

LETTER

Proximity of restored hedgerows interacts with local floral diversity and species' traits to shape long-term pollinator metacommunity dynamics

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Abstract

Disconnected habitat fragments are poor at supporting population and community persistence; restoration ecologists, therefore, advocate for the establishment of habitat networks across landscapes. Few empirical studies, however, have considered how networks of restored habitat patches affect metacommunity dynamics. Here, using a 10-year study on restored hedgerows and un-restored field margins within an intensive agricultural landscape, we integrate occupancy modelling with network theory to examine the interaction between local and landscape characteristics, habitat selection and dispersal in shaping pollinator metacommunity dynamics. We show that surrounding hedgerows and remnant habitat patches interact with the local floral diversity, bee diet breadth and bee body size to influence site occupancy, via colonisation and persistence dynamics. Florally diverse sites and generalist, small-bodied species are most important for maintaining metacommunity connectivity. By providing the first in-depth assessment of how a network of restored habitat influences long-term population dynamics, we confirm the conservation benefit of hedgerows for pollinator populations and demonstrate the importance of restoring and maintaining habitat networks within an inhospitable matrix.

Keywords

Agriculture, graph, hedgerow, metapopulation, network, restoration, wild bee.

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INTRODUCTION

Agricultural and pastoral landscapes occupy *c.* 40% of Earth's ice-free terrestrial surface. This habitat conversion has contributed extensively to biodiversity loss (Foley *et al.* 2005). However, within these managed landscapes, it is possible to restore and manage certain habitat elements that are favourable to a wider array of species (Daily *et al.* 2001; Kremen 2015; Kremen & Merenlender 2018), many of which supply key services such as pest control or pollination (Zhang *et al.* 2007). Since restored habitat within a matrix of intensively managed agriculture is inevitably isolated, understanding the dynamics of re-established metacommunities that occupy these dispersed patches is necessary to mitigate the effects of fragmentation (Montoya *et al.* 2012; Burkle *et al.* 2017).

In metacommunities, community assembly is influenced by the interplay of local and landscape processes and the dispersal abilities of multiple, interacting species (Logue *et al.* 2011; Leibold & Chase 2017). In most landscapes, habitat is heterogeneous and varies in its ability to attract and support specific species (Mouquet *et al.* 2005). Species are more likely to colonise and persist at sites with biotic and abiotic conditions to which they are adapted (habitat selection), shaping patterns of both local community composition and landscape-level

patterns of species turnover (Vellend 2010; Leibold *et al.* 2004). A network of patches linked by dispersal is less likely to lose species permanently than a completely isolated patch (Hanski & Simberloff 1997); if a species goes extinct in one patch, other patches still supporting that species could act as a source, thereby promoting re-colonisation (Vellend 2010; Leibold *et al.* 2004; Brown & Kodric-Brown 1977; Hanski & Simberloff 1997). This leads to higher apparent species persistence and enhances species occupancy as well as richness at the landscape scale relative to isolated habitat patches (Brown & Kodric-Brown 1977; Hanski & Simberloff 1997; Hanski 1999; Hanski & Ovaskainen 2000; Gilpin 2012).

Dispersal between sites is only possible when the distance between sites is not too great (Vellend 2010; Leibold *et al.* 2004; MacArthur & Wilson 1964; Levins 1969; Hanski 1999; Hanski & Ovaskainen 2000; Gilpin 2012). These concepts of the roles of habitat selection and dispersal in community assembly and persistence rely on a body of theory that has been informed by community ecology (Vellend 2010), metapopulation theory (Levins 1969; Hanski 1999; Hanski & Ovaskainen 2000; Gilpin 2012), including rescue effects (Brown & Kodric-Brown 1977; Hanski & Simberloff 1997), and metacommunity theory, including the concepts of species-sorting, mass effects and patch dynamics (Leibold *et al.* 2004).

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Together, habitat selection and dispersal shape both the local composition and spatial heterogeneity of communities. To promote the restoration of site networks with a high probability of persistence, we must understand the importance of these processes in structuring metacommunity dynamics and their interaction with local and landscape characteristics.

Though community spatial heterogeneity determines regional biodiversity (i.e. β -diversity), species sharing between sites (i.e. community similarity) shapes metacommunity connectivity – an important indicator of long-term persistence (Rezende *et al.* 2009; Macfadyen *et al.* 2011; Timóteo *et al.* 2018). Connectivity is maintained spatially through the exchange of individuals between sites where certain sites act as ‘hubs’ or bridges in the landscape (Kininmonth *et al.* 2011; Timóteo *et al.* 2018). Spatial hubs are often sites with high local habitat quality and may also occupy a central location within the landscape (Bodin & Norberg 2007; Estrada & Bodin 2008; Urban *et al.* 2009). From a species perspective, hub species will be those that maintain spatial metacommunity connectivity through linking sites across the landscape. Similarly, species that consistently occupy a site though time will maintain temporal connectivity, and be most consistent in their support of ecosystem functions such as pollination. Because species must have high occupancy across the landscape in order to make a high contribution to metacommunity connectivity, hub species will likely be those that are not strongly dispersal or resource limited. Understanding the local, landscape and species’ characteristics that constitute spatial and temporal hubs is essential for identifying how to promote metacommunity persistence (e.g. Kininmonth *et al.* 2011).

Here, we study 10 years of wild bee metacommunity dynamics at on-farm habitat restoration patches, known as hedgerows, within an intensive agricultural landscape. On a local scale, earlier work has shown that, in this landscape, hedgerows enhance rates of colonisation and persistence for insect pollinators (M’Gonigle *et al.* 2015), leading to resultant increases in species abundance and richness (Morandin & Kremen 2013; M’Gonigle *et al.* 2015), as well as functional richness (Kremen *et al.* 2018; Ponisio *et al.* 2016). On local and landscape scales, pollinator community composition tracked plant community composition, indicating that floral preferences play an important role in determining pollinator community assembly (Ponisio *et al.* 2016; Kremen *et al.* 2018). Pollinator community similarity also declined with the distance between sites, suggesting bees are dispersal-limited (Ponisio *et al.* 2016). Here, we use multi-species, multi-season occupancy models to disentangle how habitat selection and dispersal structure these metacommunities. We examine how species colonisation and persistence are affected by bee floral resource generalisation (habitat selection) and movement potential (dispersal). We also ask how the interaction between these species’ traits and a site’s floral resource diversity (local) and distance to hedgerows and remnant habitat (landscape) affect population dynamics. Lastly, using network theory, we identify the characteristics of species and site ‘hubs’ that are most important for maintaining metacommunity network connectivity through space and time. Our study provides one of the first in-depth, empirical assessments of how dispersal and habitat selection by species interacts with local and landscape characteristics to influence metacommunity dynamics.

