On-farm habitat restoration counters biotic homogenization in intensively managed agriculture

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Abstract

To slow the rate of global species loss, it is imperative to understand how to restore and maintain native biodiversity in agricultural landscapes. Currently, agriculture is associated with lower spatial heterogeneity and turnover in community composition (*β*-diversity). While some techniques are known to enhance *α*-diversity, it is unclear whether habitat restoration can re-establish *β*-diversity. Using a long-term pollinator dataset, comprising $\sim$9,800 specimens collected from the intensively managed agricultural landscape of the Central Valley of California, we show that on-farm habitat restoration in the form of native plant 'hedgerows', when replicated across a landscape, can boost *β*-diversity by approximately 14% relative to unrestored field margins, to levels similar to some natural communities. Hedgerows restore *β*-diversity by promoting the assembly of phenotypically diverse communities. Intensively managed agriculture imposes a strong ecological filter that negatively affects several important dimensions of community trait diversity, distribution, and uniqueness. However, by helping to restore phenotypically diverse pollinator communities, small-scale restorations such as hedgerows provide a valuable tool for conserving biodiversity and promoting ecosystem services.

Introduction

Widespread conversion of natural ecosystems to agriculture, combined with intensification of farming practices, is causing major declines in biodiversity globally (Tilman et al., 2001; Green et al., 2005; Tscharntke et al., 2005). Agriculture is particularly associated with the homogenization of biological communities (Gabriel et al., 2006; Clough et al., 2007; Hendrickx et al., 2007; Vellend et al., 2007; Ekroos et al., 2010; Flohre et al., 2011). The turnover of species through space and subsequent heterogeneity of community composition (*β*-diversity) is a primary determinant of the total species diversity present in a landscape (Flohre et al., 2011). Thus, by homogenizing communities, agriculture can act to reduce biodiversity on both local and regional scales (Hendrickx et al., 2007; Ekroos et al., 2010; Flohre et al., 2011).

Spatial heterogeneity in community composition can be influenced by a variety of deterministic (niche-based) and stochastic (neutral) processes. Species are thought to 'deterministically' track the biotic and abiotic conditions to which they are adapted and, in a heterogeneous environment, this will contribute to the spatial structuring of communities (Whittaker, 1960;

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Condit et al., 2002; Chase, 2007; Püttker et al., 2014). Stochastic processes, such as priority effects or rare long distance dispersal events, can then amplify or weaken these signals (Condit et al., 2002; Chase, 2003; Püttker et al., 2014).

Ecological filters are one deterministic process that can shape community assembly because only species with particular sets of physical, functional, and life-history traits are able to persist (Chase, 2007; Püttker et al., 2014). The diversity and distribution of ecological filters in a landscape contributes to spatial heterogeneity. By reducing the diversity of filters, habitat homogenization (e.g., the conversion of complex landscapes into simplified landscapes such as monocultures) can reduce *β*-diversity and species' trait diversity (Chase, 2007; Püttker et al., 2014).

The loss of species and/or species trait diversity that can result from conventional monoculture agriculture may also compromise the provisioning of important ecosystem services such as pollination, pest control, and nutrient cycling (Tscharntke et al., 2005; Kremen & Miles, 2012). Currently, our agricultural system compensates for these lost ecosystem services by increasing external inputs (Kremen et al., 2012), which can have unwanted negative consequences on both humans and wildlife (Eskenazi et al., 2007; Gill et al., 2012). The negative ramifications of high-input agricultural systems have fostered the development and refinement of

agricultural techniques that minimize external inputs by utilizing and regenerating ecosystem services (Kremen & Miles, 2012; Kremen et al., 2012). Through local and landscape-scale diversification of crops and habitat, these techniques seek to promote biological interactions that lead to better provisioning of ecosystem services. Such systems also support higher local biodiversity (Hole et al., 2005; Gabriel et al., 2013; Gonthier et al., 2014; Tuck et al., 2014) and spatial heterogeneity in community composition (Gabriel et al., 2006; Clough et al., 2007) than conventional monoculture agriculture. Particularly, techniques that foster landscape-level diversification by maintaining or restoring fragments of natural habitat have been shown to be effective in supporting greater numbers of species and the ecosystem services that they provide (Ricketts et al., 2008; Garibaldi et al., 2011; Kennedy et al., 2013) while also increasing community level β-diversity (Kehinde & Samways, 2014). However, if landscape diversification reduces yields, it may lead to further extensification, harming biodiversity (land-sparing argument Ref. Phalan et al., 2011). Recent work suggests that land-sparing arguments promoting intensive, simplified agriculture are over-simplified (Kremen, 2015), because such forms of agriculture often also lead to extensification (Meyfroidt et al., 2014).

In the most simplified agricultural areas, natural habitat is nearly nonexistent. In some cases, farmers have adopted the habitat restoration technique by planting strips of native plants along farm edges (hedgerows) to help diversify the landscape, without removing arable land from production. Hedgerows have been shown to support higher diversity and abundance of various ecosystem service providers, including beneficial insects, and birds (Hinsley & Bellamy, 2000; Bianchi et al., 2006; Hannon & Sisk, 2009; Morandin & Kremen, 2013; Morandin et al., 2014). It remains unclear, however, whether they mimic natural habitat by re-creating spatially structured communities, by leading to higher β-diversity. In addition, communities with diverse traits can provide higher quality and more stable ecosystem services (Klein et al., 2009). Thus, if hedgerows maintain the spatial heterogeneity of communities at different hedgerows by supporting species with a diversity of traits, they may promote the provisioning of ecosystem services such as pollination in agricultural areas (Klein et al., 2009). Understanding whether simple restoration interventions such as hedgerows can counter biotic homogenization when replicated across a landscape will be critical in assessing their value for ecosystem service provision and biodiversity conservation.

