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

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A B S T R A C T

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

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1. Introduction

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

landscapes often contain little remnant habitat. As a result, re-diversification of agricultural areas has been proposed as a means of bolstering pollination services from these alternate pollinators (Steffan-Dewenter and Leschke, 2003; Kremen et al., 2007; Tscharntke et al., 2005; Brosi et al., 2008; Holzschuh et al., 2008; Winfree, 2010; Garibaldi et al., 2014).

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

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

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

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

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

2. Material and methods

2.1. Study system

Field sites were located in Yolo County, an intensively-farmed agricultural region of California's Central Valley that contains a mixture of conventionally managed row and orchard crops. The majority of natural and semi-natural habitat in the county is concentrated around the borders of agricultural lands and not embedded within them (California Department of Water Resources, 2008). We sampled 18 sunflower fields between June and July (10 fields in 2012 and 8 fields in 2013). Half of the fields were adjacent to bare or weedy edges (hereafter called controls), and half were adjacent to hedgerows (Fig. S1a). Sites were paired based on the timing of the sunflower bloom, the sunflower variety

(specific to company), and landscape context. Field pairs were a minimum of 900 m apart (range, 947–5409 m) to maintain independence (Greenleaf et al., 2007). To avoid contamination of varieties, sunflower fields are moved every year; therefore no field was sampled in multiple years although two fields were adjacent to the same hedgerow in different years.

2.2. Sunflower

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

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

2.3. Hedgerows and control edges

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

hedgerows contained more plant species and more blooms than control weedy edges (Tables S1 and S2).

2.4. Landscape context

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

2.5. Sampling methods

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

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

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

2.6. Seed set

To determine ambient pollination rates, we collected three sunflower heads at each distance/transect combination prior to harvest. In the first year of this study we bagged one male-sterile sunflower head at each distance along both transects to determine seed set levels without cross-pollination events. No seeds were produced in any bagged sunflower head, therefore we did not account for seeds set due to selfing in our models of seed set. Heads were dried, measured, and all mature seeds were removed,

weighed and counted with a Syntron automatic seed counter. We tested for differences in head size (diameter) between companies using a generalized linear model, with site nested within pair as a random effect, in the R package lme4 (Bates et al., 2013; R version 3.1.2). Sunflower head size was similar between companies (estimated head area 25 cm^2; Table S5), although one company had a wider range of head sizes and was significantly different from the other three companies in the study ($t = -2.22$, $P < 0.05$; Table S5). All hedgerow and control sites were paired by company.

2.7. Field edge use by sunflower specialists

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

2.8. Statistical analyses

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

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

To determine which factors impacted sunflower seed set, we used negative binomial generalized linear models in the R package lme4 that accounted for overdispersion in the seed

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

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

3. Results

3.1. Aerial netting

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

We collected more bees in hedgerow edges than in control edges (Table 1 and Fig. 1a). On average, hedgerow edges supported higher species richness (5.11 ± 0.89, mean ± standard error; Fig. 1b) than control edges (2.11 ± 0.48), hedgerow fields (1.41 ± 0.20) or

Table 1

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

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

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

control fields (2.06 ± 0.20; Table 1). We detected a significant interaction between hedgerow presence and location within fields (edge or field) for abundance ($t = -3.91$, $P < 0.001$) and species richness ($t = -4.22$, $P < 0.001$; Fig. S4). Proportion of potential pollinator habitat with a 1 km radius did not influence wild bee species richness ($t = -0.83$, $P = 0.41$) or abundance ($t = -0.49$, $P = 0.62$) within sunflower fields.

3.2. Visitation rates

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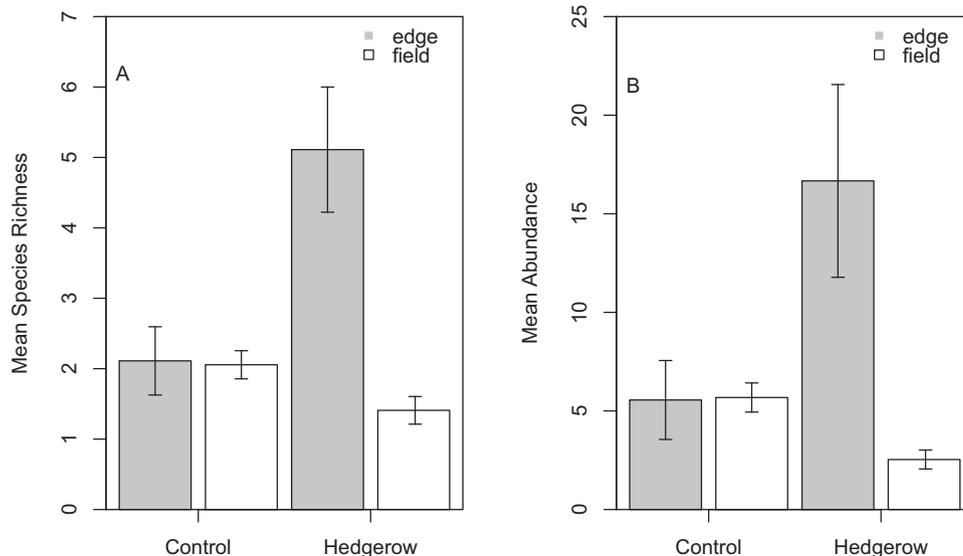