MATERIALS AND METHODS

Survey sites and collection methods

The study landscape was located in the Central Valley of California in Yolo, Colusa and Solano Counties. On-farm restoration sites consisted of hedgerows – native perennial, shrub and tree plantings (e.g. *Cercis occidentalis*, *Ceanothus* spp., *Rosa californica*, *Heteromeles arbutifolia*, *Sambucus mexicana*, *Eriogonoum* spp., *Baccharis* spp., and *Salvia* spp.) (Morandin & Kremen 2013; Kremen *et al.* 2018). Hedgerows border large (c. 30-hectare) crop fields ($N = 18$). In field margins where hedgerows have not been planted, weedy plants often establish, including *Convolvulus arvensis*, *Brassica* spp., *Lepidium latifolium*, *Picris echioides* and *Centaurea solstitialis*. We also monitored these unrestored field margin habitats, which were paired with hedgerows geographically ($N = 21$). Surveyed sites were all approximately 350 m in length. The mean distance between survey sites was 15 km, and the minimum distance between sites sampled in the same year was 1 km (Fig. S1). The entire area surveyed spanned almost 300 km² (Fig. 1, S2).

Our sites were embedded within intensively-managed agriculture – primarily monocultures of conventional row crops, vineyards and orchards. Management practices like crop rotation, pesticide application and tillage prevent fields from supporting most pollinator populations (Ullmann *et al.* 2016). Only subset of the wild bees in the landscape have been observed visiting mass-flowering crops (e.g. sunflower, squash, canola) when they are in bloom (Westphal *et al.* 2003), and these resources are transient (Kleijn *et al.* 2015). In addition, in our study landscape, the nest densities of ground-nesting bees (which are the majority of bees) are higher in hedgerows and field margins compared to fields (Sardiñas *et al.* 2016b). We thus assume that most pollinators primarily reside in isolated hedgerows, field margins and remnant habitat within the crop matrix.

However, two native bee species (out of the 120 observed consistently in the landscape) are outliers in their generality and distribution: *Lasioglossum (Dialictus) incompletum* and *Halictus tripartitus*. We encountered these species in every survey site at least once, whereas all other species were less continuously distributed. Both are also primitively eusocial and multi-voltine, which likely contributes to their high prevalence through the landscape. The floral and nesting resources of *L. incompletum* and *H. tripartitus* are less specialised than other bee species (Kremen & M’Gonigle 2015). Evidence from previous studies in this system suggests that they nest and forage throughout the landscape, including in fields and hedgerows (Sardiñas *et al.* 2016a). Their populations may therefore be continuous rather than patchy or sub-divided. To determine whether our results were robust to excluding these species, we conducted all analyses with and without these super-generalist species.

We surveyed pollinator communities at roughly even intervals between April and August each year from 2006 to 2015, between two and five times per year (Table S1, mean $3.4 \pm$ SD 1 samples per year). The number of sampling rounds and the number of sites sampled each year varied due to available funding. In each round of sampling, we randomised the order of when the sites were surveyed. We conducted surveys under sunny conditions when the temperature was above 21°C and wind speed was below 2.5 m/s. We netted flower visitors at

