Habitat restoration promotes pollinator persistence and colonization in intensively managed agriculture

Leithen K. M'Gonigle,[1,2,3] Lauren C. Ponisio,[1] Kerry Cutler,[1] and Claire Kremen[1]

[1]*Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720 USA*
[2]*Department of Biological Science, Florida State University, Tallahassee, Florida 32306 USA*

Abstract. Widespread evidence of pollinator declines has led to policies supporting habitat restoration including in agricultural landscapes. Yet, little is yet known about the effectiveness of these restoration techniques for promoting stable populations and communities of pollinators, especially in intensively managed agricultural landscapes. Introducing floral resources, such as flowering hedgerows, to enhance intensively cultivated agricultural landscapes is known to increase the abundances of native insect pollinators in and around restored areas. Whether this is a result of local short-term concentration at flowers or indicative of true increases in the persistence and species richness of these communities remains unclear. It is also unknown whether this practice supports species of conservation concern (e.g., those with more specialized dietary requirements). Analyzing occupancies of native bees and syrphid flies from 330 surveys across 15 sites over eight years, we found that hedgerow restoration promotes rates of between-season persistence and colonization as compared with unrestored field edges. Enhanced persistence and colonization, in turn, led to the formation of more species-rich communities. We also find that hedgerows benefit floral resource specialists more than generalists, emphasizing the value of this restoration technique for conservation in agricultural landscapes.

Key words: agro-ecosystem; habitat restoration; hedgerows; occupancy; persistence; pollinators.

INTRODUCTION

By restoring habitat, conservation biologists and restoration ecologists seek to promote the reassembly of diverse ecological communities, while also enhancing the ecosystem services these communities provide (Funk et al. 2008, Rey Benayas et al. 2009). Restoration of pollinator communities is of particular concern because pollinators play a critical role in plant reproduction in both natural and agricultural systems (see Plate 1; Ollerton et al. 2011, Garibaldi et al. 2013). With managed honey bees (*Apis mellifera*) declining at unprecedented rates in many regions of the world (Neumann and Carreck 2010) and increasing evidence of declines in populations of native pollinators (Biesmeijer et al. 2006, Cameron et al. 2011, Carvalheiro et al. 2013, Weiner et al. 2014), conservation and restoration of native pollinator communities has become a conservation imperative (Potts et al. 2010, Garibaldi et al. 2011). Little is known, however, about how effectively current restoration methods are curtailing or reversing the declines of native pollinators (Menz et al. 2011, Winfree 2010).

In agricultural landscapes, where pollinators are at risk from pesticides (Brittain et al. 2010) and habitat loss

(Kennedy et al. 2013), multiple studies have shown that increasing vegetative diversity locally boosts pollinator species richness and abundance (e.g., Kohler et al. 2008, Kennedy et al. 2013, Morandin and Kremen 2013*a*). However, it is unknown from these snapshot studies whether such techniques contribute to the conservation of these pollinators by enhancing population persistence or if they simply attract pollinators from the surrounding landscape, leading to transient increases in local abundance and/or richness. Additionally, earlier work in intensively managed agricultural landscapes has found that local floral enhancements increase pollinator richness but do not promote the conservation of rare, endangered, or specialized species (Kleijn et al. 2006). Thus, small-scale floral enhancements alone may fail to conserve biodiversity adequately and, consequently, not fully restore functioning communities and the services they provide (Klein et al. 2009, Isbell et al. 2011).

In order to assess whether restoration promotes pollinator conservation (i.e., via enhancing population persistence), it is necessary to examine temporal trends in species occurrence or occupancy by tracking individual species across multiple seasons. Recently developed occupancy models are designed for this task (MacKenzie et al. 2006, Royle and Kéry 2007). These models account for imperfect species detection, and thus permit inferences about species occupancy that might otherwise be obscured by differences in species-specific detectabilities. In order to estimate species persistence, occupancy

models require substantially more data than models that do not account for the detection process; specifically, they require that multiple surveys or collection episodes take place at each site in each year. Due, in part, to the high data requirements, these occupancy models have seldom been applied to invertebrates (although, see Pellet et al. 2007, Dorazio et al. 2011) and, to our knowledge, have never been applied to insect pollinators, leading to a critical knowledge gap.

The most widely used restoration technique to promote pollinators in agricultural landscapes is the planting of flowering native shrubs and forbs along farm edges, where they do not remove arable land from production. These hedgerows are designed to include a variety of plant species which provide a continuous or near continuous sequence of floral resources over the flight seasons of many pollinators (Menz et al. 2011). Plantings may also create nesting habitat and function as refuges from pesticides and soil disturbances such as tilling (Morandin and Kremen 2013a, b). Here we show how restoration of hedgerows facilitates assembly and long-term temporal stability of native pollinator populations and communities. We do this by tracking five hedgerows from their inception through their maturation and comparing them against 10 non-restored control sites in a hierarchical multi-season, multi-species occupancy model. To determine whether hedgerows promote pollinator conservation or simply function as transient pollinator sinks, we tested (1) whether the establishment of diverse native plant hedgerows increased pollinator occupancy, (2) whether this increase was a consequence of reduced extinction, enhanced colonization, or both, (3) whether hedgerow restoration had differential effects on specialist vs. generalist species, and (4) if effects on occupancy translated into species richness patterns. We found, as expected, that restoration led to increases in species richness and, furthermore, that it did this by increasing both rates of between season persistence and colonization. Additionally, we found that this latter effect was most pronounced for more specialized foragers which are less likely to survive in highly modified environments (e.g., Burkle et al. 2013). These findings suggest, therefore, that restoration via hedgerows is an important conservation technique effecting the temporal stability of pollinator populations and communities, including more specialized species.

