

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 syrphid 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)

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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.

² <http://nassgeodata.gmu.edu/CropScape>

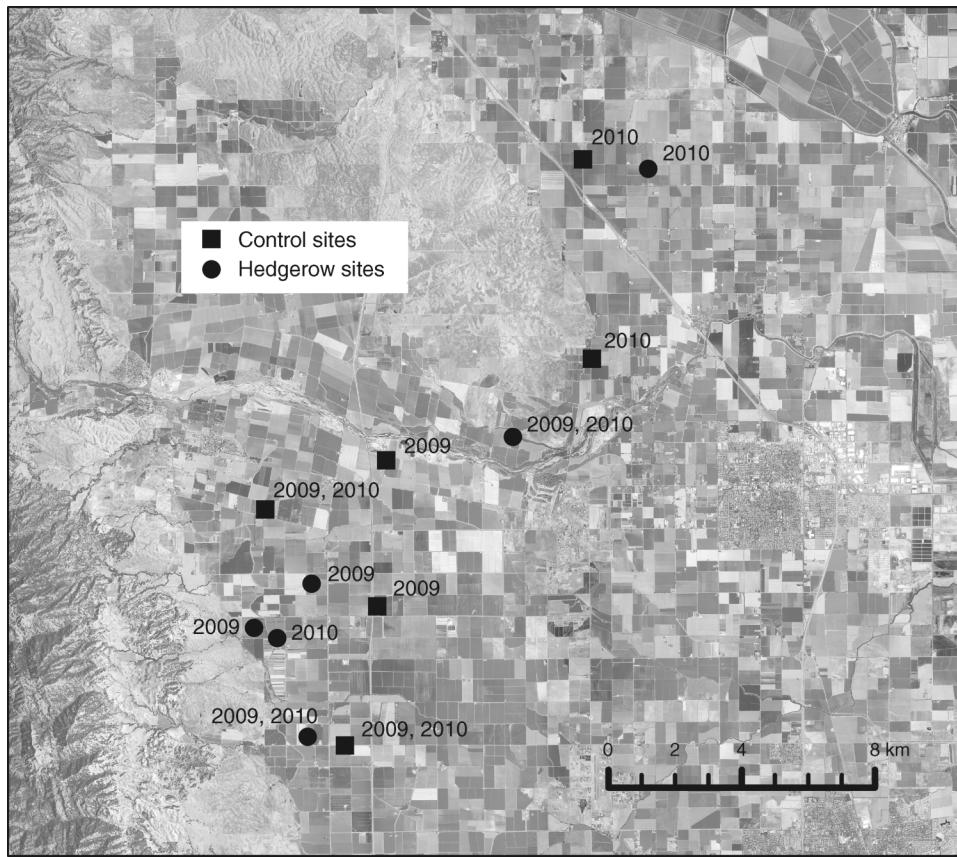


FIG. 1. Hedgerow and control sites from 2009 and 2010 in Yolo County, California, USA. Four hedgerows were matched with four control sites each year. Two hedgerow edges and two control edges were the same in 2009 and 2010, but due to rotation of tomato crops, the other sites were different between years.

Floral, nesting, and pollinator assessment

At each sample round, floral cover was assessed by placing 50 1-m² 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-m³ 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 \times 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 \pm 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 \pm 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

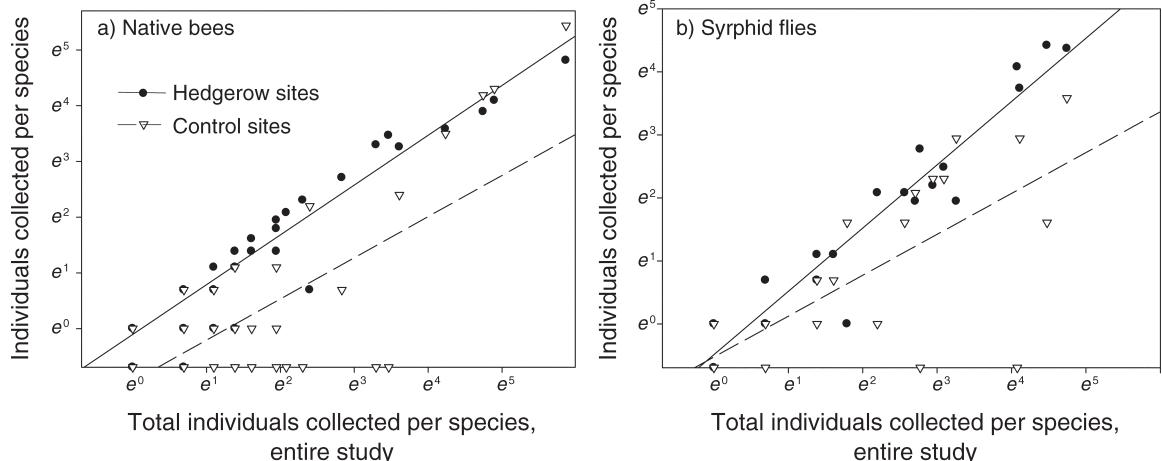


FIG. 2. For (a) native bees and (b) syrphid flies, the number of individuals of each species collected from flowers at either hedgerow or control sites in relation to the total number of individuals collected for that species in both site types. The axes are on a natural logarithm scale ($e = 2.7182818$). 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.