Focusing on pollinators, key ecosystem service providers (Klein et al., 2007), here we ask whether hedgerows support more spatially rich communities with more diverse suites of species traits. We do so using a long-term dataset from the highly simplified and intensively managed agricultural landscape of California's Central Valley. We also identify which mechanisms are likely responsible for driving the spatial trends we find. Specifically, we uncover the processes leading to the observed patterns in pollinator β-diversity and, further, investigate whether there is evidence that pollinator species track biotic and abiotic resources. Lastly, we test whether simplified agriculture imposes an ecological filter on insect pollinators by favoring species with particular set of traits. In our study landscape, hedgerows augment the richness and abundance of pollinators (Morandin & Kremen, 2013) and the occurrence, persistence, and colonization of both resource generalists and specialists (Kremen & M'Gonigle, 2015; M'Gonigle et al., 2015), while also exporting pollinators into agricultural fields (Morandin & Kremen, 2013). Understanding whether hedgerows support spatial heterogeneity of communities is the next step toward understanding whether they can conserve biodiversity and promote the provisioning of ecosystem services in agricultural areas.

Materials and methods

Study sites and collection methods

We surveyed pollinators from 21 hedgerow sites and 24 unrestored control sites, located in the Central Valley of California in Yolo, Colusa, and Solano Counties (Fig. 1). This is an intensively managed agricultural area dominated by monocultures of conventional row crops, vineyards, and orchards. The monitoring sites represent a sample of field margin conditions across the northern Central Valley. Hedgerows, which consist of native, perennial, shrub, and tree plantings (Morandin & Kremen, 2013), are ca. 3–6 m wide and approximately 350 m long and border large (ca. 30-hectare) crop fields. They are typically planted along field margins where they do not remove valuable land from production. Hedgerows differ in age from newly established, 'maturing' (1–10 years postplanting) to 'mature' (established >10 years ago). By investigating hedgerows at different stages of maturity, we can determine whether the effects of hedgerows on β-diversity accumulate with hedgerow maturation. We also monitored unrestored control sites which are weedy edges that represent a variety of relatively unmanaged field edges found in the region. Control sites were selected to match conditions surrounding the hedgerow sites. For each hedgerow, we selected 1–2 unrestored controls adjacent to the same crop type (row, orchard, pasture, or vineyard), within the same landscape context. The crop fields adjacent to hedgerows and controls were similarly managed as intensive, high-input monocultures. The mean distance between monitoring sites was 15 km, and
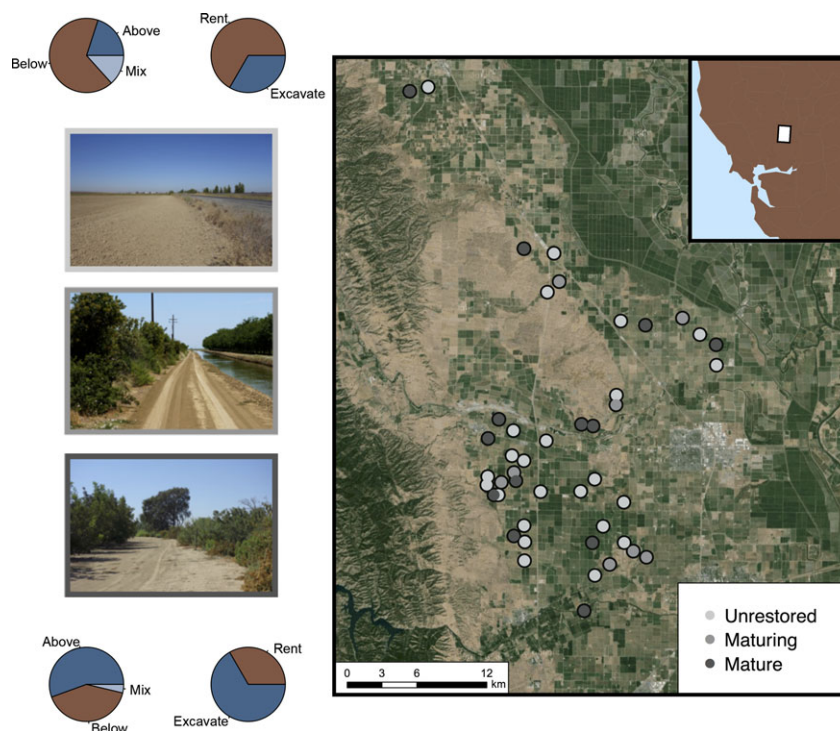
Fig. 1 Location of hedgerow and unrestored control sites in California (inset) and surrounding landcover. Pie charts represent the selected trait makeup of species found only at controls (top) or hedgerows (bottom). The left pie charts represent the nest location of the species, and the right charts depict the nest construction behavior.

the minimum distance between sites of the same type sampled in the same year was 2 km. The entire area surveyed spanned almost 300 km^2.

