Title

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Authors

Kremen, Claire
M'Gonigle, Leithen K

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Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species

Claire Kremen[1]* and Leithen K. M'Gonigle[1,2]

[1]*Department of Environmental Sciences, Policy and Management, University of California, 130 Mulford Hall, Berkeley, CA 94720-3114, USA; and* [2]*Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA*

Summary

1. Agriculture now constitutes 40–50% of terrestrial land use globally. By enhancing habitat suitability and connectivity, restoration within agricultural landscapes could have a major influence on biodiversity conservation. However, habitat management within intensive agricultural landscapes may primarily boost abundances of common, highly mobile generalists, rather than vulnerable or endangered species. We studied pollinator community response to small-scale habitat restoration in the intensively farmed Central Valley of California to determine whether restoration could also promote more specialized, less common and/or less mobile species.

2. Composition of pollinator communities was assessed in five experimental and 10 control (unrestored) sites before and after restoration of native plant hedgerows over an 8-year period, using a before-after control-impact design.

3. We characterized bee and fly species based on functional response traits [floral specialization, habitat specialization, abundance, body size and sociality (bees only)] known to influence the response to habitat change.

4. We modelled how species occurrences changed with habitat restoration over time as modulated by their response traits.

5. We found that hedgerows not only significantly enhanced occurrences of native bee and syrphid fly species, but that as hedgerows matured, they had a greater positive effect on species that were more specialized in floral and nesting resources and smaller (less mobile).

6. *Synthesis and applications*. Unlike previous studies that suggest habitat restoration in agricultural landscapes only benefits mobile, generalist species, our results suggest that small-scale habitat restoration can promote species whose traits likely render them particularly vulnerable to habitat degradation. Thus, even within highly intensive agricultural landscapes, small-scale habitat restoration can be a conservation management tool. However, tailoring habitat enhancements to promote certain species or guilds may be critical for their success as a conservation intervention in agricultural landscapes.

Key-words: Apoidea, bee, before-after control-impact, conservation, hedgerow, land-use change, pollination service, response traits, syrphid fly

Introduction

Two primary goals of restoring natural habitat are to conserve biodiversity and restore ecosystem functions and services (Benayas *et al*. 2009). Agriculture is the world's largest land use and constitutes a principle driver of biodiversity loss, increased homogenization and decreased ecosystem services (Foley *et al*. 2011; Karp *et al*. 2012). Agricultural lands also constitute much of the matrix that surrounds protected patches of natural habitat. Managing this matrix both to provide resources for species in these patches and to improve connectivity among patches is perhaps the most important current task for biodiversity conservation (Driscoll *et al*. 2013).

While restoring habitat within agricultural areas might enhance species abundances in the matrix or promote

*Correspondence author. E-mail: ckremen@berkeley.edu

movement through the matrix, such schemes are thought to primarily promote common and resilient species and thus provide few conservation benefits for species of concern (Kleijn *et al.* 2006). Such species, it is thought, are likely to have specific functional traits ('response traits') like high mobility and generalist habits (Ewers & Didham 2006; Schweiger *et al.* 2007) that permit them to survive even in intensive agricultural landscapes (Flynn *et al.* 2009). Thus, trait composition could be used to assess whether restoration simply bolsters populations of such species or, alternatively, promotes species that are sensitive to habitat loss, fragmentation and degradation (hereafter, 'land-use changes'). Here, we examine how restoration of native plant hedgerows in an intensive agricultural setting influences the response trait composition of flower visitor communities, as an indicator of conservation effectiveness of this technique.

For bees and syrphid flies, two dominant groups in many flower visitor communities (Morandin & Kremen 2013; Winfree *et al.* 2014), abundance, body size, specialization in diet or microhabitat, and sociality are response traits that are sensitive to land-use changes and might, therefore, differentiate flower visitor communities in response to restoration (i.e. reversal of land-use changes). Abundance was the single most important trait influencing persistence in a study of bees and flies (Winfree *et al.* 2014), while population size, but not habitat area, was related to persistence in a solitary bee species (Franzén & Nilsson 2010). Diet specialization was associated with sensitivity to land-use changes for both bees (Bartomeus *et al.* 2013; Burkle, Marlin & Knight 2013; but see Williams *et al.* 2010) and syrphid flies (Schweiger *et al.* 2007). Microhabitat specialization also influenced flower visitor response to land-use changes. In flies, Schweiger *et al.* (2007) found that larval habitat specialists (i.e. living on water plants or in the root zone of trees) were most sensitive to land-use changes. In bees, several studies found that cavity nesters were more affected by land-use changes (Williams *et al.* 2010; Burkle, Marlin & Knight 2013; but see Bartomeus *et al.* 2013), as are above-ground nesters that either used existing cavities or excavated their own nests (Williams *et al.* 2010).