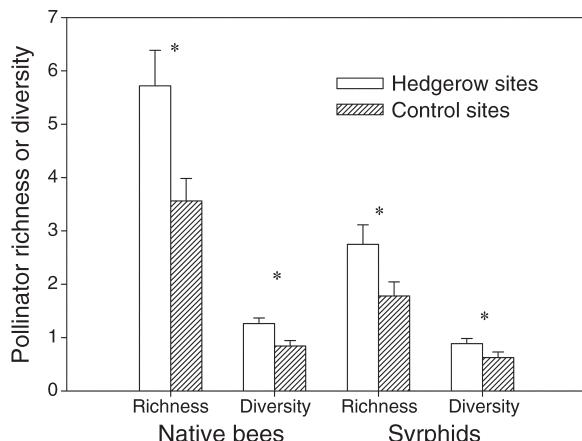


FIG. 3. Native bee and syrphid richness (number of species) and Shannon's diversity index (values are shown as mean \pm SE) on flowers in hedgerow and control edges in 2009 and 2010. Asterisks indicate a significant difference between hedgerow and control sites.

* $P < 0.05$.

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; $t = -1.9$, $P = 0.048$).

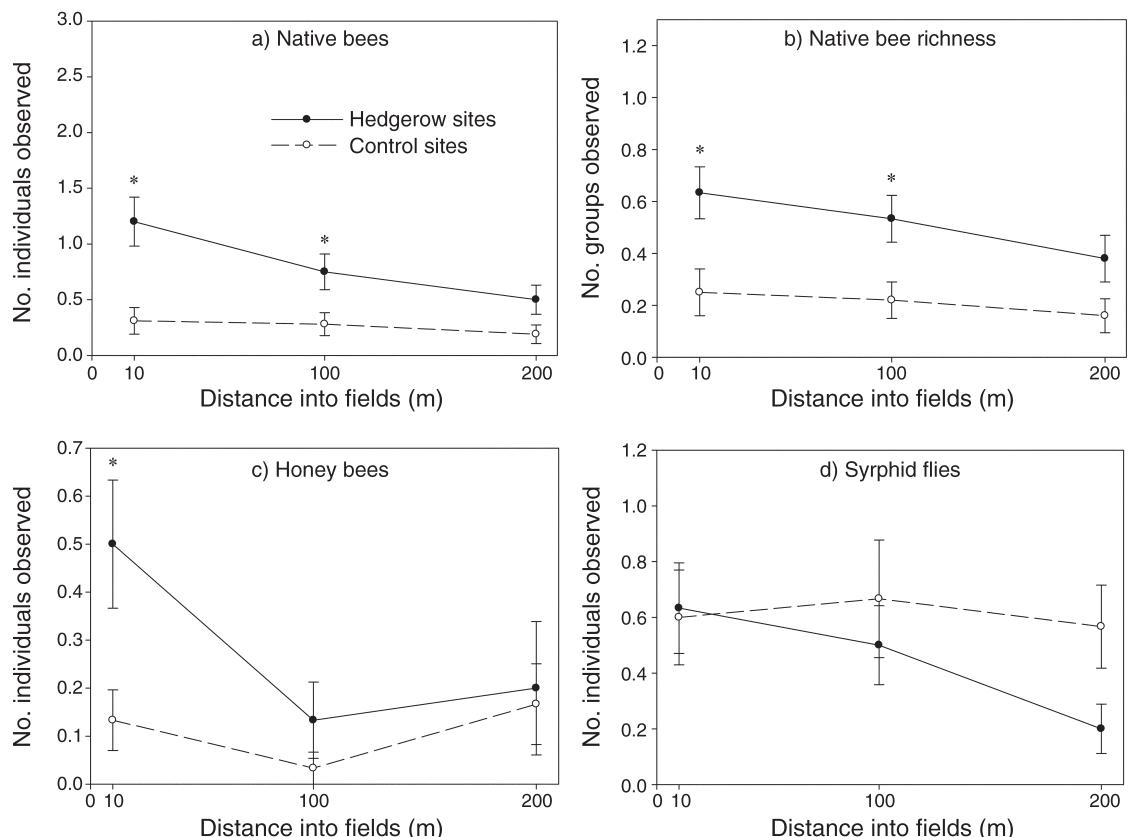


FIG. 4. Observed numbers (mean \pm SE) of (a) individuals of native bees, (b) species of native bees, (c) individuals of honey bees, and (d) individuals of syrphid flies at three distances into fields that were adjacent to hedgerow or control edges, in 2009 and 2010.

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 Circle 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 (Decourtey 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.

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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*).