive agricultural landscapes, simply increasing vegetative diversity and structure may not be simultaneously enhancing nesting habitat for ground-nesting bees.

Key words: agriculture, conservation, emergence traps, field edges, nesting resources, pollination services, restoration

Implications for Practice

- Increasing flowering vegetation does not necessarily translate into increases in nesting habitat for ground-nesting bees.
- Using indicators of nest-site quality may not correlate with ground-nesting bee abundance and richness.
- Bee species found foraging in hedgerows will not always be indicative of the bee species nesting within hedgerows.
- Some bees foraging in hedgerows use hedgerows as a partial habitat that provides critical flowering resources.
- Limited nesting habitat will limit the ability of nesting bees to establish in restored habitats.

Introduction

For restoration projects aimed at promoting specific species or guilds, it is important to enhance habitat characteristics on which target taxa rely (Miller & Hobbs 2007). Yet the autecology of many species, particularly invertebrates, is complex and often poorly understood (Murray et al. 2009). Thus, a restoration project may elect to focus on readily managed factors known to affect a species' life-history. However, if only one dimension of a species' niche is restored, other factors critical to their establishment may be inadvertently neglected. For species reliant on restored fragments, an absence or lack of specific features could cause an area either to be unoccupied or to function as a sink (Pulliam 1988). Determining whether restoration of some habitat elements can enhance other key habitat features may be important for sustaining local populations of the species of interest.

Wild bees (Hymenoptera: Apoidea) are critically important species in natural and agricultural areas (Memmott et al. 2004; Garibaldi et al. 2013), and as such, have been the focus of habitat enhancement projects (Dixon 2009; Winfree 2010; Menz et al. 2011; Garibaldi et al. 2014). Pollen and nectar are the sole food supply for bee larvae, therefore floral blooms are essential for bee reproduction. In addition, bees require nesting substrates (e.g. appropriate soil conditions for belowground nesters; pithy stems or cavities in wood for aboveground nesters) and nesting materials (e.g. mud or leaves to construct partitions between brood cells). Bees are central place foragers; thus floral and nesting resources must be within flight range of their

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Author contributions: HSS, CK designed the research; HSS carried out the research; HSS, LCP conducted the analyses; HSS, LCP, CK coauthored and edited the manuscript.

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doi: 10.1111/rec.12338
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.12338/suppinfo

nest location (Westrich 1996). Identifying appropriate floral resources is easier than targeting nesting habitat, because nest sites are hard to locate and the nesting needs of many bee species remains unknown (Roulston & Goodell 2011). The majority of pollinator-related restoration projects therefore focus on floral diversity and abundance (Winfree 2010; Garibaldi et al. 2014), and not nesting resources.

Hedgerows are a common habitat enhancement technique targeted at augmenting wild pollinator populations in agricultural landscapes. Hedgerows are linear plantings of shrubs and forbs that can be added to field margins (Long & Anderson 2010); they may contain native or non-native species, or a mixture of both. Hedgerows are multifunctional, acting as windbreaks, filter strips, and erosion control buffers (Wratten et al. 2012). Beneficial insects (e.g. wild pollinators or natural enemies of crop pests) prefer native plants (Tuell et al. 2008; Isaacs et al. 2009; Morandin & Kremen 2013*a*), therefore, when hedgerows are planted with the goal of augmenting habitat for beneficial native insects they should contain numerous flowering native plant species (Long et al. 1998; Long & Anderson 2010). By planting species with overlapping bloom periods lasting from early spring to later summer, hedgerows provide stable, attractive floral resources throughout the growing season (Hannon & Sisk 2009; Gareau et al. 2013; Morandin & Kremen 2013*b*; Morandin et al. 2014).

As hedgerow enhancement specifically involves increasing local floral availability and diversity, it is unclear whether hedgerow presence also improves wild bee nesting habitat. Hedgerows introduce woody plants into agricultural landscapes often lacking vegetative and structural diversity. Morandin and Kremen (2013*b*) found that hedgerows increased the amount of dead wood over unenhanced field edges. A subsequent study found that hedgerow maturation led to higher occurrences of aboveground nesting bees in field edges containing hedgerows (Kremen & M'Gonigle 2015). The presence of perennial shrubs in hedgerows can limit soil disturbances in field edges, such as disking, that may negatively impact wild bee nesting (Brodt et al. 2009). Hedgerows may also suppress weed populations (Wilkerson 2014), potentially increasing the proportion of available bare ground. These changes might be expected to promote ground-nesting bees; in particular, bare ground is a site characteristic that has been linked to enhancing the abundance of belowground nesting bees (Potts et al. 2005; Sardiñas & Kremen 2014). However, evaluation of habitat enhancement projects to date has focused on floral resources. There therefore exists a pressing need for assessments of nesting resources in pollinator-focused restoration projects (Winfree 2010).

In this study, we examine the ability of hedgerows to increase nesting habitat for ground-nesting wild bees. We characterize nesting habitat by quantifying characteristics thought to be linked to nesting incidence (hereafter "nesting indicators"; Potts et al. 2005; Grundel et al. 2010; Sardiñas & Kremen 2014). First, we determine whether hedgerows enhance nesting indicators when compared to unenhanced field edges. Next, we ask whether differences in nesting indicators influence the nesting rates of wild ground-nesting bees. Finally, we compare the overlap in the composition of communities found nesting with those visiting floral resources at these sites to determine whether bee species are utilizing floral resources within hedgerows but not nesting there.

Methods

Study System

We conducted our study in Yolo County, located in California's Northern Central Valley. The region is characterized by intensive agricultural production of orchard and row crops and contains little remnant natural habitat (Kremen & M'Gonigle 2015; Sardiñas & Kremen 2015), although it also contains a relatively high density of hedgerow enhancements (Brodt et al. 2009). There is little topographic variation in the farmed areas, with most slopes less than 2% (NRCS USDA 2014). Soils are typically well-drained silty loam or silty clay loam (NRCS USDA 2014).

Hedgerows in our study were at least 5 years post-planting and contained a mixture of perennial shrubs, perennial forbs, and annual forbs (see Supporting Information for plant list, Table S1; Long & Anderson 2010). The majority of plant species are California natives, though hedgerows also contained numerous colonizing weedy species (Table S1). Although there was some variation in hedgerow management (e.g. hand weeding vs. spot herbicide treatment), many factors, such as use of pre-emergent herbicide and irrigation, were similar (Wilkerson 2014). Unrestored controls are also managed in a variety of ways, including mowing, disking, burning, herbicide treatment, or no active management (Garbach & Long unpublished data; Brodt et al. 2009; Morandin & Kremen 2013*b*).

We sampled eight hedgerows and eight unenhanced field edges (hereafter referred to as controls; Fig. S1). We sampled each site three times, twice in year 1 and once in year 2, between May and August, to capture variation in the bee community over the spring and summer flight seasons, as well as to document any changes to nesting resource availability. Sites were a minimum of 1 km apart to ensure the majority of the bee individuals visiting a site were unlikely to forage between sites (Greenleaf et al. 2007).

Sampling the Bee Community

We focused on belowground nesting bees because the majority of bees nest beneath the soil and locating the nests of aboveground nesting bees is exceedingly challenging (Roulston & Goodell 2011; Sardiñas & Kremen 2014). We sampled the belowground nesting community using 0.6 m^2 emergence traps (e-traps; Bug Dorm MegaView Science, Taiwan; Sardiñas & Kremen 2014). E-traps were fitted with jars at their apex filled with soapy water to kill emerging insects. We set e-traps at dusk to ensure that bees had returned to their nest sites; the e-traps were removed the following afternoon, approximately 20 hours after being set. We only set e-traps if weather conditions the following day were predicted to have clear skies, temperatures over 18°C and wind speeds less than 2.5 m/s to ensure that weather conditions would not impede insect activity. We placed

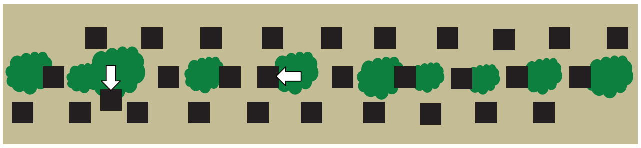

Figure 1. Sampling scheme for 30 emergence traps (black boxes) to capture ground-nesting bees in field edges with and without hedgerow plantings. If a hedgerow shrub (green) was in the location where an emergence trap was to be placed, we first tried to put the trap in line with the hedgerow, next to the shrub (left-pointing arrow); however, if another shrub was adjacent to the first, we then put the trap to another side (downward pointing arrow). In both cases, we placed the trap as close to the shrub as possible.

30 e-traps in each site during each sampling round. Ten e-traps were placed 30 m apart along three transects, one to either side of the hedgerow and one in line with hedgerow plantings (Fig. 1). If a shrub conflicted with placement of an e-trap, the e-trap was set alongside the plant as close to the base of the shrub as possible. The sides of each e-trap were weighted down to prevent bees from entering or escaping.

To document the bee species foraging on floral resources within our study sites, we netted bees from inflorescences for 1 hour, excluding time spent handling specimens. All sampling was conducted between 08:00 and 14:00 hours. Net surveys were performed within 10 days of e-trap sampling under allowed weather conditions.