Body size, sociality and parasitism displayed conflicting responses to land-use changes in different studies. Body size is a proxy for mobility in bees (Greenleaf *et al.* 2007) and flies (Schweiger *et al.* 2007). Larger-sized individuals may be more resilient to land-use changes because they can disperse further through inhospitable landscapes in search of resources. However, large-bodied species may also have larger resource needs and smaller population sizes, reducing their resilience to land-use changes. These opposing tendencies may explain the wide variation found in the responses of body size to land-use changes which include non-significant for bees (Williams *et al.* 2010), significant positive for bees (Larsen, Williams & Kremen 2005; Bartomeus *et al.* 2013) and significant negative for bees (Jauker *et al.* 2013) and flies (Öckinger *et al.* 2010). Social bees responded more strongly to land-use changes than solitary bees in several studies (Williams *et al.* 2010; Bommarco *et al.* 2010), but others found no effect of sociality (Bartomeus *et al.* 2013) or effects that varied by bee family (Jauker *et al.* 2013). Cleptoparasitic bees, which are generally specialized on their hosts and are considered to occur at a higher trophic level because they feed on the nest provisions and/or larvae of other bees (Bommarco *et al.* 2010), were found to be more sensitive to land-use changes than non-parasitic bees in one study (Burkle, Marlin & Knight 2013), but less sensitive in another (Jauker *et al.* 2013). These discrepancies among studies may reflect not only true differences among study systems, but also methodological differences, such as coding of qualitative traits.

While many studies have examined how traits of flower visitor communities change as communities disassemble in response to land-use changes (e.g. Steffan-Dewenter & Tscharntke 2000; Larsen, Williams & Kremen 2005; Schweiger *et al.* 2007; Bommarco *et al.* 2010; Bartomeus *et al.* 2013; Burkle, Marlin & Knight 2013; Winfree *et al.* 2014), only a few studies have used a trait-based approach to examine how restoration influences the reassembly of flower visitor communities (Alanen *et al.* 2011; Merckx, Marini & Feber 2012). If restoration in intensive agricultural landscapes merely promotes common generalist species, then we would expect to see increases in mean occurrence (i.e. presence) of species between restored and unrestored sites, but no relative increases in the occurrence of species that are more sensitive to land-use changes. Here, we present results from a long-term restoration study. Specifically, we examine (i) how restoration of native plant hedgerows within an intensive agricultural landscape in California's Central Valley influences species occurrences of bees and flies and (ii) how these effects on species occurrences are modulated by response traits. We predict that hedgerows promote species more sensitive to land-use changes and thus will disproportionately increase occurrence of species that have some or all of the following response traits: (i) less abundant, (ii) narrow larval and/or adult diet breadths, (iii) cavity-nesting bees, (iv) large body size for bees (based on Larsen, Williams & Kremen 2005 from the same study region), (v) small body size for flies and (vi) parasitic bees. We predict no difference in sociality for bees, however, since in our study system, some social bees are least responsive to agricultural intensification (i.e. *Halictus* and *Lasioglossum*), whereas others (*Bombus*) are most sensitive to agricultural intensification (Larsen, Williams & Kremen 2005; see also Jauker *et al.* 2013). If hedgerows promote species with these response traits disproportionately relative to controls, then hedgerows may be partially reversing the community disassembly that has occurred in response to agricultural intensification in this region (Kremen, Williams & Thorp 2002; Larsen, Williams & Kremen 2005).

Materials and methods

STUDY LANDSCAPE AND SAMPLING

Our study landscape, located in the Central Valley of California (Yolo County), is an intensively managed agricultural landscape comprised principally of conventional row crops, vineyards and orchards (Fig. 1a). The 1-km buffers around our sites contained on average <0·6 ± 0·2% (SE) natural habitat cover; thus, these areas are examples of 'cleared landscapes' (*sensu* Tscharntke *et al.* 2005). We utilized a before-after control-impact (BACI) design (Underwood 1994) to assess the impact of hedgerows on pollinator communities, as recommended for evidence-based assessment of conservation and agri-environment management schemes (Potts *et al.* 2006). We selected five farm edges to be restored and paired these with 10 control sites that would not be restored. As recommended, we selected a larger number of controls than restoration sites ('beyond BACI', Underwood 1994).