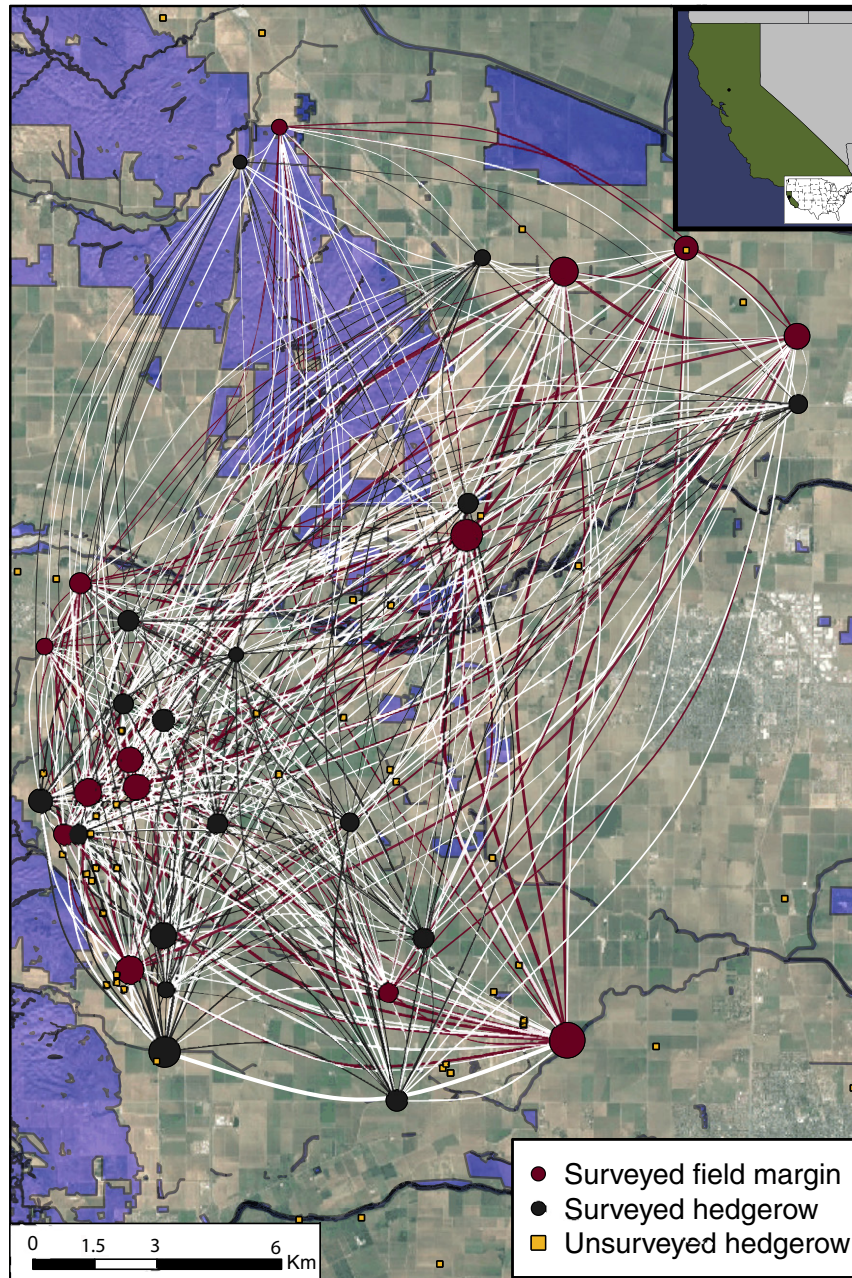


Figure 1 Map of the site network. Surveyed hedgerows and controls are represented by black and red points, respectively, weighted by the number of sites with which they share species (across all 10 years surveyed). Links between sites are weighted by the number of shared species. Hedgerow-hedgerow links are in black, field margin-field margin links are in red, and hedgerow-field margin links are white. Hedgerows that were not surveyed are depicted by yellow squares. Remnant habitat with potential floral resources is shaded in blue.

plants for one hour of active search time (pausing the timer when handling specimens). We collected all insect flower visitors that touched the reproductive parts of the flower into a kill jar; however, here we focus only on wild (non-*Apis*) bees – the most abundant and effective flower visitors in the system (representing 49% of records, C. Kremen, A. Klein and L. Morandin, unpublished data). Besides *Apis* bees, other flower visitors include wasps, flies, butterflies and other groups (Kremen *et al.* 2011). Expert taxonomists identified specimens to species (or morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*).

On the same date or within one week of the pollinator survey, we identified flowering plants in 50 one-meter quadrats along the length of the survey site to species or morpho-species. We estimated the annual abundance of each plant species as the mean number of quadrats in which the species was found flowering in that year.

We used the Yolo Habitat Conservation Plan/Natural Community Conservation Planning spatial data layer for Yolo County to estimate the remnant potential pollinator habitat, hereafter remnant habitat (ICP 2017). This landcover data includes 70 plant community types digitised from a variety of satellite imagery

sources (ICP 2017), of which we identified 46 that may provide resources that could benefit pollinators (Table S2, Fig. S2). We did not distinguish between native and non-native vegetation because many habitat types that are important to bees, such as CA annual grasslands, are predominately non-native plants. We recorded survey locations (hedgerows and unrestored field margins) using a Trimble GPS (Geo Explorer 3). We located additional hedgerows (i.e. those not sampled in the pollinator survey) on the ground and then hand-classified them from Google Earth satellite imagery in 2014–2015.

Metacommunity model

To determine the role of habitat selection and dispersal in structuring metacommunity dynamics, we developed a multi-season, multi-species occupancy model. This framework incorporates uncertainty in the detection process into species occupancy estimation (MacKenzie *et al.* 2006; Royle & Kéry 2007; Dorazio *et al.* 2010). Observed occurrences at each site and sampling period are modelled as a function of a species-specific detection probability and are allowed to vary over the season. The true probability of occurrence, having accounted for imperfect detection, is then modelled as a function of both persistence at and colonisation to a site. We do not explicitly model competitive or facilitatory interactions between species in affecting the occupancy of bee species.

Specifically, for species i , we let $z_{i,j,t}$ denote its unknown (latent) occupancy state in year t at site j . We then let $x_{i,j,t,r}$ indicate whether we detected ($x_{i,j,t,r} = 1$) or did not detect ($x_{i,j,t,r} = 0$) that species in the r^{th} visit to site j in year t . We assumed that the occupancy of the i^{th} species at the j^{th} site in the t^{th} year is a Bernoulli random variable $z_{i,j,t} \sim \text{Bern}(\psi_{i,j,t})$ with probability $\psi_{i,j,t}$. After year 1, occupancy is determined by a species' ability to persist in an occupied site or colonise a vacant site. We let $\phi_{i,j,t}$ denote the probability that species i occupying site j persists from year t to year $t+1$, and $\gamma_{i,j,t}$ denote the probability that species i , absent from site j in year t , colonises site j in year $t+1$. Local extinction is the complement of persistence ($1 - \phi_{i,j,t}$), and thus modelled implicitly. The probability of occupancy for species i at site j in subsequent years is then

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

In the first year, we assumed that a species' probability of occupancy, $\psi_{i,j,1}$, was equal to a species' average equilibrium occupancy probability (Frishkoff *et al.* 2016), based on the persistence and colonisation probabilities for that site:

$$\psi_{i,j,1} = \bar{\gamma}_{i,j} / (1 - \bar{\phi}_{i,j} + \bar{\gamma}_{i,j}). \quad (2)$$

where $\bar{\gamma}_{i,j}$ and $\bar{\phi}_{i,j}$ are the mean colonization and persistence, respectively, for each species i at site j . We included explanatory variables for the effects of local and landscape characteristics and their interaction that represented each of the following predictions:

1. **Local:** Bee persistence will be positively related to a site's floral resource diversity (Kremen *et al.* 2018). Because bees are central place foragers and able to distinguish between sites with different levels of floral diversity (observed in bumble bees, Cartar 2004), sites with high floral diversity will also

attract more colonists (M'Gonigle *et al.* 2015). Equilibrium occupancy will thus be positively related to floral resource diversity. Floral resource diversity was quantified using Shannon's diversity index using floral abundance estimates from the annual quadrant surveys ($frd_{j,t}$) (Kremen *et al.* 2018).

2. **Landscape:** Because bees are dispersal limited (Duelli & Obrist 2003; Öckinger & Smith, 2007; Jauker *et al.* 2009; Ponsio *et al.* 2016), the habitat area within the surrounding landscape (hedgerows and remnants), weighted by their distance from a focal site (proximity hereafter), will increase rates of species colonisation. Through facilitating rescue effects (Brown & Kodric-Brown 1977), habitat proximity will also increase rates of species persistence. Subsequently, equilibrium occupancy will thus be positively related to hedgerow and remnant habitat proximity.