We sampled pollinator communities between April and August each year from 2007 through 2013 (Tables S1 and S2). Sites were sampled between two and five times per year (Tables S1 and S2).

In each round of sampling, the order in which sites were sampled was randomized. Surveys were conducted under sunny conditions when the temperature was above 21 °C and wind speed was below 2.5 m s^{-1}. Flower visitors to plants in hedgerows and unrestored controls were netted for 1 h of active search time (the timer was paused when handling specimens). All insect flower visitors that touched the reproductive parts of the flower were collected; however, here we focus only on wild bees, the most abundant and effective pollinators in the system (C. Kremen, A. Klein, and L. Morandin, unpublished data). Bee specimens were identified to species (or morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*) by expert taxonomists.

Surveys of the biotic and abiotic conditions were also conducted at each site throughout the flight seasons of the pollinators. At each site, each flowering plant in 50, one meter quadrats along the length of the hedgerow or control site was identified to species or morpho-species. The abundance of each plant species was estimated as the mean number of quadrats a species was present in, each year. In addition, in 2011 and 2012, we used the same quadrats to evaluate the

physical characteristics of the site including the amount of vegetative cover and uncultivated, bare ground.

Diversity estimates and statistical analysis

To estimate the species turnover between sites of the same type (i.e., unrestored controls, maturing hedgerows, or mature hedgerows), we used the variance in community composition as a measure of β-diversity (i.e., multivariate dispersion, see Section for details, 2,3). To calculate this metric, we first calculated the pairwise dissimilarity between sites within each year of the dataset using a dissimilarity estimator that incorporates species abundances, while also accounting for unobserved species (Chao et al., 2005).

Dissimilarity estimates can be affected by the total number of species and individuals sampled at a site (Chase et al., 2011; Kraft et al., 2011). For example, sampling from a fixed species pool, the probability that two sites do not share any species is higher when there are few individuals at those sites. Confounding sampling effects and species turnover can yield misleading results (Chase et al., 2011; Kraft et al., 2011). By extending the method described by (Chase et al., 2011) to include estimates of species' abundances, we used null models to estimate the deviation of the observed dissimilarity from that which would be expected under a completely random community assembly process (see Section for details). With the corrected dissimilarity values, we then calculated the multivariate dispersion of communities as the variability in

species composition within a site type (see Section for details, Anderson et al., 2011).

To investigate effects of site type, the *β*-diversity estimates were used as the response variable in a linear mixed model with site type (unrestored control, maturing hedgerow, mature hedgerow) as an explanatory variable along with random effects for both year and site (Bates et al., 2014; Kuznetsova et al., 2014). All analyses were conducted in R, version 3.1.1 (R Core Team, 2014).

Sources of *β*-diversity

We next assessed which spatial pattern was most responsible for maintaining *β*-diversity within each site type in our landscape. Communities that turnover in species composition across space (i.e., those that exhibit *β*-diversity) are thought to arise via two processes: (i) species replacement and (ii) predictable species loss/gain (Gaston & Blackburn, 2000; Baselga, 2012). In the latter case, species-poor sites will often be subsets of species-rich sites, and thus, communities should exhibit some degree of nestedness. Such a pattern might occur when, for example, species assemble along a resource gradient (Baselga, 2012). In contrast, species replacement should lead to communities that turnover in composition via substitution of species. This pattern could result when species track their preferred resource or, somewhat randomly *via* colonization and priority effects. Unlike species loss/gain, these communities would not be expected to exhibit any patterns in nestedness. Thus, to identify which of these two scenarios best describes the patterns in the landscape within each year, we determined whether our communities were significantly nested (Almeida-Neto et al., 2012). We used the index NODF to measure nestedness (Ulrich & Gotelli, 2007; Almeida-Neto et al., 2012).

To further uncover the processes contributing to spatial heterogeneity, we asked whether the dissimilarity between pollinator communities within and between site types was related to the geographic distance between sites. To do this, we compared the pollinator community dissimilarity matrix to the geographic distance between sites using Mantel tests. To assess the significance of the correlation, we permuted dissimilarity values among sites within each year to maintain the hierarchy of the data.

We also looked for evidence that pollinator communities track resources across the landscape. One important such resource is floral hosts; if the majority of the pollinators track specific floral resources, differences in floral community composition between sites should generate corresponding differences in pollinator communities. To test this, we used Mantel tests to compare the pollinator community dissimilarity matrix to an analogous dissimilarity matrix for flowering plant species within and between site types. As we did for the bee community, we used an abundance-based measure to estimate the dissimilarity of the floral communities (Chao et al., 2005).

Rather than tracking particular flowering plant species, bees may track floral resources generally. Therefore, we also characterized floral communities according to their species richness, diversity, and total floral abundance, all proxies for floral resource availability. We then used a Gower dissimilarity measure to characterize the changes in the floral resources between sites and then compared that to the pollinator community, again using Mantel tests to look for associations between and within site types.

Lastly, both abiotic conditions and resources may affect which pollinator species are present. Bee species vary considerably in their nesting habits, and therefore, the availability of specific nesting materials may influence which species are able to occupy an area (Potts et al., 2005; Sardinas & Kremen, 2014). To examine this, we characterized the nesting resources at each site. Specifically, we measured the mean and variability of the amount bare ground, dead wood, hollow stems, cracks in the soil, and vegetation cover (Potts et al., 2005). We used Mantel tests to correlate pollinator community turnover with differences in the physical characteristics of sites, between and within site types, estimated using Gower dissimilarity.