Materials and Methods

Study sites and collection methods

Our study landscape, located in the Central Valley of California (Yolo County), USA, is an intensively managed agricultural landscape comprising conventional row crops, vineyards, and orchards (Fig. 1). We selected five farm edges to be restored as hedgerows and 10 non-restored control edges. Because hedgerow sites require significantly greater financial and time investments, it was not feasible to restore more than five sites.

However, because some parameters in our model (such as the rates of species detections) are shared between control sites and hedgerows, including more control sites than hedgerows increases our ability to detect trends associated with restoration. Hedgerows were planted in 2007 and 2008 with native perennial shrubs and trees (e.g., *Cercis occidentalis*, *Ceanothus* spp., *Rosa californica*, *Heteromeles arbutifolia*, *Sambucus mexicana*, *Eriogonoum* spp., *Baccharis* spp., *Salvia* spp., and others; see Appendix: Table A1 for a complete list of plantings by site). Hedgerow restorations were approximately 350 m long and 3–6 m wide and border large crop fields (~30 ha). After initial planting, hedgerows were irrigated and weeded for three years, after which no further management was needed (see Fig. 2 for an example of a restoration prior to and six years after restoration). Pollinator sampling at each restoration site began one year prior to restoration (see Table 1 for an overview of our sampling history).

Control sites were selected to match conditions surrounding restoration sites. For each restoration site, we selected two control sites adjacent to the same crop type (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. Control sites were generally weedy field edges and reflect a variety of unmanaged crop field edges found in the region and the pre-restored condition (Appendix: Fig. A1). Such edges typically contain a variety of nonnative forbs, grasses, shrubs, and trees and may at times be tilled, treated with pesticides, or left alone. The most common flowering plants at these sites are *Convolvulus arvensis*, *Brassica* spp., *Lepidium latifolium*, *Picris echioides*, and *Centaurea solstitialis*. Many of these species have also established at restoration sites.

We sampled pollinator communities at each restoration and control site three to five times each year from 2006 until 2013 (with some exceptions; see Table 1). All sampling was conducted between April and August. Dates of sampling were spread evenly across this time period. Sites were selected in random order for sampling and, once all sites had been sampled, the process began again for the next sample round. For logistical reasons, no sampling was conducted in 2010. In 2012 and 2013, the number of rounds of sampling was increased to satisfy data requirements for other projects (Table 1). However, because we use analyses here that account for imperfect detection and also temporal turnover of pollinators over the duration of the field season (described in detail below), different numbers of visits to sites across years do not bias parameter estimates.