To calculate habitat proximity in a way that reflects the dispersal limitation of bees, we weighted habitat area by its distance from a focal site. We first quantified the amount (m^2) of remnant or hedgerow habitat in concentric rings (radii from 50 m to entire study landscape on a log scale). We then used a Gaussian function to assign weights to habitat with each ring such that habitat in more distant rings is assigned a lower weight than habitat in closer rings (Karp *et al.* 2016; Chandler & Hepinstall-Cymerman 2016; Miguët *et al.* 2017). Specifically, the weight for ring r was calculated as:

$$W_r = \exp\left(\frac{-d_r^2}{2 * \alpha^2}\right) \quad (3)$$

where d_r is a ring's distance from the focal site and α is the decay rate that specifies how quickly weightings decrease with increasing distance. We used three decay rates ($\alpha = 350$, $\alpha = 1000$ and $\alpha = 2500$) to capture a steep to more gradual decay in the weighting of habitat area with distance for all species. $\alpha = 350$ represents 98.5% reduction in weight by 1 km (the average movement potential for the average sized bee, Greenleaf *et al.* 2007) whereas $\alpha = 2500$ represents a 98.5% reduction in weight by 7 km (nearly the entire study landscape) (Fig. S3). We then calculated the log of the weighted sum of the area of remnant ($RemnantWtProx_j$) or hedgerow habitat ($HRwtProx_j$) by summing the area of habitat within each ring ($area_r$), multiplied by that ring's weight (W_r), across all of the rings:

$$wtProx_j = \log\left(\sum_{r=1}^{all} W_r * area_r\right) \quad (4)$$

3. **Landscape*local:** Sites with high floral diversity will benefit the most from the proximity-weighted area of neighbouring hedgerows and remnant habitats because they will be more likely to be colonised or rescued. We included an interaction between a site's floral resource diversity and the weighted area of neighbouring hedgerow and remnant habitats.

We also included explanatory variables for the effect of species' traits related to habitat selection and dispersal on colonisation and persistence and their interaction with local and landscape characteristics representing the following predictions:

1. **Habitat selection*landscape:** Because floral resource generalists will be more likely to find the interaction partners they need at any given site, they will have higher persistence and colonisation across the landscape (Tschardt *et al.* 2002). Similarly, the proximity-weighted area of neighbouring hedgerows and remnant habitats will enhance the colonisation and persistence rates of generalist floral resource users will mostly strongly.

Floral resource generalisation (k_i) was measured as the rarefied floral diet breadth of a species (i.e. rarefied species' degree, Chao *et al.* 2009; Winfree *et al.* 2014; Ponisio *et al.* 2017) calculated from interaction observations from an extensive dataset from Yolo County (*c.* 20,000 interaction records) that included both the data in this study and additional data from other sites in the region, collected using the same sampling methods (M'Gonigle *et al.* 2015; Ponisio *et al.* 2016).

2. **Dispersal*landscape:** Because pollinators are dispersal limited (Duelli & Obrist 2003; Öckinger & Smith, 2007; Jauker *et al.* 2009; Ponisio *et al.* 2016), species with higher movement potential will have higher colonisation across the landscape. Species with higher movement potential will also be better able to rescue populations (Brown & Kodric-Brown 1977), leading to higher apparent persistence. Furthermore, the colonisation and persistence rates of species with higher movement potential will benefit most from the proximity-weighted area of neighbouring hedgerows and remnant habitats. In pollinators, body size is related to movement potential because it is strongly related to the size of flight muscles (Greenleaf *et al.* 2007). Body size ($BodySize_i$) was quantified using the intertegular span (mm) (Cane 1987).

Site-level intercept and slope parameters were modelled as species-specific but linked together by community-level distributions (i.e. borrowing from frequentist terminology, random intercepts and slopes).

$$\begin{aligned} \text{logit}(\phi_{i,j,t}) = & \alpha_i + \beta[1]_i * \text{HRwtProx}_j + \beta[2]_i * \text{RemnantWtProx}_j \\ & + \beta[3]_i * \text{frd}_{j,t} + \beta[4]_i * k_i + \beta[5]_i * \text{BodySize}_i + \beta[6]_i \\ & * \text{frd}_{j,t} * \text{HRwtProx}_j + \beta[7]_i * \text{frd}_{j,t} * \text{RemnantWtProx}_j \\ & + \beta[8]_i * k_i * \text{HRwtProx}_j + \beta[9]_i * B_i * \text{HRwtProx}_j \\ & + \beta[10]_i * k_i * \text{RemnantWtProx}_j + \beta[11]_i * B_i \\ & * \text{RemnantWtProx}_j \\ \alpha_i \sim & N(\mu_\alpha, \sigma_\alpha) \\ \beta[s]_i \sim & N(\mu_{\beta[s]}, \sigma_{\beta[s]}), s = 1 \dots 3 \\ \text{logit}(\gamma_{i,j,t}) = & A_i + B[1]_i * \text{HRwtProx}_j + B[2]_i * \text{RemnantWtProx}_j \\ & + B[3]_i * \text{frd}_{j,t} + B[4]_i * k_i + B[5]_i * \text{BodySize}_i + B[6]_i \\ & * \text{frd}_{j,t} * \text{HRwtProx}_j + B[7]_i * \text{frd}_{j,t} * \text{RemnantWtProx}_j \\ & + B[8]_i * k_i * \text{HRwtProx}_j + B[9]_i * B_i * \text{HRwtProx}_j \\ & + B[10]_i * k_i * \text{RemnantWtProx}_j + B[11]_i * B_i \\ & * \text{RemnantWtProx}_j \\ A_i \sim & N(\mu_A, \sigma_A) \\ B[s]_i \sim & N(\mu_{B[s]}, \sigma_{B[s]}), s = 1 \dots 3 \end{aligned} \quad (5)$$

Here α_i and A_i denote species-specific intercepts of persistence and colonisation, respectively. The $\beta[s]$ and $B[s]$ parameters

proceeding each of the explanatory variables represent the effect of those variables on persistence and colonisation respectively. All explanatory variables were centred.

We also assumed that detection was distributed according to a Bernoulli random variable such that $x_{i,j,t,r} \sim \text{Bern}(p_{i,j,t,r} * z_{i,j,t})$, where $p_{i,j,t,r}$ is the probability that the i^{th} species was detected at site j in the r^{th} sample period of the t^{th} year, given that it was present. The detection probability of each species was allowed to vary over the season according to species-specific phenologies (M'Gonigle *et al.* 2015). Specifically, the detection probability of the i^{th} species at the j^{th} site in the r^{th} replicate of the t^{th} year was specified as

$$\text{logit}(p_{i,j,k,t}) = p[1]_i + p[2]_i * \text{date}_{j,k,r} + p[3]_i * (\text{date}_{j,k,r})^2 \quad (6)$$

denote the effect of day of the year on detectability of species i . We used orthogonal polynomials for the linear and quadratic terms on day. The inclusion of the quadratic term allowed species-specific rates of detection to have a seasonal peak.