Monitoring began in 2006 prior to restoration and continued through 2013. Hedgerows were planted in 2007 or 2008 with native perennial shrubs and trees (e.g. *Cercis occidentalis*, *Ceanothus* spp., *Rosa californica*, *Heteromeles arbutifolia*, *Sambucus mexicana*, *Eriogonum* spp., *Baccharis* spp., *Salvia* spp. and others). Hedgerows are approximately 350 m long and 3–6 m wide, bordering an irrigation ditch or slough and adjacent to large (*c.* 80 acre) crop fields. After initial planting, hedgerows were irrigated and weeded for 3 years until well-established (see Fig. 1b and 1c for an example of a restoration site prior to and 6 years post-restoration).

Control sites (Fig. 1a) were selected to roughly match conditions surrounding paired restoration sites, including adjacency to an irrigation ditch or slough and similar crop system (row, orchard, pasture or vineyard), within the same landscape context (i.e. within 1–3 km of the restoration site, but >1 km from all other study sites to maintain independence). Controls reflect the variety of potential conditions on edges of crop fields that could be restored (see Fig. S1, Supporting information). Such edges may at times be tilled, treated with pesticides or left alone; plants on these edges include predominantly non-native forbs and grasses, with occasional shrubs and trees. The most common flowering plants at these sites are the non-native weeds: *Convolvulus arvensis*, *Brassica* spp., *Lepidium latifolium*, *Picris echioides* and *Centaurea solstitialis*. Many of these weeds also occurred at restoration sites.

We sampled flower visitor communities at each site a minimum of three times between April and August each year, except for two sites which were sampled only twice in the first year (Table S1). For logistical reasons, no sampling was conducted in 2010. In each sample round, sites were sampled in random order during allowed weather conditions, which were bright overcast to clear skies, wind speed <2·5 m s^{-1}, temperature >21 °C. Beginning in the morning, all flower visitors that contacted the reproductive parts of the flower (except *Apis mellifera*) were netted along a 350-m transect for 1 h, pausing the timer while handling specimens and recording the plant species on which each specimen was collected. Honeybees (*A. mellifera*) were not collected because their abundance is determined largely by the placement of hives throughout the region by bee-keepers. Here, we focus our analyses on the two most abundant and effective wild pollinator groups in the data set: bees and syrphid flies (representing 47% and 20% of records, respectively). Bee specimens were identified to species or morpho-species by expert taxonomist Dr. Robbin Thorp (Professor Emeritus, University of California, Davis), and syrphid specimens were identified to species by expert taxonomist Dr. Martin Hauser (California Department of Food and Agriculture).

RESPONSE TRAITS

Qualitative traits for bees included sociality, nesting location and nesting habit. Following Burkle, Marlin & Knight (2013), we classified bees as social (including primitively social to eusocial), solitary or cleptoparasitic, based on Michener (2000). Following Williams *et al.* (2010), we classified nesting location as above- or below-ground or mixed and nesting habit as constructing a nest (excavator) or using a pre-existing cavity

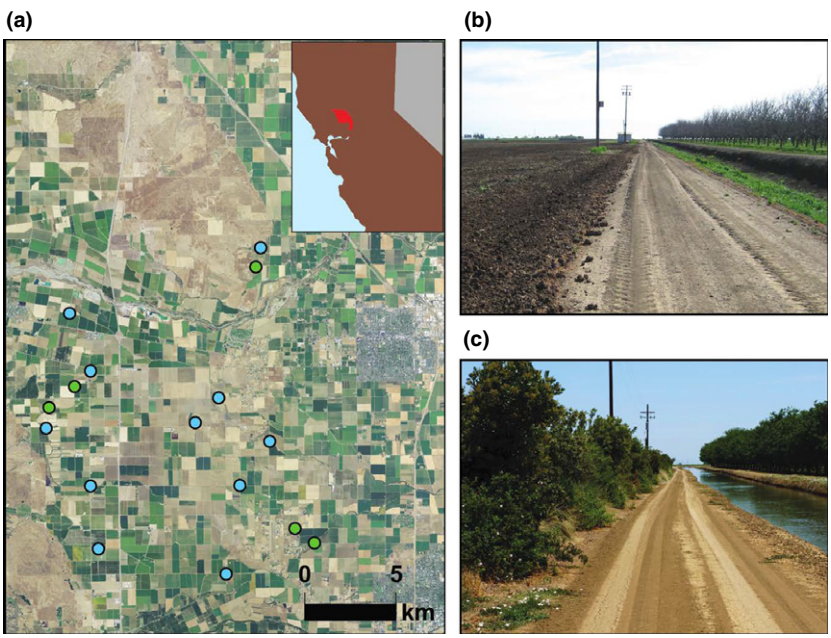

Fig. 1. Study region and sites. (a) Location of hedgerow and control sites in California (inset) and surrounding land cover (Data available from the U.S. Geological Survey, National Aerial Imagery Program). Green dots are restored sites and blue are control sites. (b) A hedgerow site prior to restoration. (c) Same site 6 years post-restoration.