Flower-visiting insects were netted along a 350-m transect for one hour, pausing the timer while handling specimens and identifying the plant species from which each specimen was collected. Pollinators were only surveyed under sunny conditions when the temperature was above 21°C and wind speed was below 2.5 m/s. While all insect visitors that contacted the reproductive
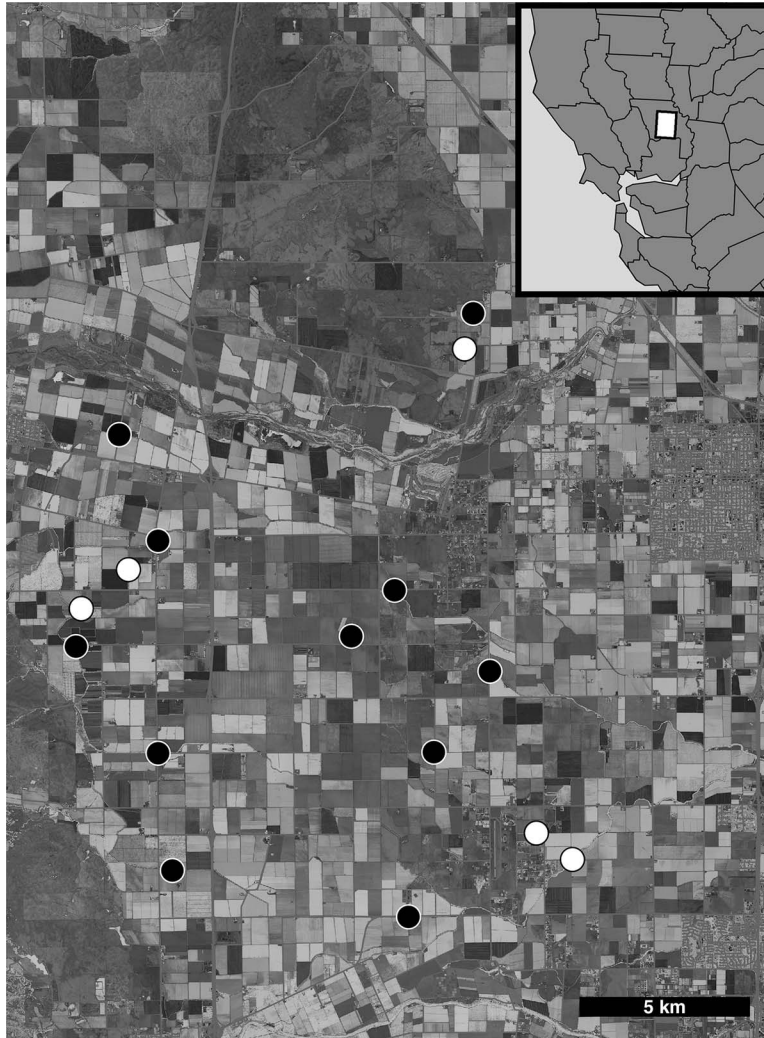
Fig. 1. Location of hedgerow and control sites in California (inset) and surrounding landcover (National Aerial Imagery Program, 2012). White dots are restored sites and black dots are control sites.
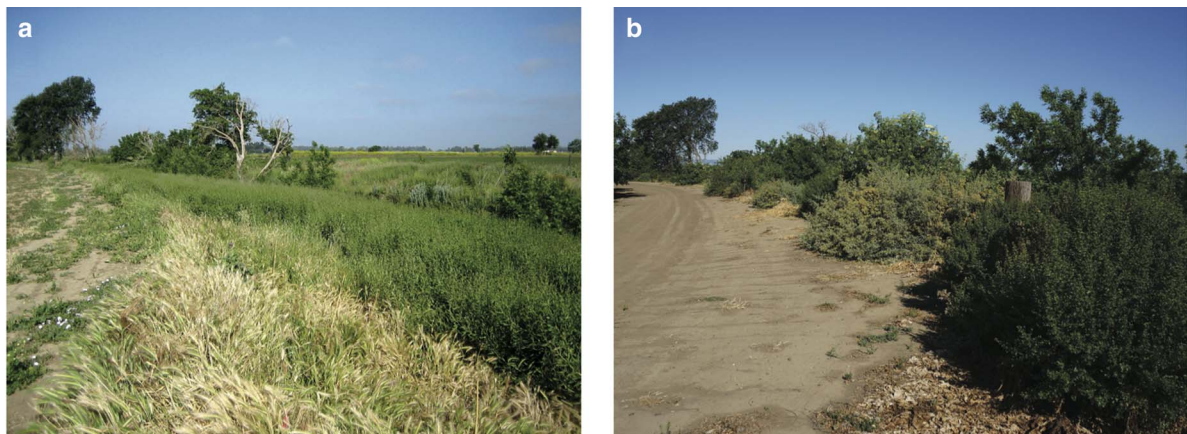

Fig. 2. Photographs of a restoration site (H1) (a) immediately prior to its restoration in the early spring of 2008 and (b) in its sixth year post-restoration in late summer of 2013. Photo credits: K. Ullman (a) and L. K. M'Gonigle (b).

TABLE 1. Number of samples per year at each site.

Site	2006	2007	2008	2009	2010	2011	2012	2013
Hedgerows								
H1	2	3	3†	3		3	4	5
H2	4	3†	3	3		3	4	5
H3		3	3†	3		3	4	5
H4	2	3†	3	3		3	4	5
H5		3	3†	3		3	4	5
Controls								
C1a	4	3	3	3		3	4	5
C1b		3	3	3		3	4	5
C2a	4	3	3	3		3	4	5
C2b		3	3	3		3	4	5
C3a		3	3	3		3		
C3b	4	3	3	3		3	4	5
C4a		3	3	3		3	4	5
C4b		3	3	3		3	4	5
C5a	4	3	3	3		3	4	5
C5b		3	3	3		3	4	5

Note: Sampling was not conducted in 2010 because resources were allocated to other projects.

† Year of planting for each restoration site.

parts of the flower were collected, here we focus our analyses only on wild bees and syrphid flies (for more information about the efficacy of syrphids as pollinators; see Kearns 2001, Rotheray and Gilbert 2011). Bee and syrphid specimens were identified to species (or morpho-species for some bee specimens in the genera *Lasioglossum*, *Nomada*, and *Sphecodes*) by expert taxonomists.

Using plant–pollinator interaction data from a more extensive data set from Yolo County (18 000 interaction records) that included both the data collected in this study and additional data from sites where we collected flower visitors with identical methods (Morandin and Kremen 2013*a, b*; C. Kremen, *unpublished data*), we quantified each pollinator species' level of floral resource specialization by calculating the metric d' for each pollinator species in our data set (Blüthgen et al. 2006). This metric measures the deviation of the observed interaction frequency from a null model in which all partners interact in proportion to their abundances. It ranges from 0 for generalist species to 1 for specialist species. The distribution of specialization values for the species investigated here are shown in Appendix: Fig. A2 and a full list of species with specialization scores is provided as a supplementary data file, along with the rest of our raw data (see Data Availability). To simplify interpretation of model coefficients, specialization values were standardized prior to running analyses.

