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

Hillary S. Sardiñas,[1,3] Kathleen Tom,[1,2] Lauren Catherine Ponisio,[1] Andrew Rominger,[1] and Claire Kremen[1]

[1]*Department of Environmental Science, Policy, and Management, University of California, 130 Mulford Hall, Berkeley, California 94720 USA*
[2]*New England Interstate Water Pollution Control Commission, 650 Suffolk Street, Suite 410, Lowell, Massachusetts 01854 USA*

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.

Key words: 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 (Lonsdorf et al. 2009, Benjamin et al. 2014). 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 overestimate 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 (Morandin and Kremen 2013, M'Gonigle et al., 2015). 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 and Whitney 2011). Brosi et al.'s (2008) 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 belowground nesting. A meta-analysis found that the relative abundance of belowground 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 (1) native bees would only nest in edges, and that (2) field margins containing the floral enhancements provided by hedgerows would provide better nesting habitat than unenhanced field margins. We also expected to (3) 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 County, in California's Central Valley, USA, from June to July in 2012 and 2013 (Appendix S1: Fig. S1). To maintain independence between fields, we ensured fields were a minimum of 900 m apart (range, 947–5409; 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 four to six 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 and 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 *Materials and Methods: Nesting*). Only a portion of the plant species present within the hedgerows bloomed during our study period (Appendix S1: Table S1). 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 (Appendix S1: Table S1); 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 (Appendix S1: Fig. S1). We set ten 0.6 m² 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 h 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 (Harry H. Laidlaw Jr. Honey Bee Research Facility, University of California, Davis), and stored in the Essig Museum at University of California, 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 (>2 mm). We calculated average particle size with a laser diffraction particle size analyzer (Sequoia
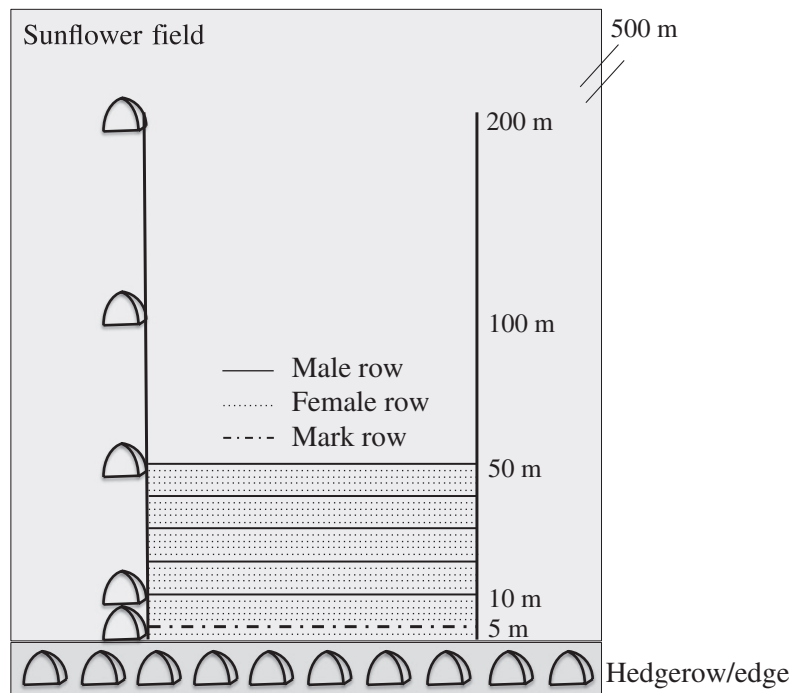

Fig. 1. We sampled ground-nesting bees using 20 emergence traps, ten in edges alongside fields and ten at 5, 10, 50, 100, and 200 m along two transects spaced 100 m apart, in sunflower fields. We marked bees with fluorescent dye in the first row of male sunflowers (dot and dash line). We then searched 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.

LISST Portable XLR, Bellevue, Washington, USA). 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 (*available online*).[4]

Key habitat features that might influence nesting have also been examined as proxies for nesting (Appendix S1: Table S2; 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 and 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 Safari, Alex Brands, Fairfield, New Jersey, USA). 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, Santa Ana, California, 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 h 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 09:00 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, two people walked each transect for 30 min 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. Sardiñas, *personal observation*).

[4] http://websoilsurvey.nrcs.usda.gov

Normal bee behavior, such as grooming and flight, could result in powder loss. Over a 4 h 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, R Core Team 2013). 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 S2). 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 nonlinear 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 vs. 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 (Zuur et al. 2009, Bates et al. 2014).

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 covariance 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 m, 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 (Appendix S1: Table S3). 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 (Appendix S1: Fig. S2).

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

TABLE 1. Model results for incidence, abundance, and richness of bees nesting in sunflower fields and edges.

Covariate	Incidence	Abundance	Richness
Hedgerow presence	−4.855	−0.144	−0.081
Distance into field	−0.215*	−0.445***	−0.001*
Hedgerow presence × 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

Notes: 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. *$P < 0.1$. **$P < 0.05$. ***$P < 0.01$.