Sampling of Nesting Habitat

We visually estimated indicators of nest-site quality within e-traps following the work of Sardiñas and Kremen (2015) and Potts et al. (2005). We focused on indicators that have been found to significantly impact nesting rates: percent bare ground, variation of slope of the ground, surface soil compaction, and soil particle size (Table 1; Sardiñas & Kremen 2014; Grundel et al. 2010; Potts et al. 2005). Farmed areas in the California Central Valley are generally flat, thus the sloping ground within the e-traps was indicative of soil surface irregularity, not topographic variation. Soil surface irregularity has been found to heighten nesting rates for some species (Wuellner 1999). To capture soil surface heterogeneity, we used the coefficient of variation in slope (CV). To evaluate soil particle size, we collected two samples at 10 cm depth at each site. Samples were homogenized, dried in a forced air oven at 40°C for 2 days, and sieved to remove coarse (>2 mm) particles and other debris. We then calculated average particle size (microns) with a laser diffraction particle size analyzer (LISST Portable XLR, Sequoia Scientific, Inc., Bellevue, WA, U.S.A.).

Statistical Analysis

We evaluated sample coverage from e-traps using species accumulation curves in the R package vegan (Oksanen et al. 2013; R version 3.1.2). To determine whether differences in the characteristics of nesting habitat translated to differences in the community composition of ground-nesting species, we calculated the pair-wise dissimilarity between sites for both species composition and nesting indicators (Gower 1971; Laliberté & Legendre 2010; Anderson et al. 2011). We then assessed the correlation between the dissimilarity of species and nesting indicators using a Mantel test.

We determined whether hedgerows increased nesting habitat using generalized linear mixed models (Bates et al. 2014). In each model, the nesting indicator was the dependent variable, site status (hedgerow or control) was the independent variable, and site was a random factor.

To assess the influence of nesting indicators on belowground nesting, we constructed a zero-inflated mixed model with a binomial error (Fournier et al. 2012). We assessed nesting incidence rather than abundance because we collected many social bee species that share nests (Table S2), we were therefore unable to determine the number of independent nests. To test whether hedgerows affected nesting rates, we included site type (hedgerow or control) as an explanatory variable. In addition, we included Julian date and Julian date square to account for the seasonal phenology of bees (Kremen & M'Gonigle 2015). All continuous variables were scaled.

Next, we examined species richness (rarified; Chao et al. 2005) within e-traps using a generalized linear mixed model with a Poisson error distribution and the same explanatory variables as the incidence models (Bates et al. 2014). Rarified richness was rounded so that a generalized linear mixed model with Poisson error could be fit.

Table 1. Nesting indicators used to characterize nesting habitat within emergence traps. We focused on nesting indicators that had previously been found to affect ground-nesting bee nesting rates significantly (Wuellner 1999; Potts et al. 2005; Sardiñas & Kremen 2014; Sardiñas et al. 2015). All indicators were measured at the trap-level except soil particle size, which was assessed at the site-level.

Nesting Indicator	*Measurement*
Bare ground	% bare exposed soil
Slope variability (proxy for soil surface irregularity)	We took three measurements of slope in each e-trap: two in corners and one in the center using a pitch and slope locator (Model No. 700, Johnson Level & Tool Mfg. Co., Mequon, WI, U.S.A.)
Surface soil compaction	We took three measurements of surface resistance (range 0–4.5 kgf/cm^2) with a penetrometer (Model no. 77114, Forestry Suppliers, Inc., Jackson, MS, U.S.A.)
Soil particle size	Average particle size (microns) from a 5-g sample processed in a laser diffraction particle size analyzer (Sequoia LISST Portable XLR)

We then evaluated whether nesting indicators influenced the incidence and rarified richness of foraging bees collected using aerial netting from plants in bloom in hedgerow and control sites using the same model structure, but including a random effect of species. We then compared the assemblage of bees collected in e-traps (hereafter "nesting bees") to the assemblage of bees collected with netting (hereafter "foraging bees") with a permutational multivariate ANOVA (PERMANOVA) using a dissimilarity estimator that incorporates species abundances while also accounting for unobserved species (Chao et al. 2005; Oksanen et al. 2013). This was visualized using non-metric dimensional scaling (NMDS).

For all models we used model validation procedures to ensure that the models were not overdispersed and did not have inflated type I error rates (Ives 2015; Sardiñas et al. 2015, in press). We included only female bees of ground-nesting species in all analyses (both nesting and foraging) because male bees are not indicative of nesting rates and may only be resting in vegetation (Kim et al. 2006). We did not examine the availability of nesting resources for aboveground nesting species because we did not collect aboveground nesting species in e-traps. We also excluded any parasitic bees, as their distributions are linked to that of their host species and including them could double-count the resources preferred by their host species.

Results

Nesting Bees

We collected 893 ground-nesting bees from 10 species in e-traps (Table S2). Ninety-nine percent of all bees collected in e-traps were in the genera *Halictus* and *Lasioglossum*. Rarefaction showed that species accumulation leveled off by 30 traps—the number we set in each site during each sampling round—in half of the sites we sampled (Fig. S2). This suggests that increased sampling with e-traps likely would have detected additional species. An average of 39% of e-traps (SE = 6.4) contained belowground nesting bees per site/sampling round combination.

Nesting habitat indicators were highly similar in control and hedgerow sites (Table 2; Fig. S3), suggesting that hedgerow plantings did not alter these soil- or nesting-related characteristics. In fact, ground-nesting rates were significantly lower in sites containing hedgerow enhancements than in unenhanced control edges (Table 3). There was a downward trend in both nesting incidence and the richness of ground-nesting species in hedgerows (Table 3; Fig. 2). Seasonality (Julian date) had the strongest effect on nesting, with nesting bees peaking in incidence in late June. Soils with finer particles (clay- and silt-based soils) had marginally negative effects on nesting (Table 3). Nesting indicators did not strongly impact nesting; ground-nesting bee community dissimilarity was not correlated with site to site dissimilarity in nesting characteristics ($r = -0.13, p = 0.76$), indicating a lack of correlation between nesting species and the indicators we measured.

Foraging Bees

We netted 425 ground-nesting bees from 20 species foraging on floral resources in hedgerow and control sites (Table S2). The Chao1 estimated species richness of foraging ground-nesting bees was 38.66 ± 14.84. Although the assemblage of ground-nesting species was a subset of the overall foraging community, the composition of nesting versus foraging species assemblages of ground-nesters collected at the same site was highly differentiated (Fig. 3). Furthermore, the assemblages of ground-nesting bees in control and hedgerow edges more closely resembled one another than they did the foraging assemblage in the same site types. Soil hardness, soil particle size, and Julian date all had marginal effects on the richness of foraging ground-nesting bees, whereas foraging incidence responded to surface soil compaction (Table 3).

Table 2. Effect of hedgerow presence on nesting indicators. The estimate provides the effect size of the nesting indicator in hedgerow sites, when compared to unenhanced, control field edges. All results were non-significant.

Nesting Indicator	*Estimate*	*t*
Bare ground	−17.93	−1.60
CV of slope	−1.15	−1.44
Surface soil compaction	0.07	0.45
Soil particle size	0.02	0.862

Table 3. Model results of the influence of site status (hedgerow present or absent) and indicators of nesting quality on the abundance and rarefied richness (Chao-1) of ground-nesting bees found in emergence traps (Nesting) and netted on inflorescences in hedgerow or control sites (Foraging). $^{+}p < 0.10$; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Variable	*Nesting*	*Foraging*
Incidence		
Status (hedgerow)	−1.02 *	0.45
Bare ground	0.09	−0.17
CV of slope	-0.24^{+}	0.16
Surface soil compaction	0.08	0.61*
Soil particle size	−0.55 *	0.17
Julian date	1.15***	−0.36
Julian date^2	−1.56***	0.66*
Richness		
Status (hedgerow)	−0.20	0.04
Bare ground	0.05	−0.01
CV of slope	−0.09	0.05
Surface soil compaction	0.07	0.07^{+}
Soil particle size	−0.23*	0.10 *
Julian date	0.34**	−0.15***
Julian date^2	−0.15	0.14**

Discussion

Hedgerow presence did not dramatically alter the underlying site conditions for the nesting indicators we measured. Nesting indicators either did not vary among sites (e.g. soil hardness and slope variability), or variation within site type (hedgerow vs. control) was higher than between site types (e.g. bare ground). High weed density in both hedgerow and controls contributed to the similarity in percent bare ground in both site types, despite the presence of woody shrubs in

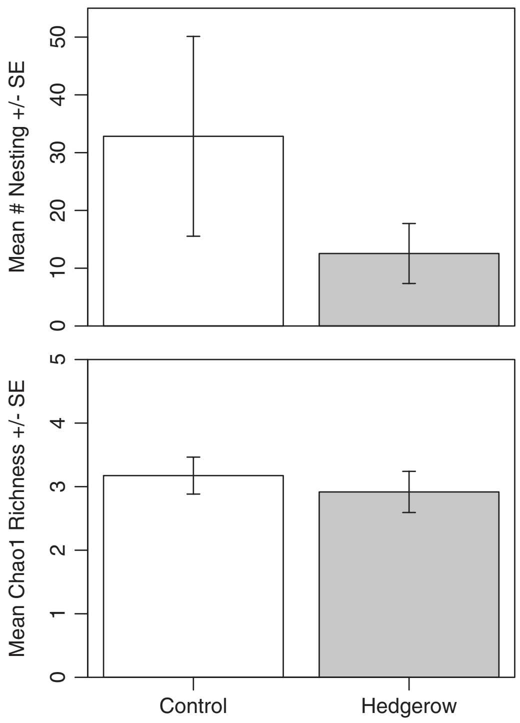

Figure 2. Mean (± SE) bee abundance per site and Chao1 (abundance-based) species richness of ground-nesting bees collected in emergence traps in hedgerow and control field edges.