Statistical model

To analyze our data, we employed a hierarchical framework that explicitly incorporated uncertainty in the detection process into the estimation of occupancy parameters (MacKenzie et al. 2006, Royle and Kéry 2007). Because our goal was to draw conclusions about communities, rather than individual species, we used a model that linked species-specific parameter estimates

together by assuming they come from common community-level distributions (Dorazio et al. 2006). By doing this, we were able to include data for species that were seldom observed and thus not amenable to analysis on their own.

We developed a multi-season, multi-species model to compare occupancy dynamics between restoration and non-restoration sites over time. For species i, we let $z_{i,j,t}$ denote its true occupancy state in year t at site j. We then let $x_{i,j,t,k}$ indicate whether we detected ($x_{i,j,t,k} = 1$) or did not detect ($x_{i,j,t,k} = 0$) that species in the kth visit to site j in year t. We assumed that the occupancy of the ith species at the jth site in the tth year is a Bernoulli random variable $z_{i,j,t} \sim \text{Bern}(\psi_{i,j,t})$ with probability $\psi_{i,j,t}$. In the first year, all sites were equivalent with respect to restoration status and so we assumed that a species probability of occupancy, $\psi_{i,j,1}$, was equal to the fraction of times we observed that species at that site. Because a species' occupancy in subsequent years is the net outcome of its ability to colonize vacant sites and persist in already colonized sites, we investigated how habitat restoration affects these two processes. Letting $\phi_{i,j,t}$ denote the probability that species i persists at site j from years t to $t+1$ (provided it was present at site j in year t, $z_{i,j,t} = 1$) and $\gamma_{i,j,t}$ denote the probability that species i colonizes site j in year $t+1$ (provided it was not present at site j in year t, $z_{i,j,t} = 0$), we then computed the probability of occupancy for species i at site j in subsequent years as

$$\psi_{i,j,t+1} = \phi_{i,j,t} \times z_{i,j,t} + \gamma_{i,j,t} \times (1 - z_{i,j,t}). \quad (1)$$

In order to investigate the effect of habitat restoration, we defined the following species-specific persistence and colonization models:

$$\text{logit}(\phi_{i,j,t}) = \phi_0[i] + \phi_1 \times d'[i] + \phi_2 \times \text{ypr}[j,t]$$
$$+ \phi_3 \times \text{ypr}[j,t] \times d'[i]$$
$$\text{logit}(\gamma_{i,j,t}) = \gamma_0[i] + \gamma_1 \times d'[i] + \gamma_2 \times \text{ypr}[j,t]$$
$$+ \gamma_3 \times \text{ypr}[j,t] \times d'[i]. \quad (2)$$

Here $\phi_0[i]$ and $\gamma_0[i]$ denote species-specific effects on persistence and colonization, respectively, ϕ_1 and γ_1 denote the effect of species specialization on persistence and colonization, respectively, and $d'[i]$ denotes the specialization level of species i. Positive values of ϕ_1 and γ_1 would indicate that specialist species have higher rates of persistence and colonization, respectively, than generalist species. For restoration sites, prior to restoration, and for control sites in all years, $\text{ypr}[j,t] = 0$. The variables ϕ_2 and γ_2 denote the effect of habitat restoration on persistence and colonization, respectively, with $\text{ypr}[j,t]$ indicating the number of years post-restoration for site j in year t. Positive values of ϕ_2 and γ_2 would indicate that rates of persistence and colonization, respectively, are higher as sites mature after restoration. Last, ϕ_3 and γ_3 denote the interaction effects between years post-restoration and species

specialization on persistence and colonization, respectively. Positive values of ϕ_3 and γ_3 would, respectively, indicate that rates of persistence and colonization for specialists are more positively affected by maturation of hedgerows than are rates of persistence and colonization for generalists.

For simplicity, both colonization and persistence in our model depended linearly on the number of years post-restoration (on a logit scale). Because the number of years post-restoration will continue to grow indefinitely, a saturating function (that requires an additional parameter) would be more appropriate here for modeling rates of persistence and/or colonization over the longer term. However, here we were interested in quantifying the effects of restoration in the years immediately following restoration and thus a linear response was appropriate.