Community traits

We determined whether agricultural areas act as an ecological filter on pollinator groups by comparing the trait distributions of pollinators found at unrestored controls to those found at hedgerows. Our unrestored control sites comprise a variety of unmanaged crop field edges and, therefore, represent the dominant conditions in our landscape. Consequently, the species visiting these sites are those that are likely present in the landscape prior to any restoration.

To characterize the trait diversity of the bee communities, we computed three metrics that capture diversity, uniqueness, and distribution of trait values in the community: trait dispersion, divergence, and evenness (Villéger et al., 2008; Schleuter et al., 2010). Trait dispersion is a measure of trait diversity, corrected for species richness (Schleuter et al., 2010); trait divergence measures how species abundances are distributed within the trait space (i.e., a measure of trait uniqueness, Villéger et al., 2008); trait evenness measures the regularity with which traits are distributed across trait space, accounting for abundance (Villéger et al., 2008). In combination, these metrics provide a relatively complete overview of the different aspects of species trait diversity (Villéger et al., 2008; Schleuter et al., 2010).

Selection of appropriate characters is essential to the characterization of the community's distribution and diversity of traits (Villéger et al., 2008). We selected resource capture and use traits that collectively influence the distribution of bee species as pollinators over space and time (Kremen & M'Gonigle, 2015) including resource specialization (quantitative, *d'*; Blüthgen et al., 2006), body size (quantitative, inter-tegular span, mm, Cane, 1987) sociality (categorical: eusocial, solitary, cleptoparasitic), nest location (categorical: aboveground, belowground or mix), and nest construction (categorical: excavate or rent; Williams et al., 2010) as described in more detail in Kremen & M'Gonigle (2015). Each trait has the same weight in trait diversity metric estimation (Villéger et al., 2008; Schleuter et al., 2010). Pollinator specialization was calculated using plant–pollinator interaction observations from a more extensive dataset from Yolo County (18 000 interaction

records) that included both the data included in this study and additional data from sites where we collected flower visitors using the same methods (M'Gonigle et al., 2015). The specialization metric measures the deviation of the observed interaction frequency between a plant and pollinator from a null expectation where all partners interact in proportion to their abundances (Blüthgen et al., 2006). It ranges from 0 for generalist species to 1 for specialist species. To determine whether trait evenness, dispersion, and divergence differed between controls and hedgerows at different stages of maturation, we used the trait diversity metrics as response variables in linear mixed models with site type as a fixed effect and year and site as random effects (Bates et al., 2014; Kuznetsova et al., 2014).

If agriculture creates an ecological filter, the trait composition of agricultural bee communities should differ from that of a community that was randomly assembled from a shared meta-community. To test whether agriculture constitutes an ecological filter, we compared the observed trait values with the distribution of traits of randomly assembled communities. Because species richness differs between hedgerow and control sites (Morandin & Kremen, 2013) and furthermore, because differences in species richness may constrain the observed trait values and trait diversity (e.g., if only one species was observed, the trait diversity will always be zero), we randomly assembled communities of the same species richness as the observed communities. For quantitative traits, we focused on the mean trait value at a site weighted by abundance, and for categorical traits, we calculated the mean Simpson's diversity of traits (finite sample formulation). To generate the randomized communities, we shuffled the species between sites while maintaining the species richness and the number of occurrences of a species within each year. We then re-calculated the mean trait value and Simpson's diversity of traits for 9999 randomly assembled communities (Schleuter et al., 2010). Lastly, to calculate the probability of the observed trait value given a random assembly process, we computed the fraction of randomly assembled communities that had trait values greater than or equal to that of our observed community. For a given trait, if that probability was <0.025% (two-tailed test), we concluded that site type exerted an ecological filter on that trait.

To complement the previous analysis, we also asked whether the trait diversity and Simpson's diversity of traits was significantly different between hedgerows and unrestored controls. We compared the mean trait value or Simpson's diversity across site types using linear mixed models, with site status as an explanatory variable and site and year as random effects, as before (Bates et al., 2014; Kuznetsova et al., 2014).

Lastly, we asked whether the pollinator composition of communities supported by between hedgerows and unrestored controls differed using a permutational multivariate analysis of variance (PERMANOVA) (Anderson & Walsh, 2013). When comparing community composition, PERMANOVAs can be too liberal when the experimental design is unbalanced and the multivariate dispersions are heterogeneous because it is testing multiple hypotheses simultaneously (Anderson & Walsh, 2013). As the number of sites was nearly

equal for hedgerows and controls within but not between years, we compared the community composition within each year.

Results

Over seven years and 545 samples, we collected and identified 9898 wild bees comprising 114 species. The species came from five families and 30 bee genera. Most species occurred infrequently in the landscape: nearly 20% of species were observed two or fewer times.