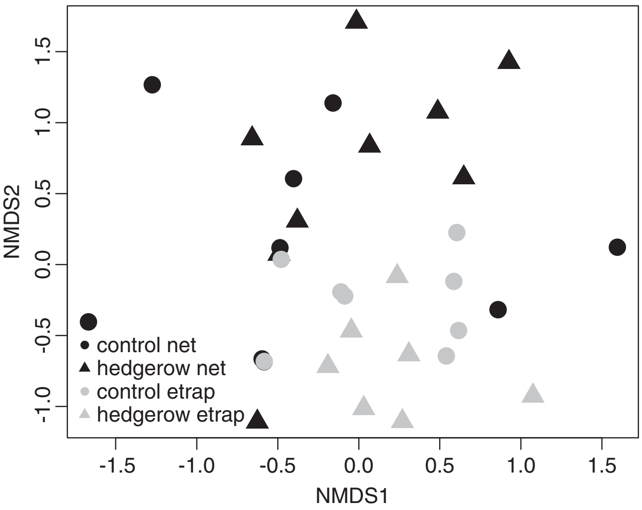

Figure 3. Chao dissimilarities between ground-nesting bee assemblages nesting and foraging in hedgerow and control edges visualized using NMDS. Communities of foraging (aerial net) versus nesting (e-traps) of ground-nesting bees are distinct.

hedgerows that have the potential to shade out weedy species (Wilkerson 2014).

The lack of turnover of nesting species that we observed across sites could be a result of this low variation in nesting characteristics between sites; if species rely on specific nesting habitat that is absent in both hedgerows and control sites, we would expect to find a homogeneous community characterized by low turnover rates. This observed homogeneity of nesting habitat within agricultural field margins may function as an ecological filter, limiting colonization by species with different nesting requirements (Ponisio et al. in press).

Despite their lack of measureable differences in nesting habitat, hedgerows may nevertheless function as a refuge for bees nesting in agricultural areas. Hedgerows contain undisturbed ground that is free from tilling and herbicide use, methods frequently used to control weeds in unenhanced field margins (Wilkerson 2014). Although we collected equal numbers of ground-nesting bees in hedgerow and non-hedgerow sites, their offspring may be more likely to survive until emergence the following year in hedgerow sites. Ullmann (2015) found that tilling within agricultural fields containing active nests led to high mortality rates in ground-nesting bee offspring. To date, nesting success of ground-nesting bees in hedgerows has not been evaluated.

Ground-nesting wild bees did not respond to most of the nesting indicators that we measured, except for soil particle size. Soils with smaller particles adversely impacted nesting rates. In our study, system soils are predominantly silty clay loams (NRCS USDA 2014). Clay-based soils have been found to be the least-utilized soils for nesting bee species (Cane 1991), and may limit the species that can colonize agricultural field margins in our area. The most abundant bees in our e-trap samples (sweat bees in the genera *Halictus* and *Lasioglossum*) may be less sensitive to poor soil conditions or disturbance, contributing to their dominance in our study region (Morandin & Kremen 2013*b*). A meta-analysis examining bee response to disturbance found that small-bodied, social species (including sweat bees) were less sensitive to intensified agriculture (Williams et al. 2010). Thus, agricultural landscapes may only provide suitable nesting habitat to bee species with certain traits (Kremen & M’Gonigle 2015).

The nesting biology of the majority of bee species remains undescribed (Roulston & Goodell 2011), therefore the range of variables influencing wild bee nesting behavior is largely unknown. Although we focused on nesting characteristics that have been previously shown to influence community composition (Potts et al. 2005; Grundel et al. 2010; Sardiñas & Kremen 2014), most did not strongly impact nesting patterns in the agricultural field edges we studied, nor were they differentiated between hedgerows and controls. Other factors that we did not measure may influence nesting, such as insolation (Potts & Willmer 1997) or soil moisture (Xie et al. 2013), however, these can be variable within and between days, making it challenging to accurately assess their influence on nesting rates.

The edaphic characteristics preferred by wild bees for nesting may be slow to respond to restoration efforts that do not directly target soil properties. For example, although hedgerows in our study were between 5 and 12 years post-planting (Morandin & Kremen 2013*b*; Sardiñas & Kremen 2015), this short time frame might not be sufficient to affect significant changes in soils in agricultural field edges. Thus, once edaphic conditions suitable for bee nesting are identified (such as with alkali bees; Stephen

1960), specific techniques aimed at creating such conditions may need to be implemented at restoration sites.

We collected many species of bees foraging in hedgerows that we did not capture in e-traps. Foraging bees that we did not encounter in our e-trap sample could have been nesting elsewhere in the landscape, using flower-rich hedgerows as partial habitats (Westrich 1996). Nearby natural or seminatural habitat, such as rangelands, have been suggested as potential nesting habitat (Kremen et al. 2002). Adjacent agricultural fields could have also provided nest site locations (Kim et al. 2006; Sardiñas et al. 2015, in press). Alternately, foraging species could have been nesting in our study sites but were undetected by e-traps. Despite the low area covered by e-traps (<1% of the study site during each sampling round), sampling effort curves showed that capture rates saturated at just four species. We were unable to sample all locations within hedgerows, for example, e-traps did not fit directly underneath hedgerow plants; we therefore may have inadvertently missed potential nesting sites. Shady areas, however, are not thought to provide attractive nesting areas as direct sunlight has been observed to stimulate bee activity (Potts & Willmer 1997).

As bees are mobile, small-scale habitat enhancement projects in heterogeneous landscapes or natural habitats may not need to focus on enhancing nesting habitat, because bees may be able to forage from their nesting sites in adjacent habitat into the restored site to utilize available floral resources (Westrich 1996). In highly altered, homogenous landscapes, such as intensified agricultural areas, nesting habitat is likely limited, therefore improving local nest-related conditions may be critical. Our findings suggest that only a subset of bees nest within hedgerow plantings, while many more species forage there. These foraging species may use hedgerows as a "partial habitat" (Westrich 1996). Although hedgerows may only provide some of the resources required for the majority of the species utilizing hedgerows, hedgerows providing a diverse array of sequential floral resources likely contribute to maintaining local bee populations (M'Gonigle et al. 2015) and communities (Kremen & M'Gonigle 2015). In order to maintain and enhance pollinator populations, it is important to continue increasing floral diversity and abundance in agricultural regions while also exploring alternate methods for enhancing nesting habitat.

Acknowledgments

We thank R. Thorp, H. H. Laidlaw Jr., Honey Bee Research Facility, University of California, Davis for specimen identification. K. Cutler made essential contributions to field and lab work. L. Larsen, C. Pallud, and E. Lewis greatly assisted with soil analyses. This project would not have been possible without the assistance of undergraduate interns and field assistants. We also thank the growers who supported our research on their farms. This project was funded by a Western Sustainable Agriculture Research and Education graduate grant (to H.S.S.), a National Science Foundation Graduate Research Fellowship (to H.S.S.), a National Institute for Food and Agriculture Fellowship (to H.S.S.), the Natural Resources Conservation Service (WLF-69-7482-6-277 to The Xerces Society/C.K.), the National Science Foundation (DEB23 0919128 to C.K.), the U.S. Department of Agriculture (USDA-NIFA 2012-51181-20105 to R. Isaacs, Michigan State University), and the Army Research Office (W911NF-11-1-0361 to C.K.).

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Hedgerow (red) and control (yellow) field edges in our study landscape, Yolo County, in the CA Central Valley.

Figure S2. Rarefaction curves of species collected in emergence traps (e-trap) in hedgerow and control sites over three sample rounds.

Figure S3. Histograms of site characteristics we measured as indicators of nesting habitat quality.

Table S1. Plant species flowering in hedgerow only (H), control only (C), and both site types during e-trap sampling.

Table S2. Bee species collected from emergence traps (nesting species) and from inflorescences in hedgerow and control sites (foraging species).