We also assumed that detection was distributed according to be a Bernoulli random variable such that $x_{i,j,t,k} \sim \text{Bern}(p_{i,j,t,k} \times z_{i,j,t})$, where $p_{i,j,t,k}$ is the probability that the ith species was detected at site j in the kth sample period of the tth year, given that it was present. When species i was absent, $z_{i,j,t} = 0$, and thus $x_{i,j,t,k}$ was 0. We allowed detection probabilities to vary by species and also to change over the course of the year in a species-specific manner. Specifically, the detection probability of the ith species at the jth site in the kth replicate of the tth year was specified as

$$\text{logit}(p_{i,j,t,k}) = p_0[i] + p_1[i] \times \text{date}_{j,t,k} + p_2[i] \times (\text{date}_{j,t,k})^2 \tag{3}$$

where $p_0[i]$ denotes a species-specific effect and $p_1[i]$ and $p_2[i]$ denote the effect of day of the year on detectability of species i. In addition to their low rates of detection, another difficulty in working with communities of pollinators is that many species' flight seasons do not span the entire duration of the field season (i.e., not all species are active during some of the early or late season samples). By including $\text{date}_{j,t,k}$ and $(\text{date}_{j,t,k})^2$ in the above model, the detection probability of each species was allowed to vary over the season according to that species' phenology. The inclusion of the quadratic term allowed species-specific rates of detection to peak at some point during the season.

We used a hierarchical community model that links together species-specific parameter estimates by assuming that they come from a common distribution. Specifically, the values for ϕ_0, γ_0, p_0, p_1, and p_2 were each drawn from common distributions whose defining parameters were also estimated. We assumed that each of the aforementioned quantities was distributed normally such that $x_i \sim \mathcal{N}(\mu_i, \sigma_i)$ where $\mu_i \sim \mathcal{N}(0, 1000)$ and $\sigma_i \sim \mathcal{U}(0, 100)$. Pollinator specialization scores were standardized before analysis to facilitate interpretation of coefficients and convergence of parameter estimates.

We analyzed the model in a Bayesian framework using uninformative priors throughout. Markov chain Monte Carlo (MCMC) chains were run for 10^5 iterations after an initial burn-in of 10^3 iterations. Each of 10 independent chains was sampled every 10^3 iterations to create samples for analyses. Models were run in R, version 3.1.0 (R Core Team 2014) using JAGS (Plummer et al. 2003). JAGS code and data are available online (see Data Availability. Model parameters were considered to be significantly different from zero if the 95% credible interval did not overlap zero.

Results

Across all of our samples and all 15 sites, we observed 1347 bee and 893 syrphid fly occurrences which, in total, comprise 6143 specimens from 97 bee species and 2732 specimens from 30 syrphid species. For bees, 553 of the 1347 occurrences and 73 of the 97 species were observed at the five hedgerow sites compared to 794 and 79 at the 10 control sites (note that the latter numbers are higher due to the greater number of control sites). For syrphids, 353 of the 893 occurrences and 27 of the 30 species were observed at the hedgerow sites compared to 540 and 26 at the control sites. Despite substantial sampling effort (330 collection days across 15 sites over eight years), many species were detected only a few times. For example, 63% of bee species and 27% of syrphid species were detected fewer than five times. For this reason, we analyzed bee and syrphid species in a single multi-species analysis; we did not have sufficient data to analyze each of these groups on their own.

Restoration increased both rates of pollinator persistence and colonization and, for the latter, this effect was most pronounced for specialist pollinators (see Fig. 3 and Appendix: Table A2). Years post-restoration had a significantly positive effect on rates of persistence. (i.e., the estimate of ϕ_2 was positive and its 95% Bayesian credible interval did not include zero; Fig. 3a, Table A2). For colonization, on the other hand, there was no evidence for a strong main effect of years post-restoration (the 95% CI for the parameter γ_2 overlapped zero) but there was a positive interaction between years post-restoration and the level of pollinator resource specialization (Fig. 3b, Table A2). While there was no evidence for a main effect of pollinator specialization on rates of persistence, rates of colonization were much lower for more specialized species (Fig. 3, Table A2). Species-specific rates of persistence and colonization for sites at zero and five years post-restoration are shown in Figs. A3 and A4.

By substituting model estimates for parameters into Eq. 2, we can compute the expected change in a species' rate of persistence and/or colonization for sites of different maturities. For example, for a species with mean intercept $\phi_0[i] = \bar{\phi}_0$ and a specialization value of $d'[i] = 0.5$, we compute its rate of persistence at non-restored sites (i.e., those with ypr = 0) as $\text{logit}^{-1}(\bar{\phi}_0 + \phi_1 \times 0.5 + \phi_2 \times 0 + \phi_3 \times 0 \times 0.5) = \text{logit}^{-1}(1.32 - 0.14 \times 0.5 + 0.47 \times 0 + 0.16 \times 0 \times 0.5) = 0.78$ We can then compare this to its rate of persistence at sites that have matured
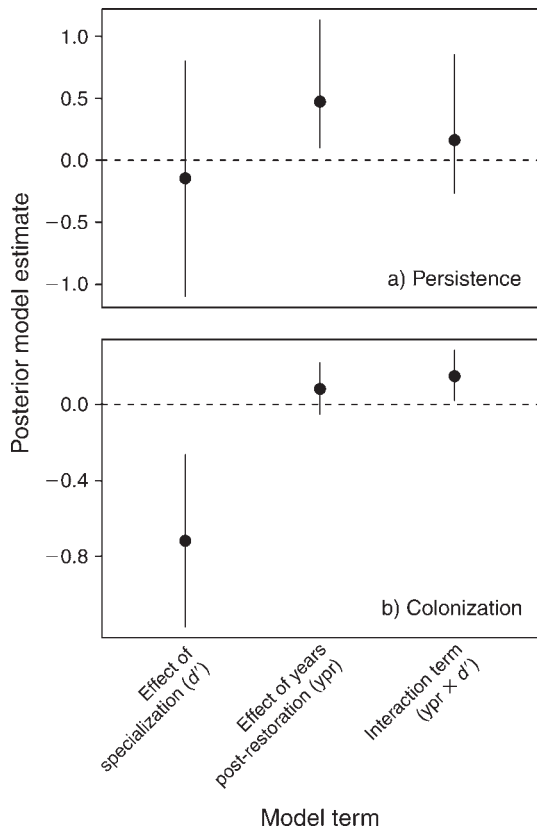
LEITHEN K. M'GONIGLE ET AL.