We found that β-diversity was higher in mature hedgerows than unrestored controls (estimate for the difference between mature hedgerows and controls, $\pm$ standard error of the estimate, 0.134$\pm$0.045, P-value = 0.005, Fig. 2). β-diversity across maturing hedgerow sites was not, however, significantly different from that for control sites. These findings were robust to our use of different methods when generating the randomly assembled communities that we used to account for the expected β-diversity given the observed differences in the number of individuals and species (compare Fig. 2 and Fig. S3). We found that pollinator communities were not significantly nested, except for a single year and site type (Table 1), suggesting that species replacement, rather than species loss/gain, was the primary determinant of spatial heterogeneity in species composition for each site type.

Dissimilarity of pollinator communities at unrestored sites and between all site types was significantly correlated with the geographic distance (Fig. S1, Table 2). In addition, we found that the bee community dissimilarity was significantly correlated with the floral community dissimilarity between site types (Fig. S1, Table 2). The bee community was also significantly correlated
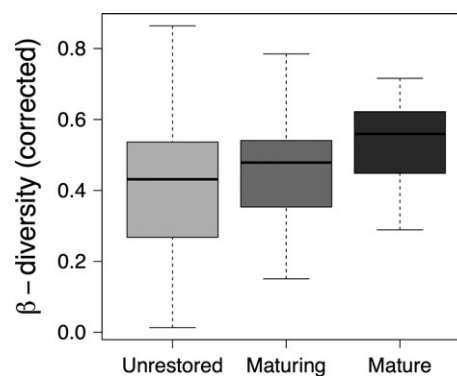
Fig. 2 Mature hedgerows support significantly higher corrected β-diversity than maturing hedgerows and unrestored controls. Corrected β-diversity values represent the dispersion of site community composition to the centroid of each site type. Boxplots represent medians (black horizontal line) first and third quartiles (box perimeter) and extremes (whiskers).

Table 1 The nestedness of pollinator communities, by year, for each site type. The z-scores were calculated by generating 9999 null communities, subtracting the mean of the calculated nestedness from the observed nestedness, and dividing by the standard deviation of the nestedness (Ulrich & Gotelli, 2007). Empirical *P*-values were calculated as the probability that the nestedness of the null communities was equal to or greater than the observed community nestedness. Pollinator communities were significantly nested only in 2013 for the unrestored site type

	Year	z-Score	P-value
Unrestored control	2007	−2.357	0.971
	2008	0.403	0.369
	2009	0.766	0.23
	2010	2.864	0.019
	2011	−0.787	0.78
	2012	−0.314	0.607
	2013	3.634	0.001***
Maturing hedgerow	2009	−0.391	0.644
	2011	1.617	0.059
	2012	1.062	0.153
	2013	−1.55	0.957
Mature hedgerow	2009	−1.15	0.892
	2010	−0.788	0.769
	2011	−0.785	0.781
	2012	0.524	0.287
	2013	−0.786	0.79

Symbols denote significance, with *** indicating 0.001.

with the floral community at mature hedgerows and controls, although the strength of the association at controls was weak (Table 2). Thus, the dissimilarity of floral communities between sites predicts the dissimilarity of the pollinator communities within mature hedgerows, while geographic distance more strongly structures the compositional turnover in controls. Maturing hedgerows may still be undergoing community assembly, and therefore, pollinator communities do not significantly respond to floral communities. The bee community was not correlated with floral or nesting resources, however (Fig. S1, Table 2).

Mature hedgerows positively affected each of the three trait diversity metrics compared to unrestored controls (estimate for the difference between mature hedgerows and controls, evenness: 0.100 ± 0.0366, $P = 0.009$; dispersion: 0.0759 ± 0.023, $P = 0.002$; divergence: 0.100 ± 0.0367, $P = 0.009$, Fig. 3). Compared to control sites, mature hedgerows therefore better support individuals with unique traits, as well as a greater diversity of trait values that are more evenly distributed across trait space. The trait diversity supported by maturing hedgerows, however, was not significantly different from controls.

Table 2 The correlation between the dissimilarity of pollinators communities and floral communities, nesting and floral resources, and geographic distance within and between site types

	Geographic distance		Floral community		Floral resources		Nesting resources	
	Mantel statistic r	P-value	Mantel statistic r	P-value	Mantel statistic r	P-value	Mantel statistic r	P-value
Across all site types	0.029	0.02*	0.134	0.0003***	−0.002	0.588	0.139	0.159
Unrestored controls	0.076	0.003**	0.085	0.019*	0.024	0.156	0.063	0.286
Maturing hedgerows	0.03	0.205	0.011	0.373	−0.061	0.697	−0.042	0.517
Mature hedgerows	−0.011	0.298	0.187	0.004**	−0.035	0.738	−0.619	0.979

Symbols denote significance, with *, **, and *** indicating 0.05, 0.01 and 0.001, respectively.