(renter). Nesting location was based on Krombein *et al.* (1979), Michener (2000), Cane, Griswold & Parker (2007), Sheffield *et al.* (2011), and nesting habit was based on Michener (2000). Cleptoparasitic bees were not scored for nesting habit since they do not collect pollen or construct nests. For flies, we assessed the type of larval diet (aphids, detritus/bacteria, oozing tree sap, rotting cactus), but dropped the latter two classes because they were utilized by only one species each. Fly traits were provided by taxonomists Dr. Martin Hauser (California Department of Food and Agriculture) and Dr. Francis Gilbert (University of Nottingham).

Quantitative traits for bees and flies included mean body size, abundance and floral resource specialization. We used intertegular distance for bees and wing length for flies as proxies for mobility (Greenleaf *et al.* 2007; Rotheray *et al.* 2014), measuring from one to five specimens under a dissecting microscope. We calculated floral resource specialization and abundance, using not only the data from this study, but also data collected in the same study area on an additional 56 hedgerow and control sites using identical sampling methods during the same sample years (Morandin & Kremen 2013). For floral resource specialization, for each pollinator species in our data, we calculated the metric d', which measures the deviation of the observed interaction frequency from a null model in which all partners interact in proportion to their abundances (Bluthgen, Menzel & Bluthgen 2006); thus, it is not confounded with abundance as is linkage (Winfree *et al.* 2014). It ranges from 0 for generalist species to 1 for specialist species. Body size metrics and abundance were log-transformed.

For syrphid flies, larval diet is entirely distinct from adult floral resource use; thus, larval diet type and d' provide non-overlapping information. However, for bees, measurements of d' include floral visits both for pollen to provision larvae and for nectar and pollen for adult food, reflecting both larval and adult diet breadth. We therefore used only d' and not assessments of lecty classes (specialization in larval diet of bees within plant taxa), since these traits would constitute overlapping measurements. Since d' is measured from our network data, it is available for all of our bee species, whereas data on lecty are poor or absent for a number of our species.

We were able to measure or obtain all traits for 80 of 97 bee species in our data set (Table S4) and for 26 of 30 syrphid fly species (Table S5).

ANALYSES

To evaluate the effect of habitat restoration over time on bee communities and traits, we model species occurrence data (presence = 1 or absence = 0 of species at a given site and sample date) as a function of the number of years post-restoration (*ypr*) for a particular site in a particular year. *ypr* values for restoration sites begin at 0 and increase each year following restoration, but remain at 0 for controls in all years. Thus, sites restored in 2007 have a value of *ypr* = 0 in 2006 and 2007 and a value of 6 in 2013. Use of the continuous *ypr* variable permits more flexibility in analyses then a classic before–after coding scheme. The before–after coding is better suited for analysing a pulse disturbance, whereas we studied a press disturbance (the maturation of hedgerows and their effects on flower visitor communities and traits). Further, since different sites were restored in different years, the *ypr* variable permits us to isolate changes associated with restoration from annual fluctuations in insect population dynamics.

Bee and syrphid fly data sets were analysed separately. In order to maximize the number of species that could be included in analyses, we first analysed each trait separately (see also Williams *et al.* 2010) and then considered the subset of species with full trait data in a multitrait analysis. All quantitative traits were centred and scaled ($(u - \hat{u})/2$ SD) to facilitate comparison of effect sizes (Gelman & Hill 2006, p. 54). All analyses were conducted in R v. 3.1.1. (R Core Team 2013) using 'LME4' (Bates *et al.* 2014).

For single-trait analyses, we used generalized linear mixed effect models with a binomial error and a logit link function to model species occurrences for each site and date, with *ypr* (years post-restoration), a trait and the interaction between *ypr* and that trait as fixed effects. We were specifically interested in this interaction because, for a given trait, a significant interaction indicates that restoration differentially affects species differing in that trait. Site, species and year were all included in each analysis as random effects. Using Akaike information criterion (AIC) values, we compared each single-trait model to a 'no-trait' model based on the same species set (the subset of species analysed for that trait), constructed as before but with only *ypr* included as a fixed effect. Comparison of these two AIC values enabled us to assess whether the trait or its interaction with *ypr* contributed substantially to the model. We considered models with ΔAIC $\leq$4 to be equivalent (Burnham & Anderson 2002).