Fig. 1. Hedgerow edges supported higher species richness (a) and abundance (b) of wild bees than control edges and sunflower fields.
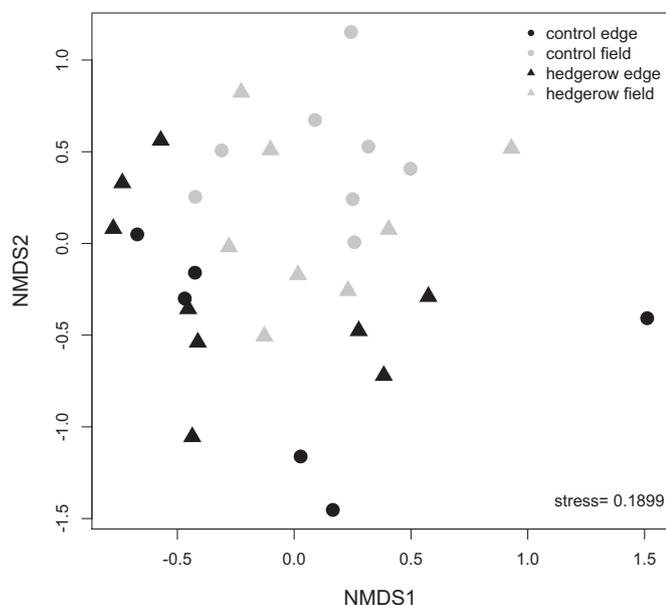
Fig. 2. Chao1 (abundance-based) dissimilarities between wild bee communities found in control edges, hedgerows, control fields and hedgerow fields; visualized using non-metric dimensional scaling. All sites with fewer than one specimen were excluded from this perMANOVA analysis.

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

3.3. Wild bee habitat use

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

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

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

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

[***] $P < 0.001$.

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

3.4. Sunflower seed set

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

4. Discussion

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

We detected distinct differences in community composition of wild bees present in edges versus fields. This difference was likely driven by the fact that the dominant bee species found within fields, sunflower specialists, were either rare visitors to or absent from both hedgerow and control edge habitats. We only sampled each site once, therefore increased sampling could lead to more convergence or divergence between bee communities in these habitats. There can be significant overlap between species found in MFC fields and adjacent hedgerows (Stanley and Stout, 2014), however species composition in hedgerows has also been shown to more closely resemble bee communities in forest habitat than adjacent crop fields (Hannon and Sisk, 2009). One factor likely driving the differences in species composition in our study region is the absence of sunflower planted within hedgerows due to concerns about genetic contamination of sunflower crop varieties. Because female sunflower specialists collect only sunflower pollen
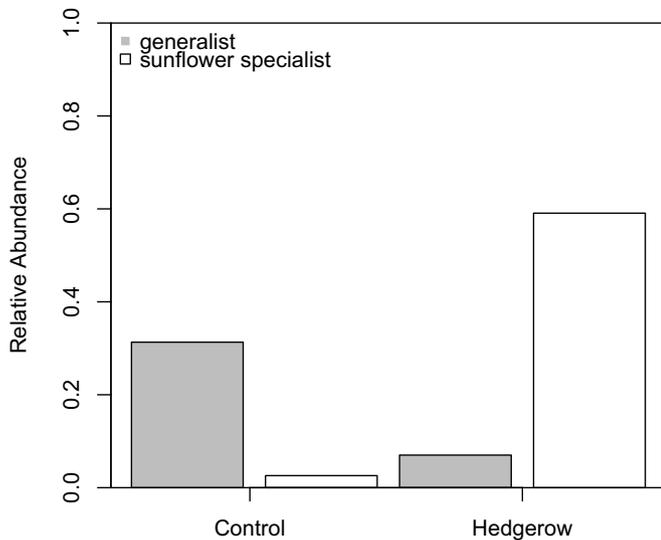
Fig. 3. In the independent data set, more sunflower specialists were found in sites with hedgerows, indicating a significant interaction between hedgerow presence and wild bee specialization on sunflower.

