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Authors

Sardiñas, HS
Ponisio, LC
Kremen, C

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RESEARCH ARTICLE

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

Hillary S. Sardiñas[1,2], Lauren C. Ponisio[1], Claire Kremen[1]

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

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
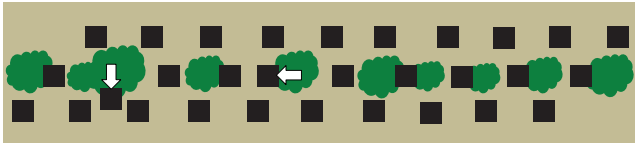
Figure 1. Sampling scheme for 30 emergence traps (black boxes) to capture ground-nesting bees in field edges with and without hedgerow plantings. If a hedgerow shrub (green) was in the location where an emergence trap was to be placed, we first tried to put the trap in line with the hedgerow, next to 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 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**

(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).

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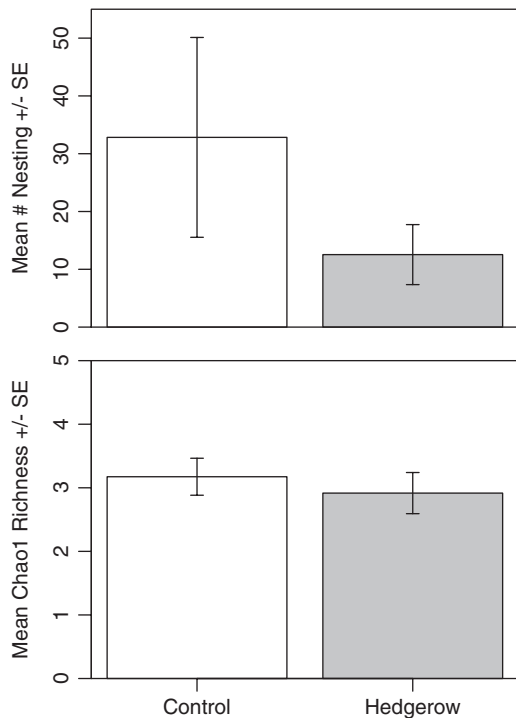
Figure 2. Mean (± SE) bee abundance per site and Chao1 (abundance-based) species richness of ground-nesting bees collected in emergence traps in hedgerow and control field edges.
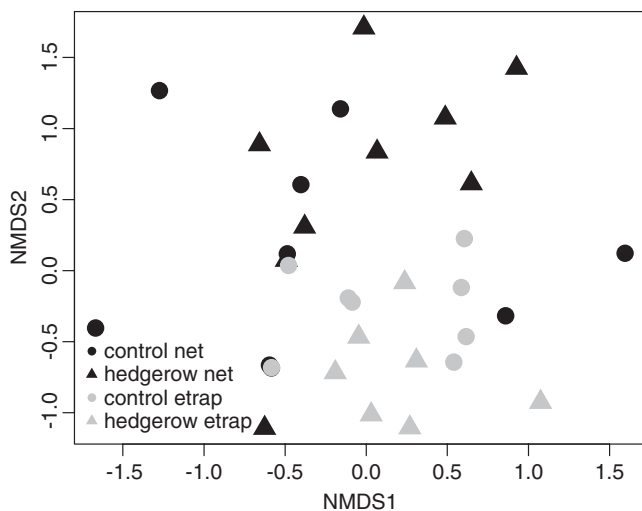

Figure 3. Chao dissimilarities between ground-nesting bee assemblages nesting and foraging in hedgerow and control edges visualized using NMDS. Communities of foraging (aerial net) versus nesting (e-traps) of ground-nesting bees are distinct.

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

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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).