Using the same basic model structure, we also constructed multitrait models using the subset of species for which we had a complete set of trait values. Here, we included each trait and an interaction between that trait and *ypr* in a single model, with species, site and year as random effects, as above. The advantage of including all traits within the same model is that one can assess the relative importance of each trait while also accounting for their combined effects. However, since functional traits are intercorrelated (Table S2), we used variance inflation factors (VIF), calculated using the AED package (Zuur *et al.* 2009) to remove collinear variables from the model. We successively removed the covariate with the largest VIF exceeding 3 and recalculated VIFs until all VIFs were <3 (Table S3), following Zuur *et al.* (2009). This covariate set was then used in the multitrait model.

By combining data from all of our species into a single analysis and including species identity as a random effect, we were able to accomplish our goal of making inferences at the community level. While some species occurred infrequently in the data, such species only exert a small influence on the estimation of effect sizes. Analyses with infrequent species removed (defined as <than five site–date occurrences in the entire data set) produced similar results to analyses including all species, except for lack of convergence in one of the 12 analyses; therefore, we present only the analyses with all species included.

Since no species-level phylogeny of our specific taxa yet exists, we could not fully account for potential phylogenetic non-independence in our analyses. However, Bartomeus *et al.* (2013) recently showed that, for bees, nesting species within genus and genus within family as random effects produced essentially the same results as a more sophisticated analysis that accounted for phylogenetic non-independence using generic-level phylogenetic trees created from GenBank sequences. Therefore, we also conducted analyses nesting species within higher-order taxonomy (genus and family for bees, and genus and tribe for syrphid flies). For all single-trait models, these analyses yielded equivalent out-

comes. Multitrait models fit the data much better without the inclusion of taxonomy (i.e. ΔAIC ≥20). Therefore, for all analyses, we present only the analyses without taxonomy.

Results

We collected 6145 bees from 97 species resulting in 1349 occurrences (i.e. presences) and 2744 syrphid flies from 30 species in 899 occurrences (Tables S4 and S5). Species occurrences of bees and flies increased significantly with *ypr* (no-trait model, bees, $N = 97$, effect size for *ypr* ± SE = 0·08567 ± 0·02653, $P = 0{\cdot}00124$; flies, $N = 30$, effect size for *ypr* ± SE = 0·14956 ± 0·02783, $P = 7{\cdot}68\text{e-}08$).

The addition of many of the single traits and their interactions with *ypr* improved models for both bees and syrphid flies (Tables 1 and 2, see ΔAIC values). We found significant positive interactions between *ypr* and the level of floral specialization (d') for both bees and flies (Figs 2a and 3a), indicating that hedgerow maturation favours specialized flower visitors. For bees, *ypr* interacted significantly with nesting habit, favouring renters that rely on pre-existing cavities over bees that excavate their own nests (Fig. 2b). We also found that restoration favoured occurrence of above-ground-nesting bees over below-ground-nesting bees (Fig. 2c), although the model including nest location was equivalent to a model without it (ΔAIC = −4). We found no significant interaction for abundance, body size or sociality in bees. For flies, we also found a significant negative interaction with wing length (Fig. 3b) but no significant interactions with larval diet or abundance. Significance and trends of trait main effects are also noted in Tables 1 and 2.

Traits were intercorrelated (Table S2). Cavity-nesting bees had higher floral specialization, lower abundances and larger body size than excavators. Solitary bees were more specialized (d') and less abundant than social bees. Parasitic bees were less abundant than solitary bees but similar in floral specialization to social bees. Body size and floral specialization were positively correlated in bees. Nest location and nesting habit were non-randomly associated with each other and with sociality. In flies, aphid feeders had smaller wing sizes. Wing size was negatively correlated with abundance.

Multitrait models, adjusted to remove correlated traits using VIF (Table S3), largely supported the single-trait models (Tables 1 and 2). For bees, we again found a significant positive interaction between *ypr* and both floral specialization and nesting habit (favouring renters). In addition, we found a significant negative interaction between *ypr* and body size. For flies, we found only a significant negative interaction with body size (wing length) but no longer an interaction with floral specialization.