Examining each trait individually, we also found evidence that only species characterized by particular trait values are found in unrestored, agricultural areas. We found that, compared to randomly assembled communities, control sites exhibited significantly lower trait values for floral specialization and body size, and lower diversity than expected for each categorical trait except sociality (Fig. 4) suggesting that the species that visit or inhabit unrestored controls comprise only a subset of the available species pool. Mature and maturing sites had trait values expected by randomly assembled communities. Similarly, the linear mixed models indicated
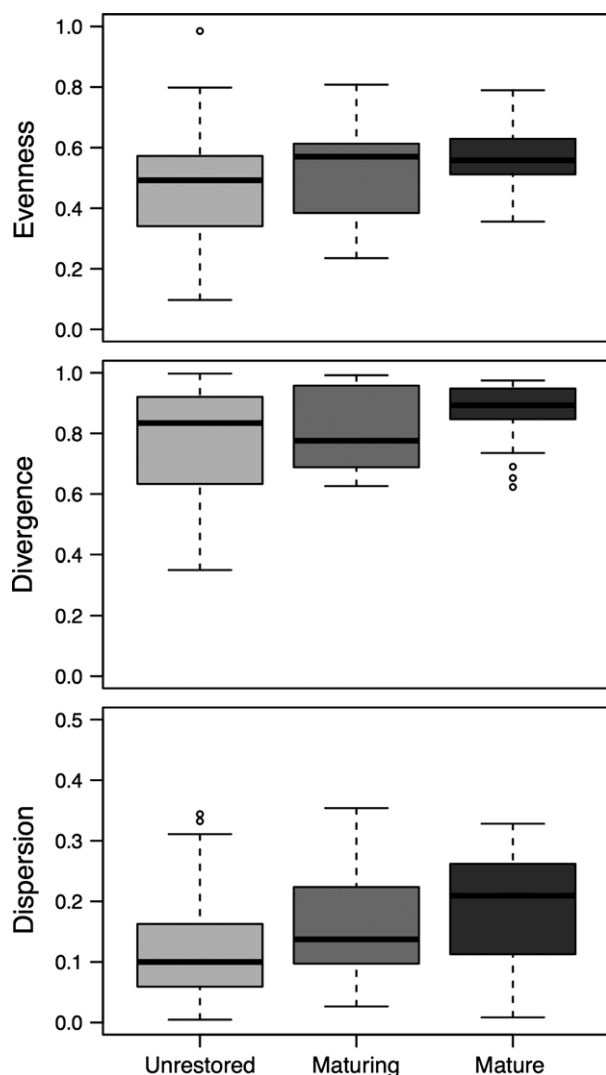
Fig. 3 The evenness, divergence, and dispersion of the pollinator traits for communities at control sites, maturing hedgerows, and mature hedgerows. Pollinator communities at mature hedgerows had significantly higher values for all metrics. Relative to the range of trait values in the landscape, mature hedgerows had 12% higher evenness, 15% higher divergence, and 21% higher dispersion than unrestored controls.

that, compared to bee communities occupying unrestored controls, bee communities at both mature and maturing hedgerow sites were comprised of species that are significantly larger (estimate for the difference between controls and mature 0.278 ± 0.080, $P = 0.001$; controls and maturing: 0.223 ± 0.092, $P = 0.02$) and more specialized (controls and mature: 0.048 ± 0.013, $P = 0.0004$; controls and maturing: 0.058 ± 0.015 $P = 0.0003$, Figs 4 and S4). Bees at hedgerows also exhibited more diversity in nesting locations and nest construction behaviors (nest location diversity, estimate for the difference between controls and mature: 0.137 ± 0.057, $P = 0.022$, controls and maturing: 0.172 ± 0.067, $P = 0.014$; nest construction trait diversity, controls and mature: 0.121 ± 0.051, $P = 0.02$, controls and maturing: 0.158 ± 0.060, $P = 0.012$, Figs 4 and S4). Sociality diversity was not significantly different between site types.

Although the trait diversity at hedgerows and unrestored controls differed significantly, the composition of communities did not significantly differ between controls and hedgerows (Table S4, Fig. S2).

Discussion

We have shown that on-farm restorations in the form of hedgerows, when replicated across a landscape, can promote the assembly of spatially heterogeneous and phenotypically diverse pollinator communities in intensively managed and simplified agriculture. Such restorations may thus help to slow or even reverse the biotic homogenization that is characteristic of such landscapes. Without hedgerows, intensive and simplified agriculture imposed a strong ecological filter that eroded patterns of spatial structuring between communities and diminished almost every aspect of community trait diversity and distribution that we investigated. This ecological filter affected a variety of phenotypic traits including nesting habits and also selected for smaller, less specialized bees. In concordance with a number of other studies conducted across a wide variety of taxa, we found that, by homogenizing communities, agriculture has the potential to affect the distribution of species over large scales (Gabriel et al., 2006; Hendrickx et al., 2007; Ekroos et al., 2010; Flohre et al., 2011).