Coordinating Editor: Stephen Murphy

Received: 3 September, 2015; First decision: 15 November, 2015; Revised: 25 November, 2015; Accepted: 23 December, 2015

Title: Sunflower (*Helianthus annuus*) pollination in California's Central Valley is limited by native bee nest site location

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Word counts:
Total- 7675
Title- 16
Summary-349
Main text- 5355
Acknowledgements- 120
References- 1499
Tables and figure legends-361
Number of tables and figures- 6
Number of references- 59

Abstract

The delivery of ecosystem services by mobile organisms depends on the distribution of those organisms which is, in turn, affected by resources at local and landscape scales. Pollinator-dependent crops rely on mobile animals like bees for crop production, and the spatial relationship between floral resources and nest location for these central-place foragers influences the delivery of pollination services. Current models that map pollination coverage in agricultural regions utilize landscape-level estimates of floral availability and nesting incidence inferred from expert opinion, rather than direct assessments. Foraging distance is often derived from proxies of bee body size, rather than direct measurements of foraging that account for behavioral responses to floral resource type and distribution. The lack of direct measurements of nesting incidence and foraging distances may lead to inaccurate mapping of pollination services. We examined the role of local-scale floral resource presence from hedgerow plantings on nest incidence of ground-nesting bees in field margins and within monoculture, conventionally managed sunflower fields in California's Central Valley. We tracked bee movement into fields using fluorescent powder. We then used these data to simulate the distribution of pollination services within a crop field. Contrary to expert opinion, we found that ground-nesting native bees nested both in fields and edges, though nesting rates declined with distance into field. Further, we detected no effect of field-margin floral enhancements on nesting. We found evidence of an exponential decay rate of bee movement into fields, indicating that foraging predominantly occurred in less than 1% of medium-sized bees' predicted typical foraging range. Although we found native bees nesting within agricultural fields, their restricted foraging movements likely centralize pollination near nest sites. Our data thus predict a heterogeneous distribution of pollination services within sunflower fields, with edges receiving higher coverage than field centers. To generate more accurate maps of services we advocate directly measuring the autecology of ecosystem service providers, which vary by crop system, pollinator species and region. Improving estimates of the factors affecting pollinator populations can increase the accuracy of pollination service maps and help clarify the influence of farming practices on wild bees occurring in agricultural landscapes.

Keywords

Agriculture; Bee conservation; Ecosystem service provider; Floral enhancements; Fluorescent dye; Foraging; Hedgerows; Mass-flowering crops; Mobile agent-based ecosystem services; Nesting.

Introduction

For ecosystem services provisioned by mobile organisms, the distribution and foraging range of ecosystem service providers impacts the stability and magnitude of services delivered (Kremen et al. 2007, Garibaldi et al. 2011, Jonsson et al. 2014). Resource availability at local and landscape scales is a key driver of the abundance and richness of species that provide ecosystem services (Kremen 2005). Quantifying the spatial distribution of key resources can help map ecosystem services; however, predictions of service provisioning depend on the accuracy of resource assessments. At the landscape-scale, proxies are often used to describe resource distributions. For example, in models of pollination services, proxies have been developed for each of the three main factors that influence the distribution of native bees and hence their ability to pollinate crops. Currently, land cover is used as a proxy for floral richness or abundance (Lonsdorf et al. 2009, Ricketts and Lonsdorf 2013, Schulp et al. 2014), nesting habitat quality is a proxy for nesting rates (Keitt 2009, Lonsdorf et al. 2009), and bee body size is a proxy for foraging range (Benjamin et al. 2014, Lonsdorf et al. 2009). However, if such proxies poorly capture floral resources, nesting habitat quality and foraging ranges, then maps of predicted pollinator abundances or services may not reflect actual levels of pollination provided to crops. In this paper, we make direct measurements of these parameters in order to map pollination services at the scale of a farm field.

The data used to map floral resources in current pollination models is often at large spatial scales derived from remotely-sensed data. This approach can miss finer-scale patterns in vegetation that may affect bee foraging patterns, and therefore potentially under- or over-estimate pollination services (Lonsdorf et al. 2009). Local floral resources can have strong effects on native bee communities (Potts et al. 2003, Roulston and Goodell 2011, Williams and Winfree 2013). Responses to increased floral diversity at the field-scale, through crop diversification or field-margin floral enhancements, include heightened native bee abundance within field edges and in crop fields (M'Gonigle et al. *in press*, Morandin and Kremen 2013). However, because bees are mobile and are central-place foragers, both the location of their nest sites and their foraging range can mediate the effects of floral resources. For example, specialist bees may prefer to nest in close proximity to their host plants, as exemplified by the squash specialist *Peponapis pruinosa*, which nests at higher rates within squash fields (Esther Julier and Roulston 2009). Similarly, adding floral resources to field margins could increase the attractiveness of these locations as nest sites.

It is challenging to quantify nesting incidence because nests are difficult to locate (Sardiñas and Kremen 2014); therefore, within pollination models, nesting is predominantly based on expert opinion rather than nesting surveys. By using expert opinion, however, the areas predicted to support native bee ground-nesting is limited to field edges and natural habitats (Brosi et al. 2008, Lonsdorf et al. 2009, Rands & Whitney 2011). Brosi et al. (2008)'s model, which optimizes pollination services in agricultural landscapes, divided the farmscape into natural habitat cells or agricultural cells; nesting was restricted to the natural habitat cells. The rationale for limiting nesting to specific areas is based on the assumption that bees prefer undisturbed soils, such as untilled field margins and remnant natural habitat (Chaplin-Kramer et al. 2011; Rands and Whitney 2011). Agricultural fields are therefore presumed to contain fewer nests than semi-natural habitats due to farm management practices including irrigation and tillage. There is conflicting evidence, however, concerning the effects of soil disturbance on below-ground nesting. A meta-analysis found that the relative abundance of below-ground nesting bees increased in disturbed habitats, although tilling had an overall negative effect, with the strength of the effect varying by species (Williams et al. 2010). Both generalist and specialist species have been found nesting directly within tilled sunflower fields, although nesting rates in undisturbed field margins were higher than within fields (Kim et al. 2006). The ability of bees to nest in agricultural fields calls into question the rationale for limiting nesting to field margins or non-crop areas within agricultural landscapes; relaxing this constraint could dramatically alter current model predictions.

The pollination maps produced by these models provide tools that could potentially influence on-farm land use decisions. Maps that highlight the importance of habitat features for augmenting pollinator abundances, such as proximity to field-scale diversification techniques, could enhance grower adoption of conservation practices (Stonehouse 1996, Knowler and Bradshaw 2007). Such maps and models could also affect the promotion of on-farm diversification techniques by government programs, such as the Environmental Quality Incentive Program in the United States and agri-environmental schemes in Europe (Vaughan and Skinner 2008). Improving estimates of the factors affecting pollinator populations can increase the accuracy of pollination service maps and help clarify the influence of farming practices on wild bees occurring in agricultural landscapes.

To facilitate development of models based on measurements of nesting and foraging inputs rather than expert opinion or proxies, we examined the nest location and movement of ground-nesting bees in intensively managed mass-flowering crop fields with or without local floral resource enhancements provided by bordering hedgerows. In accordance with previously published model parameterizations, we predicted that (i) native bees would only nest in edges, and that (ii) field margins containing the floral enhancements provided by hedgerows would provide better nesting habitat than unenhanced field margins. We also expected to (iii) find evidence that within crop fields, bee foraging distances are consistent with allometric predictions of their typical foraging range. We then use these data to model the coverage of pollination services within a single crop field.

Materials and Methods

Study system

This study was conducted in sunflower (*Helianthus annuus*) fields in Yolo Co., in California's Central Valley from June to July in 2012 and 2013 (Fig. A1). To maintain independence between fields, we ensured fields were a minimum of 900 m apart (range, 947-5,409; Greenleaf et al. 2007). Sunflower is an artificially gynodioecious pollinator-dependent row crop with male-sterile (female) heads that produce nectar and male-fertile (male) heads that produce both nectar and pollen (Greenleaf and Kremen 2006). There is one male row for every 4-6 female rows. To facilitate isolation of hybrid offspring, sunflower fields are moved each year; therefore none of the fields were sampled in both years.

Floral resources

To evaluate whether local-scale floral resources influenced native bee nesting, we sampled sunflower fields adjacent to either hedgerows or unenhanced field margins (hereafter "controls"). Hedgerows contained native flowering shrubs and forbs that bloom sequentially over the year to provide resources to bee species with differing flight periods (Long and Anderson 2010). Each hedgerow was between 250-300 m in length. Control sites were bare or weedy field margins. When we sampled a sunflower field adjacent to a hedgerow, we also sampled a control field containing the same sunflower variety, at the same stage of bloom (> 90% of heads flowering), and in the same landscape context (similar proportion of natural habitat within a 1 km buffer) within one week.

We collected data on floral cover and diversity in each site in the same quadrats in which we sampled nesting (see Nesting section below). Only a portion of the plant species present within the hedgerows bloomed during our study period (Table A1). Hedgerows also contained weedy species; the most predominant were *Convolvulus arvensis* (bindweed), *Brassica* spp. (wild mustard), and *Polygonum arenastrum* (common knotweed). Hedgerow composition and history are described in detail in Long et al. (1998). Controls sites did not contain any native plant species (Table A1); dominant weedy species were the same as those in hedgerows.