FIG. 3. Posterior estimates for model coefficients for both (a) persistence and (b) colonization. The effects of species specialization corresponds to the parameters ϕ_1 (panel a) and γ_1 (panel b). The effects of years post-restoration corresponds to the parameters ϕ_2 and γ_2. The terms corresponding to the interaction effects between these two quantities correspond to parameters ϕ_3 and γ_3. Positive values can be interpreted to mean that the corresponding explanatory variable has a positive effect on rates of either persistence (a) or colonization (b) and vice versa. Vertical bars denote Bayesian 95% credible intervals. When 95% credible intervals do not overlap zero, those coefficients can, in some sense, be considered to be "significantly different from zero" with a type 1 error rate of 0.05.

for a single year, $\text{logit}^{-1}(\bar{\phi}_0 + \phi_1 \times 0.5 + \phi_2 \times 1 + \phi_3 \times 1 \times 0.5) = 0.86$. Thus, we would expect this species to see an increase in its rate of persistence by approximately 8% after just one year of restoration.

Increased rates of persistence and colonization at restoration sites led to more species-rich pollinator communities in later years (Fig. 4). While restoration and non-restoration sites exhibited similar levels of richness in the early years of our study (especially prior to restoration), species richness in later years increased at restored sites compared to non-restored sites.

DISCUSSION

Habitat restoration increases rates of between-season persistence and, for more specialized wild bee and syrphid fly pollinators, colonization (Fig. 3). This, in

turn, leads to the assembly of more species-rich pollinator communities at restored sites (Fig. 4). Furthermore, these restorations do not simply facilitate recolonization from an external source population but, rather, they create the conditions that promote population persistence. It follows that they do not simply concentrate floral visitors transiently, but instead create temporally stable pollinator populations. This has also been suggested by our earlier findings that mature hedgerows (i.e., >10 years old) enhance abundances in adjacent fields, rather than dilute them through concentration (Morandin and Kremen 2013b) That these restorations could eventually even act as source populations into other parts of the landscape is an important possibility for a landscape such as California's Central Valley where there is little remaining undeveloped habitat and thus few potential source populations.

Our results corroborate recent findings that small, florally enhanced patches in agricultural areas can increase pollinator richness, although these former studies did not distinguish between transient effects on species occurrences vs. enhancement of persistence (Kohler et al. 2008, Batáry et al. 2011, Carvell et al. 2011, Pywell et al. 2011). Importantly, and unlike some earlier work (Kleijn et al. 2006), we found that restoration particularly benefits more specialized bees, likely because the critical floral resources that specialists need are at low densities or altogether absent in conventional field edges. Similarly, others have found that leguminous floral enhancements led to higher abundance and richness of legume-specialist bumble
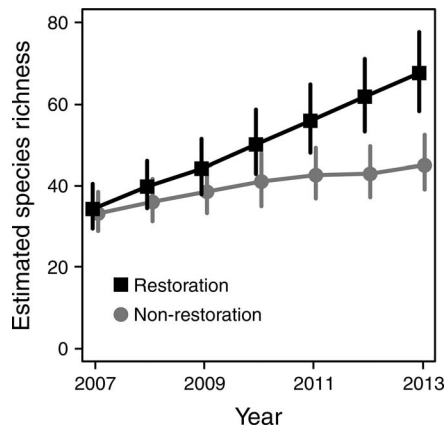

FIG. 4. Estimated mean number of species present in restoration sites (squares) and non-restoration sites (circles). The estimate of the species richness for site j in year t is computed by summing $z_{i,j,t}$ across all i. Points denote means and vertical bars 95% credible intervals. Note that because a species' occupancy at a site in any given year depends, via the process of persistence and colonization, on its occupancy in the previous year, estimates shown here are not independent between years, thus creating roughly monotonic trends. In addition, because we have focused our entire analysis only on species we have actually detected, these estimates do not include species that were potentially unobserved from our study, altogether.