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 (Appendix S1: Fig. S3). 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 (Appendix S1: Table S3). 97.2% were sunflower specialists (Appendix S1: Table S3). 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

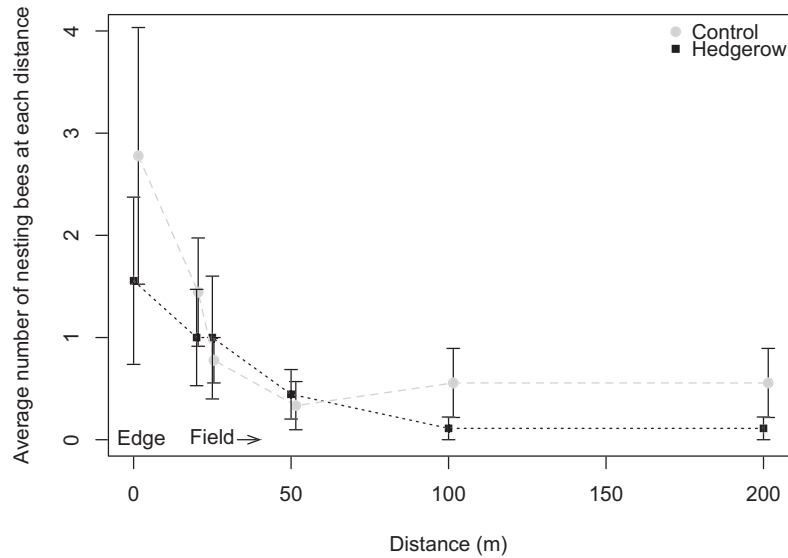Using the nesting rates and foraging distances we observed, we predict a spatially heterogeneous pattern of

Fɪɢ. 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.
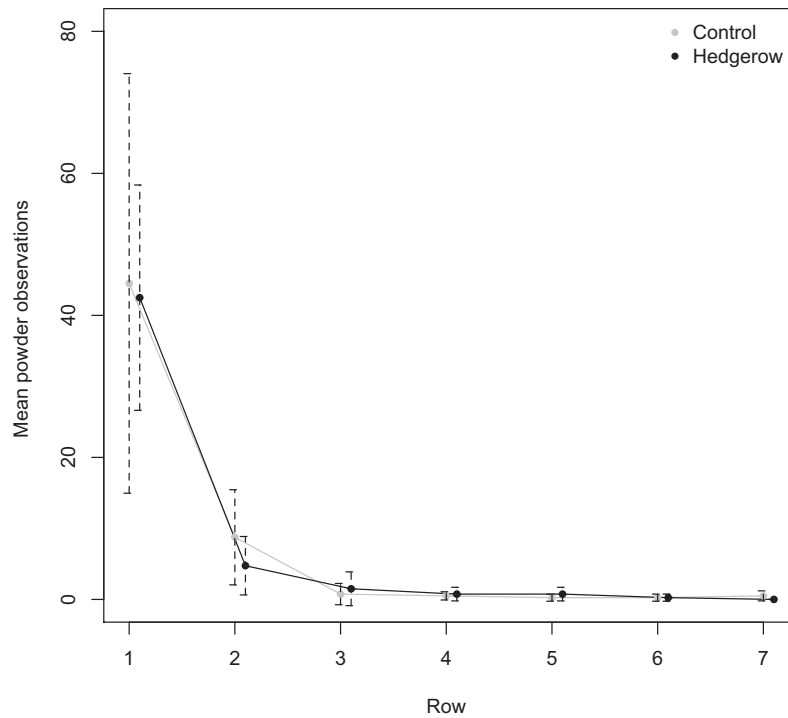

Fɪɢ. 3.   Marks deposited by medium-size sunflower pollinating bees coated with fluorescent powder exhibited an exponential rate of decay ($k = 0.99$) with increasing distance into the field. Whiskers indicate standard errors. Rows in which marks were measured contained male sunflowers; rows of female 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.

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 (Appendix S1: Fig. S4) 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

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 × distance	0.014
No. bees marked	0.559*
Proportion female:male marked	0.066

*$P < 0.05$. **$P < 0.001$.

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. [2009] 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
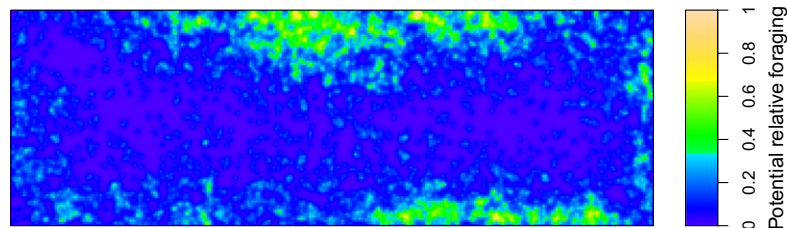

FIG. 4. Foraging rates were higher in areas of high nesting density within a sunflower field, in this case, along field edges. Nesting rates were Poisson sampled from a log-normal distribution and foraging distances exhibit an exponential decay rate of 1. This simulated field is 100×300 m; each grid cell containing a nest density is 1 m^2.

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 effect 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 (Appendix S1: 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 and 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 to 17 per m² for female plants and from 3 to 25 per m² 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.'s (2009) 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.'s (2009) 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 and Roderick (2015) 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 (Appendix S1: Table S1). In 2013, a drought year, hedgerows we surveyed 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., Lonsdorf et al. 2009, Chaplin-Kramer et al. 2011). 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.

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Supporting Information