Loss of such diversity may impact the functioning and resilience of natural systems which could have profound implications for humans and wildlife. The provisioning of ecosystem services, such as pollination, requires a stable and diverse community of wild bees (Kremen, 2005; Klein et al., 2009). These pollination services are critical both in natural communities and economically: 87% of all flowering plant species and 75%
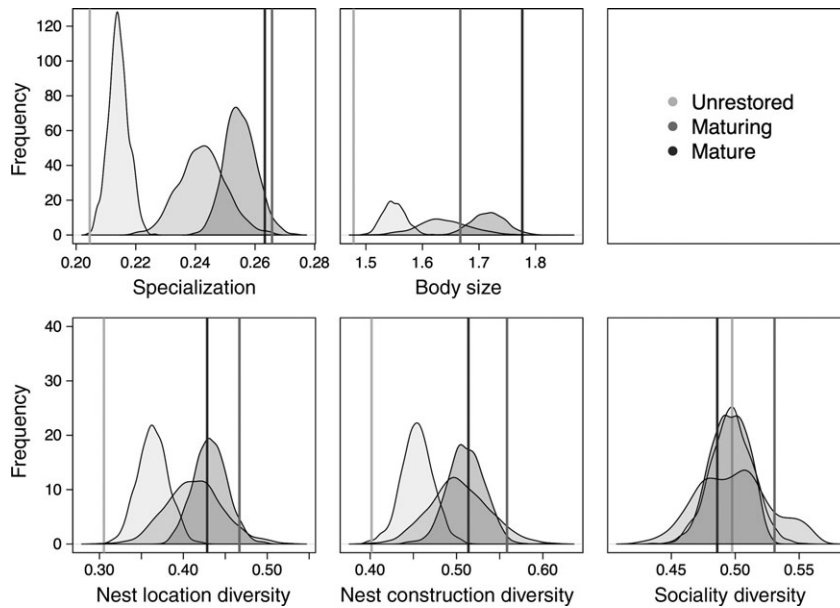
Fig. 4 The mean trait value (top panel) and trait diversity (bottom panel) of pollinator communities at different site types. The solid lines are the observed trait values, and the shaded curves are trait distributions for randomly assembled communities with the same species richness as the observed communities for each site type. The unrestored controls had significantly lower ($P < 0.025$) trait values and diversity than expected for a randomly assembled community for all trait groups except sociality diversity. In the context of the range of trait values observed in the study landscape, mature hedgerows had 21% higher specialization than controls, 16% larger bees, 12% more nest location diversity, and 11% more nest construction diversity.

of crop species depend to some extent on animal pollinators in order to produce fruits or seeds (Klein et al., 2007; Ollerton et al., 2011). Animal-pollinated crops also supply a large proportion of essential nutrients to the human diet (Eilers et al., 2011; Smith et al., 2015).

Based on findings in other cropping systems, lower functional diversity, combined with the loss of key service providers, will likely negatively affect levels of pollination in both crops and wild plant populations (Hoehn et al., 2008; Klein et al., 2009; Brittain et al., 2013). In addition, by reducing the size of the species pool, simplified agriculture may impact the stability of services (Winfree & Kremen, 2009) and thus the reliability and predictability of plant reproduction and crop yields (Garibaldi et al., 2011; Garibaldi et al., 2013). Encouragingly, however, relatively small-scale restorations such as hedgerows can mitigate the homogenization caused by simplified agriculture, when replicated across landscapes. Hedgerows have also been shown to support other ecosystem services (Hinsley & Bellamy, 2000; Bianchi et al., 2006; Hannon & Sisk, 2009), so these small-scale, on-farm restoration measures may also provide an economic benefit to growers (Blaauw & Isaacs, 2014), although this is likely to be context dependent (Sardiñas & Kremen, 2015).

We have shown that, in addition to supporting a higher diversity and abundance of pollinators (Morandin & Kremen, 2013), hedgerows also support approximately 14% higher β-diversity and approximately 10% more trait diversity, uniqueness, and evenness than unrestored field margins. In addition, because the trait diversity of the communities differed significantly between hedgerows and unrestored controls but community composition did not, the communities at controls are likely a subset of those at hedgerows. For example, 28% of the total species pool was found only at hedgerows, whereas only 13% of species were unique to unrestored controls (Table S3). Of the species only at controls, 80% were represented by a single individual. The species only at hedgerows tended to have more specialized nesting requirements (above-ground renters), whereas those only at controls were primarily generalists (below-ground excavators, Fig. 1). Also, although the majority of the species (68%) were found at both hedgerows and unrestored controls (Table S3), species ranging from relatively rare (<10 individuals) to common (between 10 and 100 individuals) were infrequent at controls and more abundant in hedgerows (Fig. S5). Interestingly, the three species observed over 100 times, *Lasioglossum incompletum*, *Halictus tripartitus* and *Halictus ligatus*, all small-bodied floral and nesting resource generalists, were at similar abundances in hedgerows and unrestored controls, if not slightly more abundant in controls (Fig. S5).

Although hedgerows may help counter homogenization of pollinator communities in simplified agricultural landscapes, comparing the spatial heterogeneity they support to that which is observed in natural communities is important in assessing their overall conservation value. In remnant chaparral/oak woodland communities in the same ecoregion and adjacent to our study landscapes (Forrest et al., 2015), an average of 30% of species were not shared across sites located within 3.5–50 km of each other. The Central Valley, which was once described as 'one vast, level, even flower-bed' (Muir, 1916), has been extensively converted to agriculture, likely limiting the species pool due to local extinctions. Even so, at hedgerows an average of 15 km apart, we found between 36% and 67% of species were not shared between sites, depending on the year. Both the spatial scale and biota of our study and that of (Forrest et al., 2015) are comparable, suggesting that hedgerows are, in fact, restoring spatial heterogeneity to approximately the same range as might occur in adjacent natural systems. In addition, in the disparate landscape of the southwestern United States, a diversity hot spot for bees (Minckley et al., 1999), 61% of species were not shared across sites within 1–5 km of each other (Minckley et al., 1999). Although the species pool is richer in the southwest, the amount of species turnover at hedgerows is not unlike what is observed in that highly heterogeneous region (Minckley et al., 1999). Thus, across many aspects of biodiversity, hedgerows might provide a valuable measure for conserving biodiversity (Hinsley & Bellamy, 2000; Bianchi et al., 2006; Klein et al., 2009; Morandin & Kremen, 2013; Garibaldi et al., 2014; Kremen & M'Gonigle, 2015).