Nesting

We examined ground-nesting rates in ten sunflower fields in 2012 and eight fields in 2013 (Fig.S1). We set ten 0.6 m^2 emergence traps (e-traps; Bug Dorm, Taichung, Taiwan) spaced 20 m apart along a single transect in field margins with and without hedgerows (Fig. 1). We then placed five e-traps at 0, 10, 50, 100 and 200 m along each of two 200 m parallel transects (T1 and T2) extending into each field (Fig. 1). Each e-trap was equipped with a kill jar at its apex filled one-third full with soapy water. The edges of the e-traps were secured with soil to prevent any bees from entering or exiting. We placed traps at dusk, after bees had retired to their nests, thus any bees collected in the e-traps were those emerging from their nests to forage. We emptied the kill jars approximately 20-22 hours after traps were set. We stored all specimens in 95% ethanol until they were pinned, after which they were identified by expert taxonomist Dr. Robbin Thorp (Professor Emeritus, Harry H. Laidlaw Jr. Honey Bee Research Facility, University of California, Davis), and stored in the Essig Museum at UC Berkeley. Only female bees are considered in analyses as male bees may have been resting in vegetation and are not indicative of nesting rates (Kim et al. 2006).

Soil characteristics may influence nesting incidence and potentially provide a proxy for nesting habitat suitability in pollination models. Therefore we measured mean particle size and soil heterogeneity. We collected four soil samples at 10 cm depth at each site, two along a transect in the field margins at 40 and 60 m, and two in each field at 10 m on T1 and 100 m on T2. Soil was then dried in a forced air oven at 40°C for two days and sieved to remove coarse particles (> 2mm). We calculated average particle size with a laser diffraction particle size analyzer (Sequoia LISST Portable XLR). To measure soil heterogeneity within a 1 km buffer around each site, we calculated Shannon's diversity index, the proportional abundance of each soil class. Soil classes were identified from the 2013 Natural Resource Conservation Service soil map (U.S. Department of Agriculture 2013).

Key habitat features that might influence nesting have also been examined as proxies for nesting (Table A2; Sardiñas and Kremen, 2014, Potts et al. 2005). We therefore visually estimated percent bare ground, percent vegetative cover, percent leaf litter, percent rocks, dead wood, cracks, cavities, slope of the ground, and surface soil compaction within each e-trap (hereafter "nesting characteristics").

Foraging

We tracked bee movement in a subset of eight sunflower fields in 2012. In each field we delineated six or seven 100 m transects (depending on row spacing within the field) in each male row between 0-50 m from the field edge (Fig. 1), measuring the distance between each transect. We walked the along the first collecting medium-sized male and female bees with nets and bug vacuums (Backyard SafariTM). We defined medium-sized bees to be approximately the size of the European honey bee *Apis mellifera*. In our study system this included the genera *Diadasia*, *Melissodes*, *Megachile*, *Pepopnapis*, and *Triepeolus*. Each bee was placed in a collecting vial containing fluorescent powder (Shannon Luminous Materials, Inc., Santa Ana, CA, USA; Frankie 1973, Stockhouse 1976). The vibration of the bees' wings caused the powder to disperse throughout the vial, coating each bee completely. Bees were released after approximately five seconds. The majority of bees then departed the transect, exhibiting a typical stress response. They were typically not seen again during collection, which lasted 2-5 hours depending on the site. We attempted to standardize the number of bees marked to 100 bees per site, but in some cases were unable to collect the full number (range, 70-120). To standardize environmental factors that could affect foraging, we began collection at 9 am at each site and only sampled when weather conditions were clear/sunny, wind speeds were below 2.5 m/s, and temperatures were above 18°C.

To quantify the marks left by bees in the field, 2 people walked each transect for 30 minutes after dusk scanning both male and female sunflower heads with UV lights for traces of luminous powder. We also searched within field margins, but did not find a single mark over the course of the study. The fact that we found marks close to release sites indicates that bees did return to the places they were originally caught. In fact, we noted dyed bees entering their nest holes in the rows where they were marked (H.S.S., pers. obs.).

Normal bee behavior, such as grooming and flight, could result in powder loss. Over a four hour period, bumble bees were found to lose approximately 6.1% of the pollen (or powder) collected on their body in ways unrelated to pollination, such as flight, grooming, or landing on other parts of the (Rademaker et al. 1997). To determine whether the amount of powder observed was affected by the physical loss of powder through activities other than pollination, we evaluated the number of powder depositions that a single marked bee is able to make by coating dead *Melissodes* specimens with luminous powder and pressing them onto sunflowers in the lab (Rademaker et al. 1997). We found specimens were still able to deposit dye after 20 presses. Many fewer than 20 powder observations per marked bee were found in the field, indicating that declines in observation with distance into the field were not solely a result of unrelated powder loss.

Analyses

We standardized all nesting characteristics (subtracted mean and divided by standard deviation), then checked them for collinearity. Because of strong negative correlation with percent bare ground, we removed percent leaf litter and vegetation, but retained all other nesting variables.

We analyzed nesting abundance using a negative binomial model in the R package lme4 (Bates et al. 2014). Although the bee nesting data contained a high number of zeros, we did not find evidence of overdispersion. However, negative binomial models are prone to high type I error rates (Ives 2015); we therefore used model validation procedures to test our abundance model for this issue (Appendix B). Fixed effects were distance into field, hedgerow presence (hedgerow or control edge), soil particle size, soil heterogeneity, and nesting characteristics. We also included an interaction between distance into field and hedgerow presence to determine whether hedgerows impacted nesting rates within fields. Site was included as a random effect. We evaluated variables using a stepwise process and comparing AIC scores (scores with 4 AIC points were considered comparable). The nesting characteristics percent rocks, wood, cracks and cavities were eliminated in this manner.

We assessed nesting incidence, coded as presence or absence (1, 0), using the same fixed and random effects as in the abundance model but with a generalized linear mixed model with a binomial distribution in the R package MASS (Venables and Ripley 2002). We analyzed raw species richness using a generalized linear mixed model in the R package nlme (Pinheiro et al. 2015). We then visually compared rarefied richness by site in fields and edges with and without hedgerows using 100 permutations of the random species accumulation method in vegan (Oksanen et al. 2013). To estimate total species richness across all sites we used a jackknife from the vegan package (Oksanen et al. 2013).

To determine the rate of decay of powder marks we used a non-linear least square regression. We then assessed the effects of the number of bees marked in each site, the ratio of female to male bees marked, distance from the marked row (shortest linear distance from “mark” row to "recapture" row), and treatment (hedgerow versus control field) on the number of powder observations using a generalized linear mixed model with a Poisson distribution with row nested within site as a random factor in the R package lme4 (Bates et al. 2014, Zuur et al. 2009).

Mapping

To map pollination coverage in a single hybrid sunflower field, we first simulated the distribution of nests. In the nesting data we found that nests were well described by a negative binomial distribution. To approximate this distribution, we used a log Gaussian Cox process (Cox and Isham 1980). The log Gaussian Cox process models nest density as a spatially explicit log-Gaussian surface and then generates exact nest locations by sampling the surface with a Poisson process. An advantage of this approach is that the Gaussian surface captures potential spatial co-variance in nest density. Using the R package spectralGP (Paciorek 2007), we parameterized the Gaussian process with an exponential covariance structure and a mean density of 0.1 nests per meter, reflecting the average number of observed nests per site. We also included a mild edge effect, allowing the mean density to increase exponentially by 5% toward the edge of the field. We computed the log of this distribution, used this spatially varying surface as the density of nests, generating exact nest locations via a Poisson process using the R package spatstat (Baddeley and Turner 2005). Next, we approximated bee foraging ranges from these nests with an exponential decay rate of 1, approximately what we found in our movement study and also the decay rate utilized in the Lonsdorf pollination services model (Lonsdorf et al. 2009). The resulting incidence of bee nests within a field combined with the foraging range around those nests depicts the expected pollination coverage from medium-sized bees predicted by our data.

Results

We collected 95 female ground-nesting bees from e-traps representing 10 species (Table A3). Our total jackknifed species richness across all sites and years was 15 ± 3. We did not find a higher number of species in hedgerows or fields adjacent to hedgerows. However, when we rarefied richness separately for field borders and fields both with and without hedgerows, we found that the number of nesting species accumulated continued to increase, particularly in control margins that lacked hedgerows (Fig. A2).

Nesting in agricultural edges and fields

Ground-nesting bees nested in both field margins and within sunflower fields; however, we found higher numbers of bees nesting in margins than within fields ($t = 9.263$, $P < 0.01$; Table 1; Fig. 2). Within fields, nests were clustered near the field borders, though we found lower densities of nests throughout fields (Fig. 2). The richness of nesting species was also slightly higher in margins ($t = -1.92$, $P = 0.056$). Hedgerow presence did not influence the abundance ($t = -0.143$, $P = 0.733$), incidence ($t = -0.51$, $P = 0.621$), or richness ($t = -0.88$, $P = 0.392$) of ground nesters. Nesting was associated with areas containing steeper slopes, but not with soil hardness (Table 1).

All soils from our study sites were classified as clay loams (Fig. A3). Soils from field margins and within fields at the same site were more similar to one another than fields were to other fields and edges were to other edges. We did not detect an effect of soil particle size on nesting however, we did find a marginally significant trend of increased nesting with higher soil heterogeneity in the surrounding landscape (Table 1).