PLATE 1. Native bee (*Melissodes robustior*) pollinating sunflower. Photo credit: L. K. M'Gonigle.

bees (Carvell et al. 2011), and that availability of particular pollen resources plays a critical role in enabling long-term persistence of populations of the specialist solitary bee, *Andrena humilis* (Franzén and Nilsson 2013). In line with these findings, our results demonstrate that small-scale restorations are an important conservation tool for sustaining diverse pollinator populations in intensively managed landscapes.

Here we have considered the age of a habitat restoration as a predictor of pollinator population responses. However, hedgerow age is only a crude proxy for the many potentially important factors that contribute to making more mature hedgerows better habitats for insect pollinators. Identifying specifically which attributes of these hedgerows (e.g., abundance of floral resources vs. quality of nesting substrates) are most critical in creating the trends we report here will provide important additional insights. We are currently in the early stages of investigating this.

More diverse pollinator communities can provide higher quality and more stable levels of pollination services to a greater variety of crops (Klein et al. 2009). Thus, by enhancing richness, hedgerow restorations may also positively affect the provisioning of pollination services. Theoretical work has also predicted that diverse communities provide more consistent levels of pollination services than less diverse communities, because these services are less sensitive to temporal fluctuations in composition (e.g., the "portfolio effect" [Tilman et al. 1998] and the "biodiversity insurance hypothesis" [Lawton and Brown 1993]). The few empirical studies that have been conducted on pollination services support these theoretical predictions (Klein et al. 2003, Steffan-Dewenter et al. 2006, Bartomeus et al. 2013). Our results indicate that restoration increases pollinator diversity by enhancing species colonization and persistence between seasons and thus may lead to communities that provide more stable pollination services.

The primary goal of conservation is the maintenance of biodiversity. Our findings demonstrate that restoration benefits specialized pollinators species more than generalists (Fig. 3, Appendix: Figs. A3, A4). Such pollinators may be lower in abundance and/or less likely to contribute to the pollination of crops (although they still could be important for selected crops that attract specialists, such as sunflower or squash; Hurd et al. 1974, 1980). In a separate work, we have examined the effects of restoration on species that are likely more vulnerable to agricultural intensification, including species that are less common, less mobile, and more specialized in floral and/or nesting resource needs (Kremen and M'Gonigle 2015). There we have shown that hedgerow restoration has the most beneficial effects on the species that are more vulnerable to habitat degradation. Thus, hedgerow restoration provides a

critical avenue for promoting the long-term conservation of biodiversity.

This study is one of the few to model the population dynamics of insect species in an occupancy framework. Unlike more traditional statistical methods, such a framework enables us to explicitly disentangle uncertainty associated with imperfect rates of species detection from actual species' presences and absences. Insect pollinators are notoriously difficult to sample due to their small size and also high rates of spatial and temporal turnover (e.g., Minckley et al. 1999). The low rates of detectability of many bee species makes the use of such a framework even more important. In our case, low detectability led to high degrees of uncertainty in species-specific estimates of occupancy, colonization, and persistence (e.g., see large credibility intervals in Figs. S3 and S4). However, by using a *multi-species* modeling framework that pools data across species, we were able to make inferences about communities with relatively high certainty. Additionally, we were able to detect these patterns despite our relatively low number of restoration sites (five).

Restoration of native habitat presents a promising avenue for conserving pollinator communities in intensive agricultural landscapes, currently in precarious decline due to land use change, pesticides, diseases, and invasive species (Potts et al. 2010). Maintaining native pollinator communities is vital for ensuring reproduction of both native plants (Ollerton et al. 2011) and crops (Garibaldi et al. 2013). Especially as resource demands on our planet continue to grow, restoration efforts within intensive agricultural landscapes that enhance biodiversity and stabilize yields will likely prove critical.

Literature Cited

Bartomeus, I., M. G. Park, J. Gibbs, B. N. Danforth, A. N. Lakso, and R. Winfree. 2013. Biodiversity ensures plant–pollinator phenological synchrony against climate change. Ecology Letters 16:1331–1338.

Batáry, P., A. Báldi, D. Kleijn, and T. Tscharntke. 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proceedings of the Royal Society B 278:1894–1902.

Biesmeijer, J. C., et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354.

Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. Measuring specialization in species interaction networks. BMC Ecology 6:9.

Brittain, C., R. Bommarco, M. Vighi, S. Barmaz, J. Settele, and S. G. Potts. 2010. The impact of an insecticide on insect flower visitation and pollination in an agricultural landscape. Agriculture and Forest Entomology 12:259–266.

Burkle, L. A., J. C. Marlin, and T. M. Knight. 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. Science 339:1611–1615.

Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. Proceedings of the National Academy of Sciences USA 108:662–667.

Carvalheiro, L. G., et al. 2013. Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. Ecology Letters 16:870–878.

Carvell, C., J. L. Osborne, A. F. G. Bourke, S. N. Freeman, R. F. Pywell, and M. S. Heard. 2011. Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. Ecological Application 21:1760–1771.