Only mature hedgerows (and not young, recently planted hedgerows) in this study supported higher trait and β-diversity when compared to nonrestored farm edges. Thus, the processes that lead to a buildup of spatial turnover in pollinator communities are slow and may take considerable time before observably affecting pollinator communities. However, we have recently shown that hedgerow restoration leads to increased rates of colonization and persistence of pollinators in maturing hedgerows and that this effect becomes stronger over time (M'Gonigle et al., 2015). Further, we found that maturing hedgerows differentially support more specialized species over time (Kremen & M'Gonigle, 2015). These two temporal studies on the early phases of hedgerow maturation (0–8 years post restoration) show that hedgerows begin to impact pollinator communities much earlier than 10 years. Combined, these findings suggest a possible mechanism whereby restoration might lead to increases in species turnover; as a hedgerow matures, species with a wider variety of life-history traits are better able to colonize and persist there, thus leading to the accumulation of differences in community composition between sites over time. This then leads to greater spatial heterogeneity in pollinator communities at hedgerows. Conversely, in unrestored areas, the rate of colonization and persistence is lower, particularly for species with more specialized habitat requirements, thereby creating an ecological filter that limits the total diversity and, thus, turnover that is possible.

This above-described process can be, in part, deterministic; restored and nonrestored farm edges differ fundamentally in which pollinator species are able to colonize and/or persist in them (Kremen & M'Gonigle, 2015; M'Gonigle et al., 2015). Thus, pollinators respond to the differences in the plant communities between hedgerows and controls, and the pollinator community at mature hedgerows tracks floral hosts. Interestingly, however, the pollinator communities at hedgerows that were closer to one another were not necessarily more similar than sites that were further apart. In addition, hedgerows maintain β-diversity in the landscape by supporting unique combinations of species, and we did not find evidence that communities at hedgerows were nested subsets of one another (Baselga, 2012). Because hedgerows are planted, the floral communities the pollinators are tracking will not necessarily be spatially structured like natural communities. In addition, bees are known to be highly spatially and temporally variable (Minckley et al., 1999; Williams et al., 2001) and thus, stochastic processes that do not result in spatial structuring are likely operating as communities assemble.

In contrast to within hedgerows, the dissimilarity of pollinators at unrestored controls responded positively to geographic distance. Because the conditions at controls are relatively uniform across space, this suggests a role for dispersal limitation in determining pollinator community composition at unrestored controls (Chase et al., 2005). In addition, the number of shared species between hedgerows and controls was also positively related to distance (Table 2), suggesting the communities at controls may be influenced by landscape context such as the presence of nearby hedgerows. Hedgerows may therefore represent a source of bee diversity in the landscape.

Here we focus on the effects of hedgerows on β-diversity, but there are likely other contributions to spatial heterogeneity in our landscape. There are a number of crops that provide floral resources to pollinators in our area, including mass-flowering sunflower, melons, and almonds (Kremen et al., 2002; Greenleaf & Kremen, 2006; Klein et al., 2012). Different crops attract different pollinators (Winfree et al., 2008) and thus may

affect the spatial heterogeneity of communities. In addition, some crops might also pull resident species from the hedgerows (Sardiñas & Kremen, 2015), while others may attract species that may subsequently colonize hedgerows (Kovács-Hostyánszki et al., 2013). Differences in adjacent crops between hedgerows and unrestored controls thus may add noise to the underlying signal of β-diversity. However, because hedgerows and controls are matched for crop type, while there may be a contribution of crop type on β-diversity, it should be a random one affecting hedgerows and controls simultaneously.

To achieve sustainable food production while protecting biodiversity, we need to grow food in a manner that protects, utilizes, and regenerates ecosystem services, rather than replacing them (Kremen & Miles, 2012; Kremen et al., 2012; Kremen, 2015). Diversification practices such as installing hedgerows, when replicated across a landscape, may provide a promising mechanism for conserving and restoring ecosystem services and biodiversity in working landscapes while potentially improving pollination and crop yields (Blaauw & Isaacs, 2014; Garibaldi et al., 2014).

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Author contributions

CK designed the study; LKM, LCP, and CK collected data; LCP analyzed output data. LCP wrote the first draft of the manuscript; and all authors contributed substantially to revisions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Supporting Methods.
Table S1. The number of sampling rounds conducted at each control site in each year of the study.
Table S2. The number of sampling rounds conducted at each hedgerow site in each year of the study.
Table S3. Bee species found at hedgerows and controls.
Table S4. The test statistics for the permutation anovas comparing pollinator community composition between mature hedgerows, maturing hedgerows and unrestored controls within each year.
Figure S1. The dissimilarity of pollinator communities as a function of the dissimilarity of the floral communities, floral resources, nesting resources, and geographic distance at each site type across all years of the study.
Figure S2. The dissimilarity of communities in multivariate space using a principal coordinate analysis.
Figure S3. The beta-diversity (corrected using random communities that have the same number of individual as observed communities) at unrestored controls, maturing hedgerows and mature hedgerows.
Figure S4. The mean trait value and trait diversity of pollinator communities at different site types.
Figure S5. The frequency of observing specific abundances at a site across years of a sample of species found in both hedgerows and controls.