Discussion

If habitat restoration chiefly benefits the common generalists that are able to survive in intensive agricultural landscapes, then we would expect to see increased occurrence of species between restored and control sites, but no increases in the occurrence of the species that are more sensitive to disturbance. In contrast, our results show that hedgerows not only significantly enhanced occurrences of native bee and syrphid fly species but differentially promoted occurrence of species with greater floral specializa-

Table 1. Bees: single- and multitrait models of species occurrence data showing Akaike information criterion (AIC) values compared to the corresponding no-trait model; effect size for the interaction between years post-restoration (*ypr*) and trait, standard error (SE) and *P*-value; and the direction of significance (+/−) if the trait's main effect was significant

Bees	Number of species	AIC (no traits, no taxonomy)	AIC (traits, no taxonomy)	ΔAIC	Interaction effect (*ypr**trait)	SE	*P*-value	Trait main effect, significance and trend
Single-trait models								
Abundance	97	7080	7027·9	−52	−0·0525	0·0406	0·1951	+
Nesting habit (rent)	82	6628·7	6601·1	−28	**0·1654**	0·0301	**3·950E-08**	−
Floral specialization (d')	97	7080	7044·6	−35	**0·1411**	0·0229	**7·410E-10**	−
Body size	91	6955·6	6952·1	−4	0·0297	0·0267	2·662E-01	−
Sociality	93	6966·6	6962·8	−4				
Social					−0·0495	0·0754	5·119E-01	+
Solitary					−0·0241	0·0739	7·446E-01	
Nest location	85	6730·6	6726·2	−4				
Below					**−0·1129**	0·0321	**4·340E-04**	
Mix					−0·0901	0·0499	7·083E-02	
Multitrait model	80	6597·4	6507·9	−90				
Abundance					0·0181	0·0524	7·293E-01	+
Nesting habit (rent)					**0·1465**	0·0369	**7·340E-05**	
Floral specialization (d')					**0·1721**	0·0328	**1·550E-07**	−
Body size					**−0·1164**	0·0347	**7·840E-04**	
Sociality (solitary)					−0·0690	0·0385	7·270E-02	

Bolded interaction effects are significant. Both single- and multitrait models have significant positive interactions with *ypr* for floral specialization and more specialized nesters (cavity nesters).

Table 2. Flies: single- and multitrait models of species occurrence data showing Akaike information criterion (AIC) values compared to the corresponding no-trait model; effect size for the interaction between years post-restoration (*ypr*) and trait, standard error (SE) and *P*-value; and the direction of significance (+/−) if the trait's main effect was significant

Flies	Number of species	AIC (no traits, no taxonomy)	AIC (traits, no taxonomy)	ΔAIC	Interaction effect (*ypr**trait)	SE	*P*-value	Trait main effect, significance and trend
Single-trait models								
Abundance	30	5107	5090·5	−16	0·0507	0·0365	0·165	+
Floral specialization (d')	30	5107	5102·2	−5	**0·0755**	0·0277	**6·35E-03**	
Larval diet (detritus/bacteria)	28	4984	4986·2	2	−0·0020	0·0323	9·51E-01	
Wing length	28	5070	5062·3	−8	**−0·0708**	0·0313	**0·0238**	−
Multitrait model	26	4947	4930·7	−16				
Abundance					0·0289	0·0453	5·24E-01	+
Floral specialization (d')					0·0252	0·0332	4·49E-01	−
Larval diet (detritus/bacteria)					0·0384	0·0364	0·2904	
Wing length					**−0·0889**	0·0361	**0·0137**	

Bolded interaction effects are significant. Both single- and multitrait models show a significant negative interaction between *ypr* and wing size. Single-trait models also show a positive interaction with floral specialization.

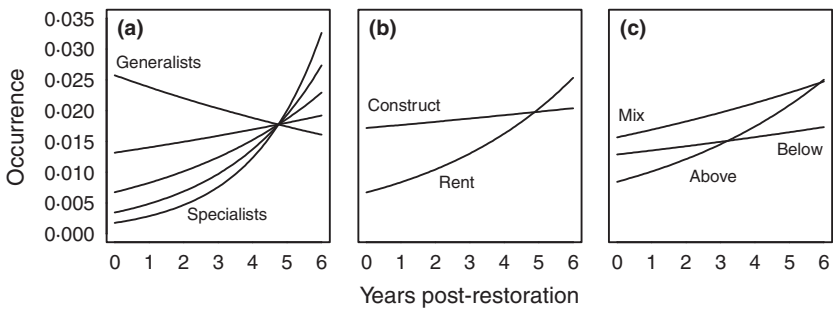

Fig. 2. Response of the mean occurrence of bee species with different traits to years post-restoration (*ypr*) based on single-trait models. Only significant relationships from Table 1 are displayed. Raw occurrence data (0 or 1 corresponding to the presence or absence of each species at each site and sample date) not shown. (a) Floral generalists vs. specialists. Five evenly spaced values of d' (specialization index from least specialized to most specialized) that fully span the range of observed values are shown. (b) Nesting habit, cavity nesters vs. excavators. (c) Nest location, above-ground, below-ground or mixed. These graphs show that as hedgerow restorations mature, they promote more specialized bees, including floral specialists and cavity nesting bees.