A limitation of the model and sampling approach is that if a species is observed within a year ($x_{i,j,t,r} = 1$ at one or more of the r sampling rounds and thus $z_{i,j,t}$ must equal 1), we cannot distinguish whether a species is resident at the site or using the resources of that site while resident elsewhere. Bees forage within a radius of their nest in proportion to their body size, which is on average less than 1 km (Greenleaf *et al.* 2007). Thus, transient resource users will only be conflated with resident species when there is nearby habitat around which species are foraging, which occurred in a small proportion of the survey sites (Fig. S3).

We used Bayesian inference and Markov chain Monte Carlo (MCMC) to estimate model parameters. To improve the sampling efficiency, we used sequential likelihood calculations (filtering) to estimate probability of all detection histories through time at one site, removing the need for many latent states (Turek *et al.* 2016). MCMC chains were run for $2 * 10^5$ iterations after an initial burn-in of $2 * 10^3$ iterations using NIMBLE (de Valpine *et al.* 2017). We used uninformative priors, $\text{Norm}(0, 10^3)$ for the means of the distributions of the top-level parameters and $\text{Unif}(0, 10^2)$ for the variances. We then used Bayesian model selection via WAIC (Watanabe 2010) to choose which decay rate had the best fit to the hedgerow and remnant habitat proximity data. For the best-fitting model, we also constructed a version of the model where the latent states were sampled, for subsequent analyses. Analyses were conducted in R 3.5.1 (R Core Team 2018).

Scripts to run all of the models and MCMC algorithms are available at https://github.com/lponisio/hedgerow_metacom or <https://doi.org/10.5281/zenodo.2575861>. Posterior probability densities were calculated to estimate the support for whether each parameter was greater than or less than zero. We defined support for a coefficient being different than zero as strong (95% of the posterior is $</> 0$) or marginal (90% of the posterior is $</> 0$).

Metacommunity network

To investigate which bee species contributed the most to metacommunity connectivity, we first constructed year-

specific, site-level spatial networks where pollinator i is linked to a site j if it is present at that site (Figs S4 and S5). We then constructed site-specific, temporal networks where a pollinator i is linked to a year t if it is present in that year (Figs S6 and S7). We based species' occurrence on the inferred occupancy of each species (latent states, $z_{i,j,t}$ Eq. Eq. 1). To estimate the networks from the inferred latent states, we selected 1000 random MCMC samples from the best-fitting occupancy model with respect to decay rate, and extracted the $z_{i,j,t}$ array. For each posterior sample of the $z_{i,j,t}$ array, we generated a spatial and temporal network. For the spatial network, we created a site by species matrix for each year. In the temporal networks, for each site, we created a year by species matrix.

We then quantified a species' contribution to network connectivity within the spatial and temporal shared species networks. We computed two network centrality metrics – degree and betweenness – to represent a species' contribution to metacommunity network connectivity (Estrada & Bodin 2008; Bodin & Norberg 2007; Rayfield *et al.* 2011). Pollinator degree is shaped by local flow of species between sites, and within a site across years, while betweenness centrality is a measure of a species' contribution to upholding the large-scale landscape connectivity (Estrada & Bodin 2008; Bodin & Norberg 2007). In the spatial metacommunity network, pollinator degree is the total number of sites within a year in which a species is present. Similarly, in the temporal metacommunity network, pollinator degree is the number of years in which a species is present at a site. Betweenness centrality quantifies the number of times a node acts as a bridge along the shortest path between all other nodes (Freeman 1978; Brandes 2001). From the perspective of a pollinator species (v), betweenness centrality, $BC(v)$, is calculated as

$$BC(v) = \sum_{s \neq v} \sum_{t \neq s, t \neq v} \frac{\sigma_{st}(v)}{\sigma_{st}} \quad (7)$$

where σ_{st} is the total number of shortest paths from node s to node t and $\sigma_{st}(v)$ is the number of those paths that pass through v . Nodes s and t are pollinators other than pollinator v , and either sites (spatial) or years (temporal). Pollinators with a high betweenness are considered to be “bridging” species, which, if removed, would break the connected metacommunity into smaller spatial and temporal compartments. For each temporal and spatial network, we calculated the mean and standard deviation of the species-level metrics across the posterior samples.

We then used linear mixed models to test whether the centrality metrics relate to species' traits (Bates *et al.* 2014; Kuznetsova *et al.* 2014), weighting the centrality metrics by their uncertainty (1/SD of the posterior estimates). As in the occupancy model, we hypothesised that floral resource generalisation (diet breadth) and body size (interregal span) would be related to a species' metacommunity network centrality. We included random effects for species. We calculated P -values for mixed models based on Satterthwaite's approximations for degrees of freedom (Kuznetsova *et al.* 2014).

We then changed the perspective from the importance of a species to that of a site in maintaining metcommunity connectivity. We used the same networks described above, but

calculated centrality metrics from the site's perspective. In the spatial networks, degree is the site's species richness. Site betweenness is the number of times a site acts as a bridge along the shortest path between all other sites and pollinators (Eq. 7, nodes s and t are all sites and pollinators). Sites with a high betweenness are considered to be “bridging” sites, which, if removed, risks separating the connected landscape into smaller spatial compartments (Estrada & Bodin 2008; Bodin & Norberg 2007). Site degree is shaped by local flow of species within a neighbourhood of the focal site, while betweenness is a measure of a site's contribution to upholding largescale landscape connectivity (Estrada & Bodin 2008; Bodin & Norberg 2007). We used weighted linear mixed models to relate a site's metacommunity network position to its characteristics, specifically floral diversity and hedgerow, and remnant proximity-weighted area. We weighted the site centrality metrics by their uncertainty (1/SD of the posterior estimates). We included a random effect for site.

RESULTS

Over 10 years and 550 hours of pollinator surveys, we collected and identified 10 491 wild bees comprising 120 species from 26 genera. Only species with five or more individuals collected over the study period were included in the occupancy analysis (57 species).