Patterns of movement detected

We dyed a total of 743 medium-sized bees with luminous powder, with a median of 101 per site. 72.4% of all bees dyed were in the genus *Melissodes*, with 428 females and 110 males (Table A3). 97.2% were sunflower specialists (Table A3). We observed 464 traces of powder on sunflower heads, with 80.7% concentrated in the first row. Powder marks decayed at a rate of 0.9964 ($t = 2.80$, $P = 0.009$) from the transect in which bees were marked (Fig. 3). Distance into the field had the strongest effect on the dye marks observed ($z = -6.50$, $P < 0.001$; Table 2). Hedgerow presence did not impact bee movement ($z = 0.47$, $P = 0.64$), nor did it interact with distance ($z = 0.42$, $P = 0.67$). We did observe more dye traces in fields where more bees were marked ($z = 2.47$, $P < 0.05$), but the sex of the bee did not influence the pattern of dye deposition ($z = 0.35$, $P = 0.73$).

Mapping services in a single field

Using the nesting rates and foraging distances we observed, we predict a spatially heterogeneous pattern of ecosystem service delivery within a single crop field (Fig. 4). The rapid decline in dye marks we observed indicates a truncated foraging range, likely centralized around nest location. Thus, the distribution and density of nests (Fig. A4) within a given field could influence foraging extent. In our e-trap sampling, we found higher numbers of nests in edges and within the first 10 m into crop fields. We would thus predict pollination services to be spatially clustered around these nests sites, and therefore higher along field edges than centers.

Discussion

Assessing model parameterizations

Contrary to our expectations, our findings did not support our specific predictions, nor did they support many of parameterizations typically used in pollination service models. First, we detected nests in both fields and field margins; however, we did find higher nesting rates in areas bordering fields. Second, we did not find that hedgerow plantings increased nesting rates. Third, the majority of bee foraging activity we detected occurred within a fraction of the predicted foraging range of the dominant genus, instead of throughout its foraging range, indicating that utilizing an exponential decay function for foraging range is critical to capturing the distances covered by native bees in pollination service models (e.g., as in the Lonsdorf et al. model). Some of the differences between these results and the expert opinions upon which pollination service models are currently based could result from factors associated with mass-flowering crops. Nevertheless, we cannot compare whether the trends we observed are particular to a mass-flowering crop system because nesting and foraging patterns have not been examined across different crop systems and regions. Thus, the divergence of our results from expert opinion strongly argues for testing expert opinion with field experiments. In addition, our findings indicate that pollination coverage in mass-flowering crop fields is likely limited by bee nest site location. Factors that affect nesting, including farm management techniques as well as soil conditions and nesting characteristics therefore require further attention in order to improve pollination service delivery at the farm scale.

Nest location and nesting resources

Our findings confirm that native bees nest in fields despite management practices that cause disturbance, although only a portion of their offspring may survive soil disturbance events (Ullmann 2015). Thus, parameterizations that limit nest site location to edge habitat, such as in the Rands and Whitney (2011) model, may not capture realistic nest distributions. A parameterization that allows bees to nest within fields, though in greater numbers along edges (modeling an edge effect), would more realistically reflect the conditions in our study system. Crop-specific pollination coverage estimates resulting from direct measurements of nesting and foraging could be used to alter the size of crop fields to maximize pollination by wild bees. The ability to nest within fields not only benefits crop pollination, but may also contribute to the sustainability of pollinator populations over time. When Keitt (2009) modeled native bee persistence in agricultural landscapes, he found that allowing bees to nest in a variety of land use types within agricultural areas promoted long-term population viability whereas constraining nest-site location to field margins and other undisturbed sites limited population growth.

Patterns of nesting, however, likely differ based on crop attractiveness, bloom density, and the attractiveness and width of field-margin plantings. Thus, the trends we observed may not be representative of other crop systems or different geographic regions, indicating a need for crop- and region-specific nesting assessments. Sunflower, for example, is visited by both generalist and specialist bees because its open blooms are easily accessed by a variety of pollinators (Parker 1981, Greenleaf and Kremen 2006). We found generalist species (e.g. *Lasioglossum (Dialictus)* spp.) nesting in both fields and edges, while sunflower specialists *M. agilis* and *M. lupina* only nested within sunflower fields. *Lasioglossum (Dialictus) incompletum* is hyper-abundant in agricultural landscapes, and known to be a generalist floral visitor. It may also be a generalist in the nesting conditions it is willing to accept. Conversely, sunflower specialists may prefer to nest in locations where sunflower is growing, although they have been found nesting in irrigation furrows adjacent to zucchini *Cucurbita pepo* plots near sunflower fields (Parker et al. 1981). Bees that are not dependent on sunflower may find nesting within fields a less attractive option.

Bees have diverse nesting habits and thus species likely exhibit a variety of preferences. Thus, having a variety of soil conditions ought to improve the diversity of nesting species. We did detect a marginally significant affect of soil diversity surrounding our study sites on the abundance and richness of ground-nesters. However, the majority of the soils in our study region, both in tilled agricultural fields and untilled margins, have high clay content (Fig. S3). Clay soils are generally considered unfavorable for nesting. Clay content has been found to decrease nesting rates, while sand and silt are more favorable because they increase drainage (Cane 1991). That both specialists and generalists were found nesting in conditions considered by bee biologists to be unfavorable suggests that expert opinion on nest site location may need revision.

Floral resources and foraging

Although we found bees nesting in crop fields, pollination coverage may be limited, if actual foraging distances are much smaller than potential foraging ranges. The majority of movements we detected were within 10 m of where bees were marked, despite the fact that marked individuals generally immediately left the field in which they were marked due to a stress response. Following their departure, they likely returned to the site of capture, and then returned to foraging. We hypothesize that this behavior indicated that they were captured near their nest sites. *M. agilis*, the most common species we collected, has an average foraging range prediction of 740 ± 250 m, based on its body size (Greenleaf and Kremen 2006). However, in the presence of abundant resources provided by a mass-flowering crop, we found the majority of foraging movement was concentrated in <1% of its potential range. With an exponential decay rate of 1, we would have expected to find a higher concentration of marks up to 75 m into fields. We curtailed searching for marks at 50 m because we did not see any between 50 - 100 m in the first two fields we surveyed. Additionally, we were unable to search the full circumference around the point of marking. We did search within hedgerows and edges adjacent to fields, never finding a single powder mark. This evidence suggests that while bees may be capable of foraging larger distances, their movement may be concentrated in certain areas, particularly when there are ample and highly attractive nearby resources.

Floral densities can affect foraging behavior (Hegland and Boeke 2006). In intensive agricultural landscapes, mass-flowering crops can provide hundreds of thousands of blooms per field (Williams et al. 2012). Honey bees, for example, have been documented to forage shorter distances when presented with higher density of blooms (Waddington 1980). Densities of sunflower in our field ranged from 1 - 17 per m^2 for female plants to 3 - 25 per m^2 for males, which often had 1 - 11 flower heads per stem. In the presence of such abundant resources, bees likely only needed to forage a short distance from their nest sites to obtain the pollen and nectar required for nest provisioning and their own alimentation. As mentioned, dyed bees returned to the site of capture, which was likely near their nest location. However, if bees nest in fields with sparse resources, which we did not study, we would then expect them to fly greater distances within their maximum foraging range to access available floral resources (Zurbuchen et al.

2010). Adding a measure of floral density to current models that alters expected foraging range predictions could help address this issue.

Spatial and temporal scales of mapping

Low resolution mapping of floral and nesting resources may capture general pollination trends within an agricultural region, but may not be informative to farmers who are interested in services within their crop fields. In the same study landscape where we conducted this study, Lonsdorf et al. (2009)'s model predicted that pollination coverage for watermelon would be very low, but relatively evenly distributed except where agricultural areas were adjacent to natural habitats, where pollination is predicted to be higher. Our visualization within a single sunflower field illustrates that pollination may be highly variable at the scale of interest to growers. Our finding supports Lonsdorf et al. (2009)'s conclusion that better quantification of fine-scale resources could alter model predictions. Reducing the scale at which key resources are modeled and including more fine-scale estimates in model parameterizations could address this issue.

Resource availability across landscapes, however, is often seasonally variable (Kremen 2005). Examining NDVI (Normalized Difference Vegetation Index), Leong (2014) found that urban, agricultural and natural areas provided pulses of floral resources at different times of year. Further, pollinator abundance tracked these changes in resource availability. In Yolo County, sunflower blooms during a lull in blooming of hedgerow plants (Table A1). In 2013, a drought year, hedgerows in this study provided virtually no floral resources during the study period. Thus, at this time, resource abundance within weedy field margins and hedgerows may have been similar to one another than during different seasons or years, although over higher average resource availability is recorded in hedgerows in the spring-summer season (Morandin and Kremen 2013). This dearth of floral resources during the study period may partially explain the lack of effect of floral enhancements on bee nesting rates observed in this study.