tion, more specialized habitat requirements (cavity nesting as opposed to ground-nesting bees) and smaller body sizes (lower mobility). These results suggest that small-scale habitat restoration within intensive agricultural landscapes has the most positive effects on species whose response traits may render them more vulnerable to habitat degradation, namely more specialized and less mobile species. (We were not able to evaluate red-listing status of these species since very few bee or syrphid species have been evaluated for threatened or endangerment status in the United States.) Thus, these plantings may be partially reversing the community disassembly that has occurred in response to agricultural intensification in this region (Kremen, Williams & Thorp 2002; Larsen, Williams & Kremen 2005).

It is important to note, however, that we did not compare communities at hedgerows with a reference natural or semi-natural community and, therefore, we cannot say to what extent hedgerows promote more specialized or less mobile species relative to the full complement of species from the region. A study on bee functional trait composition in the same biogeographic region found that farms impose strong environmental filters limiting species occurrences relative to semi-natural habitats (Forrest *et al.*, in press). This finding, coupled with our finding of enhanced success of cavity nesters with restoration, suggests that providing shrubs and trees on farms is the key to re-establishing the cavity-nesting component of native bee communities.

We found support not only for our general hypothesis that habitat enhancements differentially promote species that may be more sensitive to disturbance, but also for some of our specific predictions on response traits. For bees, however, several specific predictions were not borne out. We predicted that hedgerows might differentially promote large-bodied species, based on previous work in this

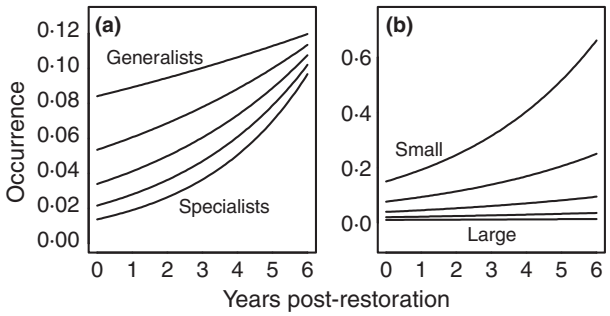

Fig. 3. Response of the mean occurrence of syrphid fly species with different traits to years post-restoration (*ypr*) based on single-trait models. Only significant relationships from Table 2 are displayed. Raw occurrence data (0 or 1 corresponding to the presence or absence of each species at each site and sample date) not shown. (a) Floral generalists vs. specialists. Five values of d' (specialization index from least specialized to most specialized) are modelled to cover the range of values in the data set. (b) Body size. Five values of wing size are modelled to cover the range of values in the data set. These graphs show that as hedgerow restorations mature, they promote floral specialists more than generalists and smaller-bodied (less mobile) flies more than more mobile flies.

region (Larsen, Williams & Kremen 2005). Instead, we found either no interaction with body size (single-trait analysis) or that smaller bees were promoted (multitrait analysis). However, both of the other traits that were promoted by hedgerow maturation, cavity nesting and floral specialization were strongly associated with larger body size (Table S2). These results suggest that, for bees, body size alone may not be an ideal indicator of species responses to small-scale habitat restoration, although it may be correlated or interacted with other traits (see also Bommarco *et al.* 2010). Also contrary to our prediction, we did not find that hedgerows differentially supported parasitic (higher trophic level) bees. Parasitic bees tend to be uncommon in our collections (2% of occurrences, Table S4), so it is possible that we are simply unable to detect such a trend, if it occurs, or that insufficient time has elapsed post-restoration for a trophic-level trend to emerge. Finally, we did not find that hedgerows differentially supported less common bee species, although cavity-nesting bees tended to be less common (Table S2), and a previous study in the same area did find greater abundances of less common species at mature hedgerows (i.e. >10 years old) than at controls (Morandin & Kremen 2013).

For bees, our principle finding – that hedgerows differentially promote more specialized flower visitors with more specialized nesting requirements – was consistent between single- and multitrait analyses. The importance of both variables in the multitrait models was evident even though cavity-nesting bees also were more specialized in floral resource use (Table S2). For flies, hedgerows differentially promoted more specialized flower visitors, but only the body size effect was consistent between single- and multitrait analyses. In bees, the main effect of hedgerow maturation became non-significant or marginally significant when traits with significant interactions were included in the single- or multitrait analyses, suggesting that hedgerows do not promote abundances of bees uniformly, but rather, a subset of bees with specific traits. In flies, the main effect of hedgerow maturation remained significant even when significant interactions were included in the models, suggesting either that our analysis failed to include some key response traits of the fly community, or that hedgerows promote the abundances of all fly species, while promoting species with certain response traits more than others. For both bees and flies, significant interactions between hedgerow status and various response traits emerged between 4 and 5 years post-restoration (Figs 2 and 3).