Metacommunity model

The model with the steepest decay rate ($\alpha = 350$) for weighting hedgerow proximity-weighted area (hereafter, hedgerow proximity) and the shallowest ($\alpha = 2500$) for weighting remnant habitat proximity was the best fit to the data (Table S3, see Fig. S8 for the distribution of hedgerow and remnant proximity). The best fitting model, therefore, included proximity effects for hedgerows at a 98.5% reduction in weight by 1 km, whereas, for remnant habitat, proximity effects included habitat within $c. 7$ km (Fig. S3). Given the landscape configuration of our study area, remnant habitat captured in the proximity metric therefore included large, continuous habitat areas in the hills to the west of the study region (Central Coast Range, Fig. 1, Figs S2 and 3) and annual grassland to the north (Fig. 1, Figs S2 and 3), that have been previously recognised for their value to pollinators and pollination services (Kremen *et al.* 2002; Klein *et al.* 2012). Most remnant habitat patches within the agricultural matrix itself were below 1000 m^2 (Fig. 1, Fig. S9).

Across the landscape, sites with higher floral diversity had a higher rate of bee persistence, as predicted (Table 1). Also as expected, bees with a wider floral diet breadth had a higher persistence than more specialised bees (Table 1). We found strong support for a negative main effect of hedgerow proximity on bee persistence modified by marginal support for a positive interaction with floral diversity (Table 1), implying that that nearby hedgerows reduce species' persistence at sites with little floral diversity (e.g. unrestored sites) while enhancing it at the highest quality sites in the landscape (e.g. other hedgerow sites, Fig. 2d). There was strong support for a positive

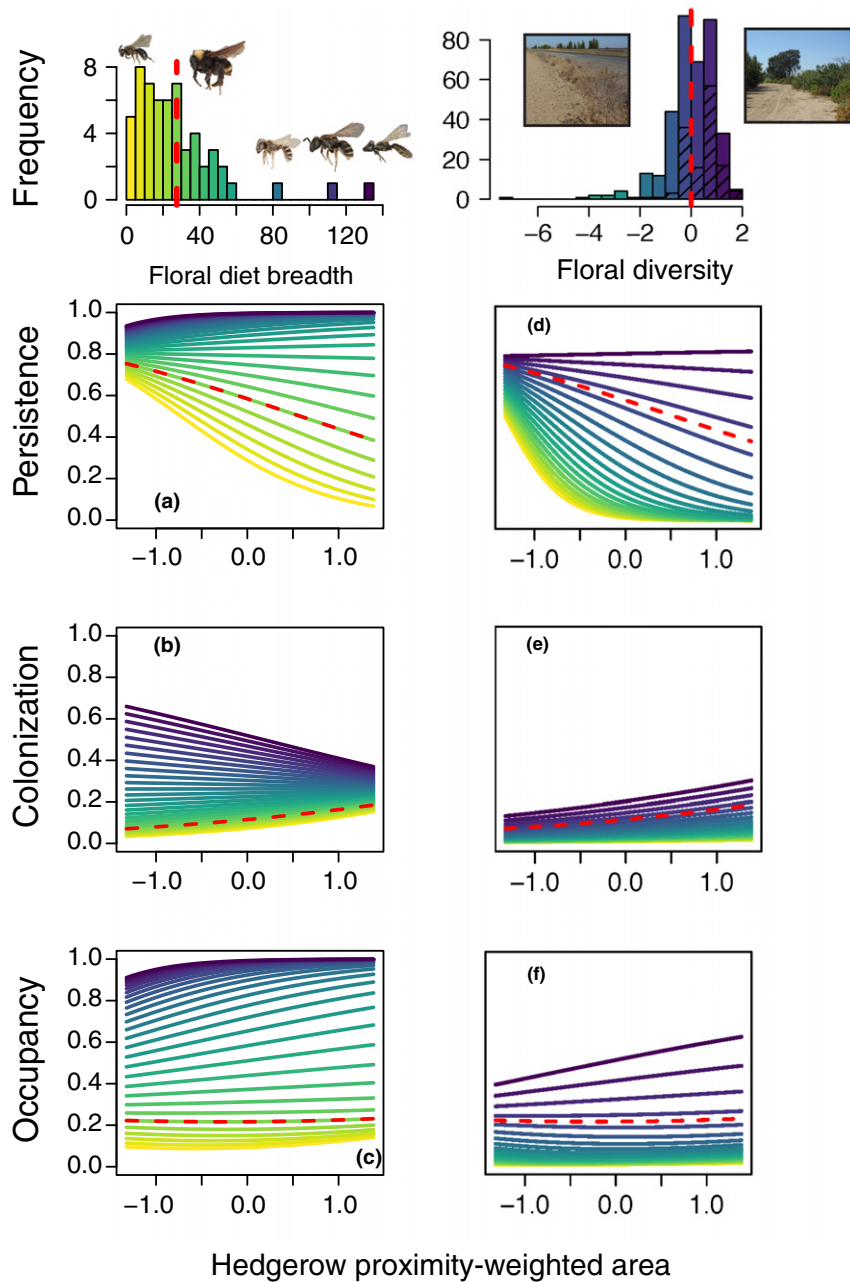
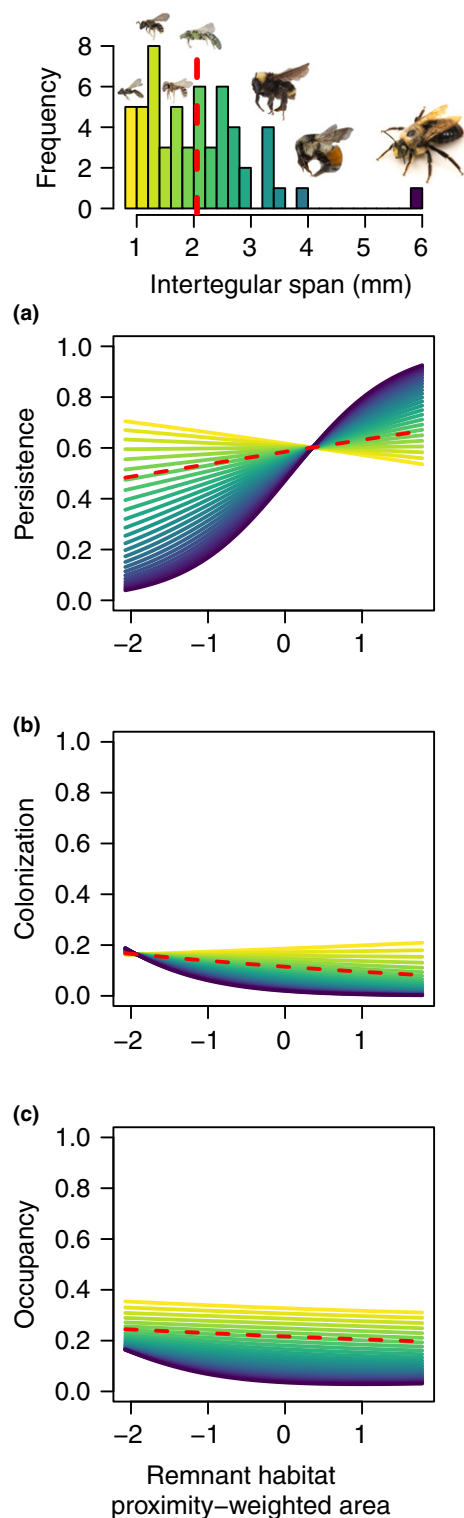