Communities of native bees also fluctuate inter-annually (Petanidou et al. 2008) and seasonally within a year, with distinct flight periods of spring and summer bees (e.g. Ginsberg, 1983; Williams et al., 2001). As a result, services may fluctuate within or across years. While pollination models can account for seasonal variation of floral resources and pollinator populations, these models sum floral resources across seasons to generate a weighted average for a given parcel. Accounting for different seasons so as to reflect bloom times for crops and natural habitats may give growers a more relevant picture of pollinator availability during times of peak need.

Conclusions

Our findings indicate that fine-scale mapping of pollination services will better reflect potential pollination trends within a single crop field while mapping at a landscape scale can capture general pollination trends across an agricultural region (e.g. Chaplin-Kramer et al. 2011, Lonsdorf et al. 2009). Both scales can help inform farmers about the pollination potential they can expect given their landscape context and the local resources provided on their farms. Despite our limited sampling effort, we show that direct assessments of pollinator nesting and foraging can lead to predictions of potentially uneven pollination services in mass-flowering crop fields. Additional field-testing of factors that impact nesting and foraging will likely yield further insights into pollination-service delivery. Until current models can be parameterized with field data from multiple crops across many regions and at different time scales, altering existing models to better assess nesting resources and scaling foraging to floral resource density may enhance predictions of pollination services across scales.

Acknowledgements

We thank two anonymous reviewers for their insightful comments on this manuscript. Ashley Ellis and our other field assistants made fieldwork possible. We appreciate the members of the Kremen lab for their ideas and editing. We thank the three anonymous sunflower seed companies and all the farmers who let us sample on their land. This project was funded by a Western Sustainable Agriculture Education Research Grant to H.S.S., a National Institute for Food and Agriculture Predoctoral Fellowship to H.S.S., a National Science Foundation Graduate Fellowship to H.S.S., a USDA Conservation Innovation Grant 69-3A75-12-253 to the Xerces Society/C.K., an Army Research Office grant W911NF-11-1-0361 to C.K, and by the U.S. Department of Agriculture (USDA-NIFA 2012-51181-20105 to Rufus Isaacs, Michigan State University).

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Appendices

Appendix A: Site and soil characteristics for hedgerow and control sites in emergence trap nesting study

Appendix B. Validation procedure for abundance model of ground-nesting bees collected in emergence traps

Tables

Table 1. Model results for incidence, abundance and richness of bees nesting in sunflower fields and edges. Values are effect sizes. Significance for the abundance model was determined using a parametric bootstrap on the likelihood ratios of models with and without the variable of interest

Covariate	Incidence	Abundance	Richness
Hedgerow presence	-4.855	-0.144	-0.081
Distance into field	-0.215†	-0.445**	-0.001†
Hedgerow presence x Distance	-0.005	-0.092†	-0.001
Soil particle size	0.038	0.210	0.006
Soil heterogeneity	1.317*	0.381†	0.183†
Percent bare ground	0.007	0.333†	0.001
Slope	0.051**	0.413**	0.009**
Soil hardness	-0.180	-0.092	-0.020

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$

Table 2. Effect of hedgerow presence, distance, and collection factors on the number of dye marks observed up to 50 m into sunflower fields.

Covariate	Estimate
Hedgerow presence	0.139
Distance into field	-0.155***
Hedgerow presence x Distance	0.014
No. bees marked	0.559*
Proportion female:male marked	0.066

* $P < 0.05$, *** $P < 0.001$

Figure legends

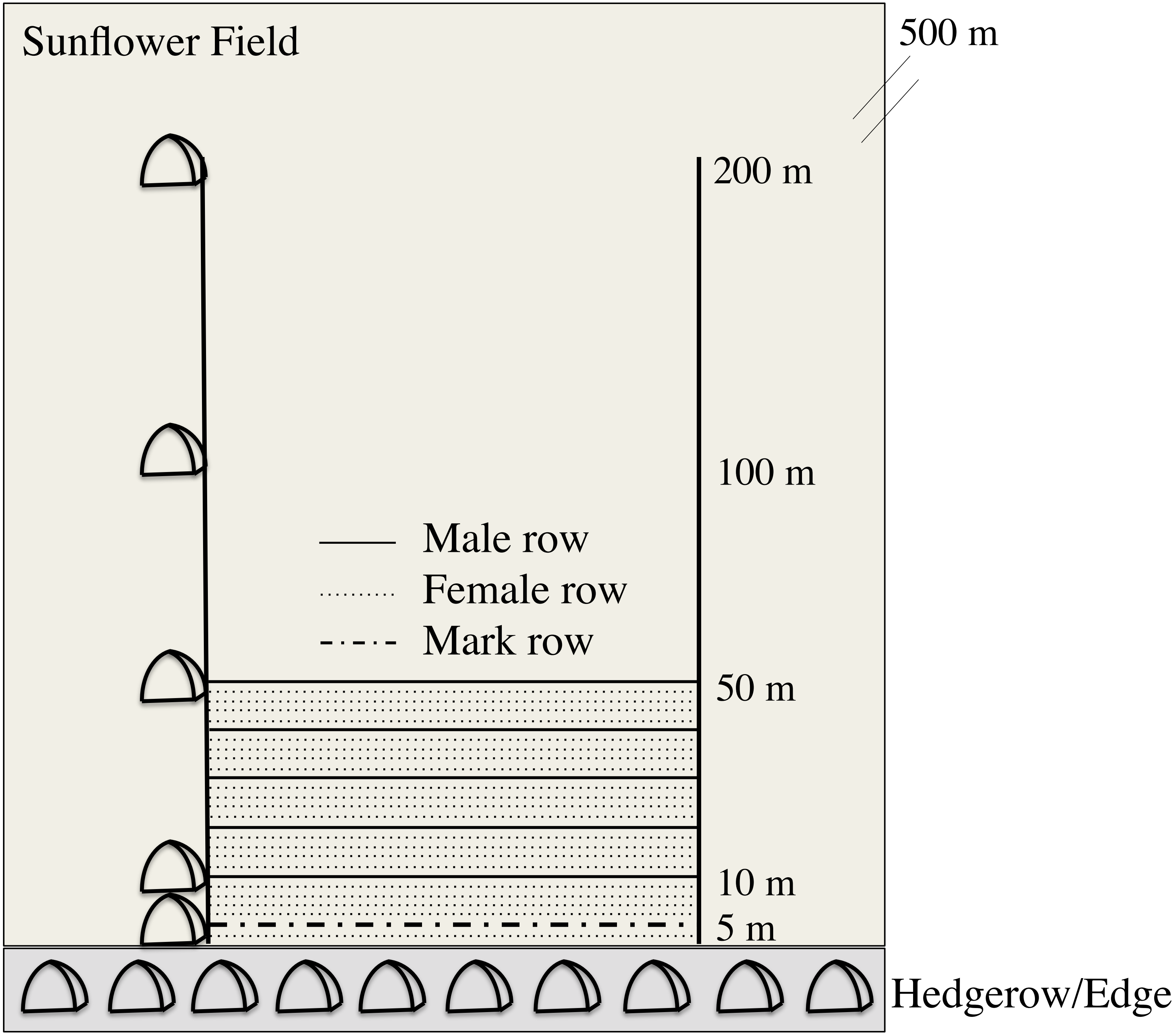
Figure 1. We sampled ground-nesting bees using 20 emergence traps, ten in edges alongside fields and ten at 5, 10, 50, 100 and 200 m along two transects spaced 100 m apart, in sunflower fields. We marked bees with fluorescent dye in the first row of male sunflowers (dot and dash line). We then searched for dye traces after dusk along parallel 100 m transects (solid lines) in male sunflower rows from the first, or mark row, to 50 m into the field. The dotted lines represent the female, seed-producing, sunflower that are interspersed with rows of male sunflower to enhance cross-pollination.