Some evidence suggests that the European Union's (EU's) 'agri-environment schemes', which subsidize growers to implement small-scale habitat enhancements and other presumed wildlife-friendly farm management techniques, increase species richness and abundance on farms primarily by promoting common and/or resilient species rather than uncommon or endangered species (Kleijn *et al.* 2006) and are effective in simple (1–20% semi-natural habitat in surrounding landscape) but not in cleared (<1% semi-natural habitat) landscapes (Scheper *et al.* 2013). In the United States, Farm Bill conservation programmes are the analogue to the EU's agri-environment schemes. Several of these programmes, such as the Environmental Quality Incentives Program and the Wildlife Habitat Incentives Program, include specific provisions to promote pollinator conservation through habitat enhancements like native plant hedgerows or insectary strips. Our results suggest that such programmes can promote not just common, resilient species, but also some disturbance-sensitive species, even in cleared landscapes. It is important to note, however, that the hedgerow plantings we studied here were specifically designed to support flower visitor communities in the region. Plant palettes were selected using bee–flower network data from the same area (Williams *et al.* 2011) to obtain bee-attractive plant species that would provide a sequence of floral resources throughout the flight season. Therefore, the conservation benefits that we observed from farm-scale habitat enhancement in our study area might only be realized in other regions if planting palettes are specifically tailored for the flower visitors found there. Similar conclusions about the need for tailoring agri-environment schemes to specific conservation objectives were reached through assessments of EU agri-environment schemes (Kleijn *et al.* 2006).

Flower-rich patches in intensive agricultural landscapes may simply concentrate existing flower visitors from the surrounding landscape, rather than promote their population growth (Scheper *et al.* 2013). Studies of species abundances or occurrences cannot distinguish between concentration vs. population effects, and demographic data instead would be needed. However, several

lines of evidence suggest that our results are not simply due to concentration effects. First, on other native plant hedgerows in the same landscape, we observed increases, not decreases, in the abundances of flower visitors in fields immediately adjacent to hedgerows, a pattern consistent with exportation, rather than concentration, of flower visitors from hedgerows (Morandin & Kremen 2013). Secondly, in multiseason occupancy analyses of this same data set, we found that, relative to controls, hedgerows enhance rates of persistence and colonization, particularly for more specialized species, suggesting that hedgerow resources promote the establishment of populations at these sites (M'Gonigle *et al.* 2015).

Restoring habitat for flower visitors in agricultural landscapes might also promote important ecosystem functions and services on adjacent farm fields like pollination and pest control (Blaauw & Isaacs 2014; Morandin, Long & Kremen 2014). While some direct evidence supports a positive role of native plant restoration in promoting pest control and crop pollination in adjacent fields (Morandin & Kremen 2013; Blaauw & Isaacs 2014; Morandin, Long & Kremen 2014), it remains to be determined whether this differential effect of restoration on response traits of flower visitor communities would translate into measurable improvements in ecosystem services. Some of the favoured traits may promote pest control or pollination services in adjacent fields (i.e. small-bodied species are likely to forage nearby; aphidophagous syrphids can provide pest control), but other traits may not (e.g. floral specialists may not visit crop flowers; small species deliver less pollen per visit). Even if these particular bee and fly species are not contributing substantially to pollination or pest control services now, they could become important in the future if environmental conditions change – for example, as a result of changes in farm management, climate or altered biotic relationships (Isbell *et al.* 2011). Further work is needed to elucidate how small-scale restoration influences pollination services (Menz *et al.* 2011) via their effects on species' response and effect traits (Suding *et al.* 2008). Meanwhile, this study shows that these habitat enhancements provide clear conservation benefits for sensitive species in flower visitor communities, even in highly intensively managed agricultural landscapes.

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Data accessibility

Species traits: uploaded as Supporting Information.

Sites information: uploaded as Supporting Information.

Species occurrences by site and sample date: doi: 10.5061/dryad.8n4p8 (Kremen & M'Gonigle 2015).

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Supporting Information

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

Table S1. Samples per site and year.

Table S2. Correlations among traits.

Table S3. Variance inflation factors.

Table S4. Bee species traits.

Table S5. Fly species traits.

Fig. S1. Variation among control sites.