



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



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ABSTRACT

Diversification of field edges is widely used as a strategy to augment pollinator populations and, in turn, supplement crop pollination needs. Hedgerow plantings, a commonly applied field-scale diversification technique, have been shown to increase wild bee richness within edges and into crop fields; however, their effects on pollination services in mass-flowering, pollinator-dependent crops typical of large-scale commercial monocultures are less well-known. We evaluated the indirect contribution of hedgerows to sunflower (*Helianthus annuus*) seed set vis-à-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

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

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 Using sentinel canola plants, Morandin, Long and Kremen (unpublished data) found that wild bees enhanced seed set, once the contribution from managed honey bees was accounted for.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

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

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

2. Material and methods

2.1. Study system

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

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

2.2. Sunflower

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

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

2.3. Hedgerows and control edges

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

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