Figure 2 The effect of the interaction between hedgerow proximity weighted area and floral diet breadth (a–c) and floral diversity (d–f) on bee persistence, colonisation, and (equilibrium) occupancy. The top histograms depict the distribution of floral diversity and floral diet breadths across the sites surveyed. Different levels of floral diversity are represented by colour darkness matched between the histogram and the panels. The mean floral diversity (the ‘average site’) and mean floral diet breadth (the ‘average bee’) are indicated by red, dashed lines in the histogram and panels. Representative sites are included as photographs, and the proportion of sites within each bar that are hedgerows is represented by a striped fill. Representative bees of a variety of floral diet breadths are depicted above the histogram. From left to right, *Andrena w-scripta* (min), *Bombus californicus* (near mean), *Halictus ligatus*, *H. tripartitus*, and *Lasioglossum incompletum* (max). Bee images from Discover Life. Floral diversity and hedgerow proximity values are centred (and thus the mean is at 0). All other explanatory variables are set to their means.

interaction between hedgerow proximity and floral diet breadth on bee persistence, suggesting more generalised species benefit from surrounding hedgerows while specialists do not (Table 1, Fig. 2a). Lastly, there was marginal support for a positive interaction between remnant habitat proximity and body size on bee persistence such that the persistence of large

bees benefited from surrounding habitat, while the persistence of the smallest bees decreased (Table 1, Fig. 3a).

As predicted, hedgerow proximity, bee floral diet breadth and local floral diversity enhanced bee colonisation across the landscape (Table 1). In contrast to our expectations, however, there was strong support for a negative effect of body size on



colonisation, implying that larger-bodied bees colonise sites at a lower rate than smaller-bodied bees (Table 1). There was marginal support for a negative main effect of remnant proximity and a negative interaction with body size on colonisation, suggesting remnant habitat augments only relatively small-bodied bee colonisation (Table 1, Fig. 3b). Interactions between hedgerow proximity and local floral diversity

Figure 3 The effect of the interaction between remnant habitat proximity and body size (intertegular span, mm) on bee (a) persistence, (b) colonisation, and (c) equilibrium occupancy. The top histogram depicts the distribution of body sizes within the landscape. Different levels of body size are represented by colour, matched between the histogram and the panels. The mean body size is indicated by a red, dashed line in the histogram and panels. Representative bees of a variety of body sizes are depicted. From left to right, *Lasioglossum incompletum* (near min), *Halictus tripartitus*, *H. ligatus*, *Agapostemon texanus* (near mean), *Bombus californicus*, *B. melanopygus*, and *Xylocopa tabaniformis orpifex* (max). Relative size differences between bees are approximately preserved. Bee images from Discover Life. The remnant proximity-weighted area values are centred (and thus the mean is at 0). All other explanatory variables are set to their means.

(Fig. 2e) or bee floral diet breadth (Fig. 2b) on colonisation were not supported by the data.

The equilibrium occupancy of the most florally diverse sites was enhanced by hedgerow proximity (Fig. 2f). Surrounding hedgerows also increased the equilibrium occupancy bees with higher than average generalisation (Fig. 2c). Remnant habitat proximity, on the other hand, did not have a strong effect on equilibrium occupancy, though there was a slight decline in the large bodied bee occupancy (Fig. 3c).

When the two super-generalist species were excluded, most of the posterior probabilities remained qualitatively the same (Table S4). This suggests that these species, though extreme in their generalisation and prevalence, are in general interacting with the landscape like other bees in the metacommunity. The posterior probability for the interaction between floral diversity and hedgerow proximity on colonisation, however, went from low support for being different greater than zero (≤ 0.90) to strong support for a positive effect (> 0.95). Similarly, support for an interaction between floral diversity and remnant habitat proximity on colonisation was low in the model including the super-generalists and strong in the model excluding them (Table S4). Lastly, the negative interaction between hedgerow proximity and diet breadth on bee colonisation also shifted from weak to strong support in the model excluding super-generalists (Table S4).

Metacommunity network

Within a year across the landscape, floral diet breadth was significantly positively related to the species' degree and betweenness within the spatial metacommunity network (Fig. 4, estimate of the slope \pm SD of degree with diet breadth, 6.662 ± 0.475 , t -value = $14.018_{53,823}$, P -value $< 2e^{-16}$; betweenness with diet breadth \pm SD, 0.0079 ± 0.0007 , t -value = $11.100_{54,090}$, P -value = $1.46e^{-15}$). Similarly, within the temporal metacommunity network, floral diet breadth was positively related to species degree and betweenness (Fig. 4, estimate of the slope \pm SD of degree with diet breadth, 1.489 ± 0.0923 , t -value = $16.137_{51,916}$, P -value $< 2e^{-16}$; betweenness with diet breadth \pm SD, 0.014 ± 0.0008 , t -value = $15.455_{53,945}$, p -value $< 2e^{-16}$). Floral generalist species are thus most connected both across the landscape and through time, or more simply, there is a set of generalist species that are pervasive in this system.