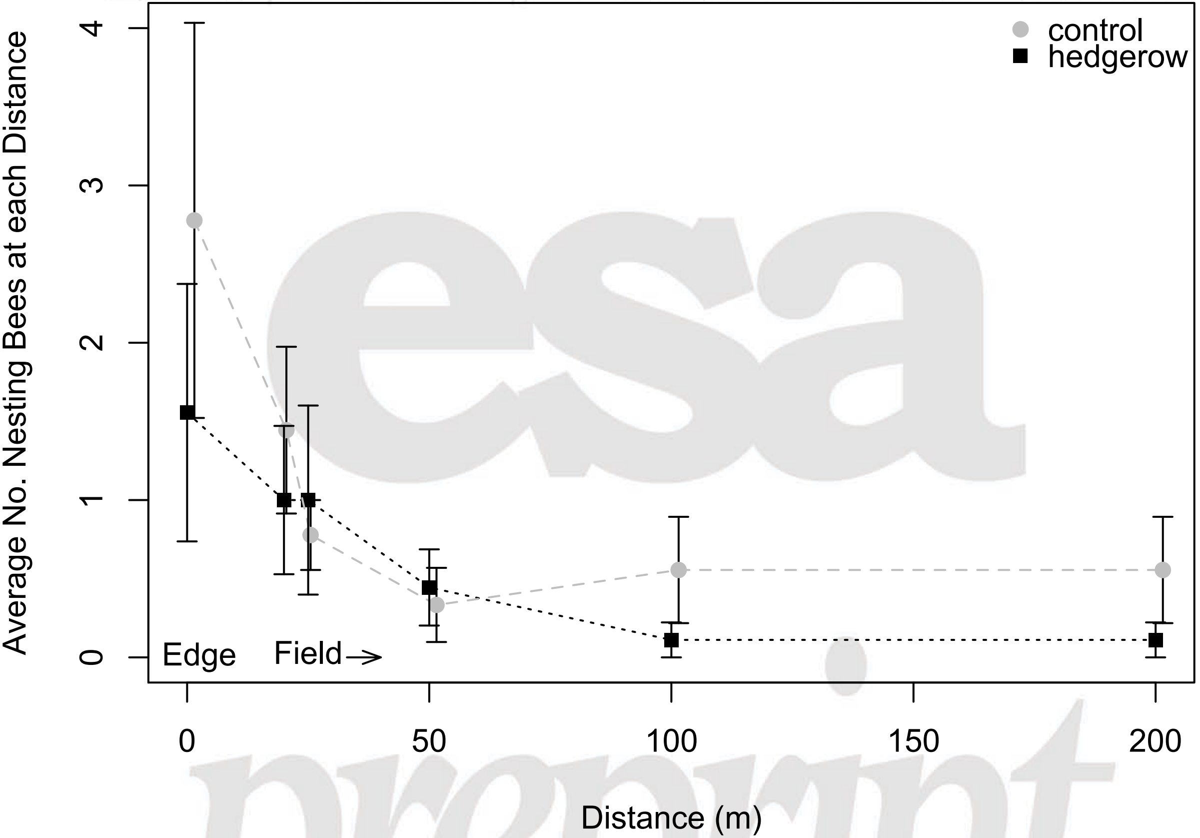
Figure 2. The average number of bees collected with emergence traps declined with distance into the field, demonstrating a spatial clustering of nests around field edges. Nesting rates were not different between hedgerow and control sites.

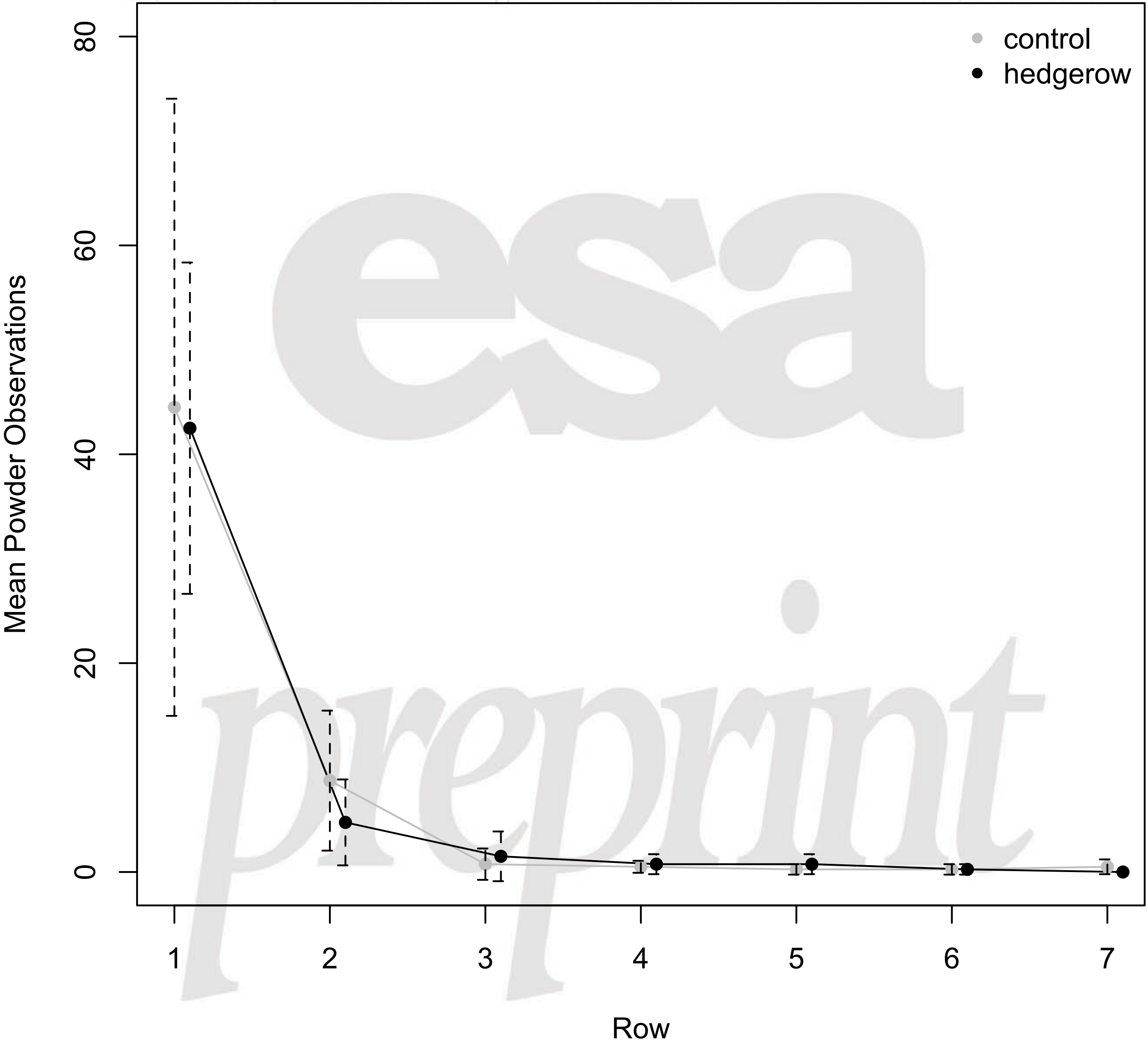
Figure 3. Marks deposited by medium-size sunflower pollinating bees coated with fluorescent powder exhibited an exponential rate of decay (k = 0.99) with increasing distance into the field. Whiskers indicate standard errors. Rows in which marks were measured contained male sunflowers; rows of female sunflower were interspersed with the male rows. Rows were approximately 7 m apart. Row 1 was the first male row within a sunflower field in which bees were marked and was 5 - 7 m from the field edge, and row 7 was approximately 50 m into sunflower fields.

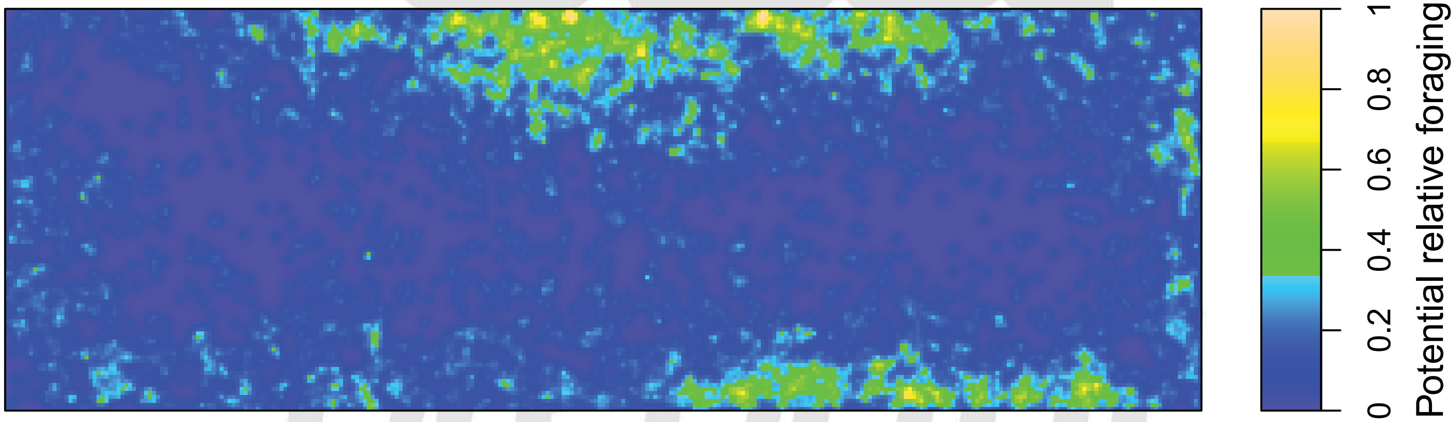
Figure 4. Foraging rates were higher in areas of high nesting density within a sunflower field, in this case, along field edges. Nesting rates were Poisson sampled from a log-normal distribution

and foraging distances exhibit an exponential decay rate of 1. This simulated field is 100 x 300 m; each grid cell containing a nest density is 1 m^2.


Sunflower Field
500 m
200 m
100 m
Male row
Female row
Mark row
50 m
10 m
5 m
Hedgerow/Edge


Average No. Nesting Bees at each Distance
0
1
2
3
4
● control
■ hedgerow
Edge
Field →
0
50
100
150
200
Distance (m)


Mean Powder Observations
0
20
40
60
80
1
2
3
4
5
6
7
Row
control
hedgerow


Potential relative foraging
0
0.2
0.4
0.6
0.8
1