Dorazio, R. M., N. J. Gotelli, and A. M. Ellison. 2011. Modern methods of estimating biodiversity from presence-absence surveys. Pages 277–302 in Oscar Grillo, editor. Biodiversity loss in a changing planet. InTech, Rijeka, Croatia.

Dorazio, R. M., J. A. Royle, B. Söderstrom, and A. Glimskär. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology 87:842–854.

Franzén, M., and S. G. Nilsson. 2013. High population variability and source-sink dynamics in a solitary bee species. Ecology 94:1400–1408.

Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution 23:695–703.

Garibaldi, L. A., et al. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology Letters 14:1062–1072.

Garibaldi, L. A., et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339:1608–1611.

Hurd, P. D., E. G. Linsley, and A. E. Michelbacher. 1974. Ecology of the squash and gourd bee, *Peponapis pruinosa*, on cultivated cucurbits in California (Hymenoptera: Apoidea). Smithsonian Institution Press, Washington, D.C., USA.

Hurd, P. D., E. Wallace-LaBerge, and G. E. Linsley. 1980. Principal sunflower bees of North America with emphasis on the Southwestern United States (Hymenoptera: Apoidea). Smithsonian Contributions to Zoology No. 310. Smithsonian Institution, Washington, D.C., USA.

Isbell, F., et al. 2011. High plant diversity is needed to maintain ecosystem services. Nature 477:199–202.

Kearns, C. A. 2001. North American dipteran pollinators: assessing their value and conservation status. Conservation Ecology 5:5.

Kennedy, C. M., et al. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecology Letters 16:584–599.

Kleijn, D., et al. 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecology Letters 9:243–254.

Klein, A. M., C. M. Müller, P. Hoehn, and C. Kremen. 2009. Understanding the role of species richness for pollination services. Pages 195–208 in S. Naeem, D. E. Bunker, A.

Hector, M. Loreau, and C. Perrings, editors. Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective. Oxford University Press, Oxford, UK.

Klein, A. M., I. Steffan-Dewenter, and T. Tscharntke. 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. Proceedings of the Royal Society B 270:955–961.

Kohler, F., J. Verhulst, R. van Klink, and D. Kleijn. 2008. At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? Journal of Applied Ecology 45:753–762.

Kremen, C., and L. K. M'Gonigle. 2015. Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. Journal of Applied Ecology 52:602–610.

Lawton, J. H., and V. K. Brown. 1993. Redundancy in ecosystems. In E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer, New York, New York, USA.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, Burlington, Massachusetts, USA.

Menz, M. H. M., R. D. Phillips, R. Winfree, C. Kremen, M. A. Aizen, S. D. Johnson, and K. W. Dixon. 2011. Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. Trends in Plant Science 16:4–12.

Minckley, R. L., J. H. Cane, L. Kervin, and T. H. Roulston. 1999. Spatial predictability and resource specialization of bees (Hymenoptera: Apoidea) at a superabundant, widespread resource. Biological Journal of the Linnean Society 67:119–147.

Morandin, L. A., and C. Kremen. 2013a. Bee preference for native versus exotic plants in restored agricultural hedgerows. Restoration Ecology 21:26–32.

Morandin, L. A., and C. Kremen. 2013b. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecological Applications 23:829–839.

Neumann, P., and N. L. Carreck. 2010. Honey bee colony losses. Journal of Apicultural Research 49:1–6.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos 120:321–326.

Pellet, J., E. Fleishman, D. S. Dobkin, A. Gander, and D. D. Murphy. 2007. An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. Biological Conservation 136:483–495.

Plummer, M., et al. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 20–22 in Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003). http://www.ci.tuwien.ac.at/Conferences/DSC-2003/Drafts/Plummer.pdf

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology and Evolution 25:345–353.

Pywell, R. F., W. R. Meek, L. Hulmes, S. Hulmes, K. L. James, M. Nowakowski, and C. Carvell. 2011. Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes. Journal of Insect Conservation 15:853–864.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Rey Benayas, J. M., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325:1121–1124.

Rotheray, G. E., and F. S. Gilbert. 2011. The natural history of hoverflies. Forrest Text, Ceredigion, Wales, UK.

Royle, A. J., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88:1813–1823.

Steffan-Dewenter, I., A. M. Klein, V. Gaebele, T. Alfert, and T. Tscharntke. 2006. Bee diversity and plant–pollinator interactions in fragmented landscapes. In N. M. Waser and J. Ollerton, editors. Plant–pollinator interactions. from specialization to generalization. University of Chicago Press, Chicago, Illinois, USA.

Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity–stability relationships: statistical inevitability or ecological consequence? American Naturalist 151:277–282.

Weiner, C. N., M. Werner, K. E. Linsenmair, and N. Blüthgen. 2014. Land-use impacts on plant–pollinator networks: interaction strength and specialization predict pollinator declines. Ecology 95:466–474.

Winfree, R. 2010. The conservation and restoration of wild bees. Annals of the New York Academy of Science 1195:169–197.

SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-1863.1.sm

Data Availability

Data associated with this paper have been deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.2vj67