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

We found a slight positive effect of wild bee species richness on seed set rates, indicating that a higher number of bee species benefits pollination function in sunflower. Functional complementarity between species can enhance fruit and seed production in a variety of crops (Hoehn et al., 2008; Blüthgen and Klein, 2011). Bee

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

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

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

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

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

It is hypothesized that the effectiveness of field-edge vegetation re-diversification is maximized in landscapes that retain a small percentage of natural areas that can facilitate recolonization of restored habitats (Tscharntke et al., 2005). The added benefits of diversification efforts may be minimal in complex landscapes with high proportions of natural habitat since ecosystem service providers are often already supported. Diversification efforts may not support ecosystem providers in highly intensified (cleared) landscapes with no remaining natural habitat, either because there are no source areas to colonize the new habitats or because the new habitats alone cannot support populations of ecosystem service providers (Tscharntke et al., 2005). Although the landscape where we conducted our study constitutes a "cleared" landscape, and we did not detect landscape effects, other studies in the same location have found that hedgerows increase wild bee abundance, richness and population persistence and promote rare and/or more specialized species (Morandin and Kremen, 2013; M'Gonigle et al., 2015; Kremen and M'Gonigle, 2015). Nevertheless we did not find evidence that these biodiversity benefits translated into higher rates of pollination services in adjacent sunflower crop fields. Although both wild bee richness and abundance were important factors contributing to sunflower seed set, these contributions may be attributable to factors other than hedgerows. For example, wild bee visitors to sunflower were predominately sunflower specialists; the amount of sunflower maintained in the
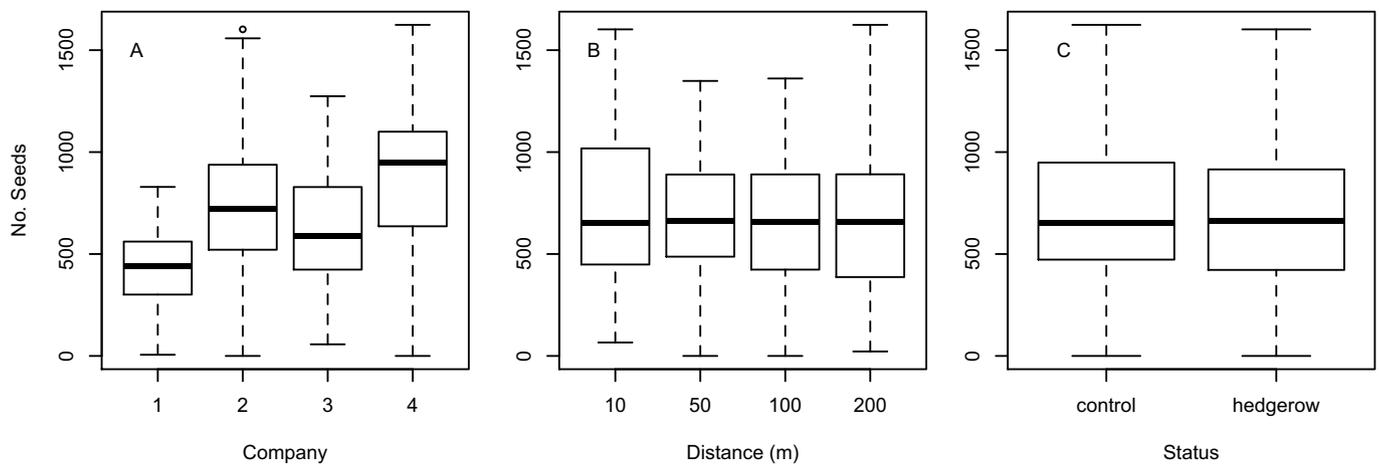
Fig. 4. Sunflower variety, which was associated with seed company (a), strongly influenced rates of sunflower seed set. Neither distance from the edge (b) nor hedgerow presence (status; (c)) impacted seed set. The dark line in each box shows the mean, the outer lines of the box denotes the 1st (lower) and 3rd (upper) quartiles, and the whiskers show the minimum and maximum values.

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

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

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

The benefits of field-edge diversifications may also differ based on crop identity and landscape context (Garibaldi et al., 2014). For example, sunflower has easily accessible florets that attract both generalist and specialist pollinators. However, in systems where flowers have specific requirements, such as highbush blueberry (*Vaccinium corymbosum* L.) that requires buzz-pollination, the identity of pollinator species may be of more importance (Button and Elle, 2014). Further, species-specific responses to habitat features may differ. Carvell et al. (2011) found bumble bees had differential responses to wildflower patch size and landscape heterogeneity, indicating that local and landscape habitat factors can also interact with one another, and with crop-specific

attributes, to affect crop pollination. In a tropical region, Carvalheiro et al. (2012) found that wildflower plantings worked in concert with natural habitat to heighten mango (*Mangifera indica*) production. There are a paucity of studies on the ecosystem service benefits from field-edge plantings, therefore the complex range of factors, including farming type, crop system, landscape context, and region (Holzschuh et al., 2007), influencing their performance is still relatively unknown (Garibaldi et al., 2014).

5. Conclusion

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

Appendix A. Supplementary data

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

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