Table 1 The mean and standard deviation of the posterior distributions of the occupancy model coefficients, as well as posterior probabilities (proportion of the posterior greater than zero or less than zero) for the model parameters. The coefficients reported for the effects of hedgerow proximity, remnant proximity and floral diversity are the means of the community-level distributions (Eq. 5, $\mu_{\beta_{[s]}}$ and $\mu_{B_{[s]}}$). * and † indicate that 95% (strong support), or 90% (marginal support) of the posterior is either greater than or less than zero, respectively. Strongly and marginally significant variables and posterior probabilities are bolded

Scale/process	Variable	Persistence			Colonisation		
		Mean (SD)	<i>prob</i> >0	<i>prob</i> <0	Mean (SD)	<i>prob</i> >0	<i>prob</i> <0
Landscape	Hedgerow proximity	-0.59(0.26)	0.01	0.99*	0.4(0.17)	0.99*	0.01
	Remnant proximity	0.2(0.23)	0.81	0.19	-0.21(0.16)	0.08	0.92†
Local	Floral diversity	0.64(0.18)	1.00*	0	0.38(0.11)	1.00*	0
Habitat selection	Floral diet breadth	1.23(0.28)	1.00*	0	0.5(0.17)	1.00*	0
Dispersal	Body size	-0.11(0.21)	0.3	0.7	-0.45(0.17)	0	1.00*
Local*Landscape	Floral diversity*Hedgerow proximity	0.37(0.24)	0.93†	0.07	-0.01(0.22)	0.48	0.52
	Floral diversity*Remnant proximity	-0.11(0.2)	0.28	0.72	-0.16(0.18)	0.19	0.81
Habitat selection*Landscape	Floral diet breadth*Hedgerow proximity	0.65(0.25)	0.99*	0.01	-0.2(0.17)	0.11	0.89
	Floral diet breadth*Remnant proximity	0.06(0.22)	0.61	0.39	-0.16(0.16)	0.16	0.84
Dispersal*Landscape	Body size*Hedgerow proximity	0.07(0.22)	0.63	0.37	-0.02(0.16)	0.47	0.53
	Body size*Remnant proximity	0.31(0.22)	0.92†	0.08	-0.24(0.16)	0.07	0.93†

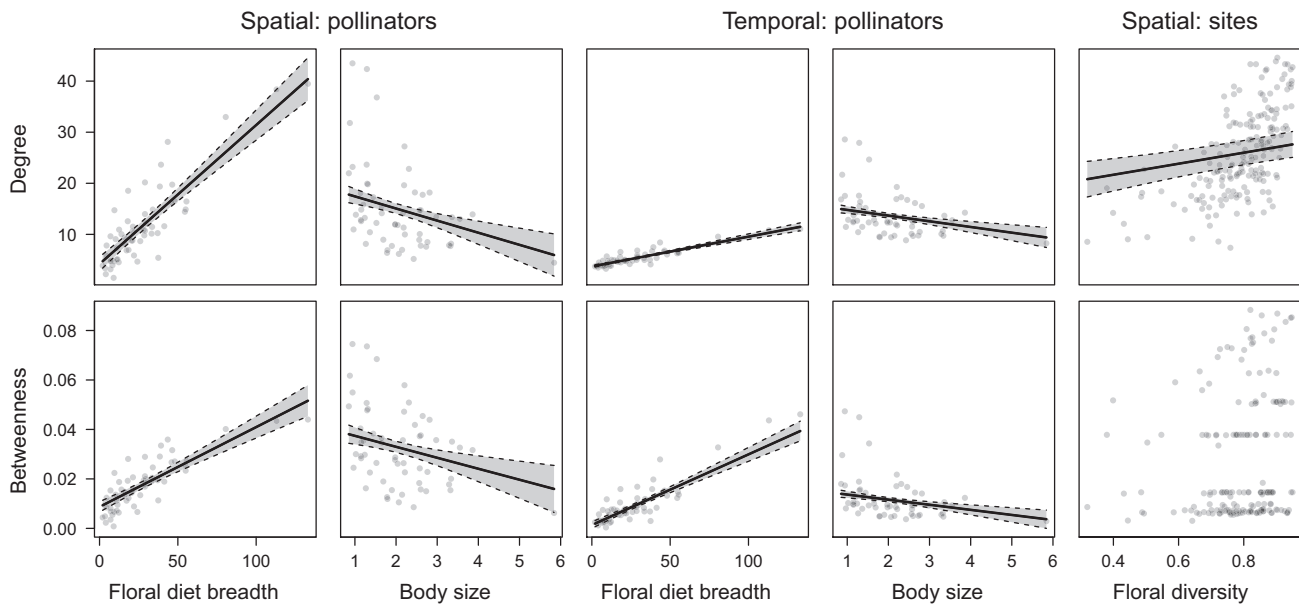


Figure 4 The relationship between species' traits and survey site characteristics and their position in the metacommunity network. Floral diet breadth was positively related to both species' degree and betweenness within a year across the landscape (spatial network) and within a site across years (temporal network). Body size (mean intertegular distance, mm) was negatively related to species' degree and betweenness in the both the spatial and temporal metacommunity network. In addition, the local floral diversity was positively related to a site's degree and betweenness (marginally significant, thus no is slope represented) across the site network within a year. Points represent means for each species or site. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

Body size was significantly negatively related to species' degree and betweenness within both the spatial temporal metacommunity network (Fig. 4, estimate of the slope \pm SD of degree with body size, -2.121 ± 0.475 , t -value = $-4.461_{53,903}$, P -value = $4.19e^{-5}$; betweenness with body size \pm SD, -0.003 ± 0.0007 , t -value = $-3.629_{53,774}$, P -value = 0.0006), and the temporal (Fig. 4, estimate of the slope \pm SD of degree with body size, -0.409 ± 0.093 , t -value = $-4.395_{53,522}$, P -value = $5.28e^{-5}$; betweenness with body size \pm SD, -0.004 ± 0.0009 , t -value = $-4.325_{52,968}$, p -value = $6.78e^{-5}$). Small-bodied species are thus most connected both across the landscape and through time.

The degree of a site (i.e. species richness) in the spatial metacommunity network was significantly positively related to the site's floral diversity, but not to hedgerow or remnant habitat proximity-weighted area (Fig. 4, estimate of the slope \pm SD of site degree with floral diversity, 0.941 ± 0.238 , t -value = $3.953_{152,782}$, P -value = 0.0001). Site betweenness was marginally significantly related to floral diversity (Fig. 4, slope \pm SD of site betweenness with floral diversity, $9.090e-04 \pm 5.379e-04$, t -value = $1.690_{182,0}$, P -value = 0.09). Floral diversity and not proximity to other habitat is thus most important for metacommunity connectivity both across space and time.

DISCUSSION

Our study provides one of the first in-depth, empirical assessments of how dispersal and habitat selection of species interact with local and landscape characteristics to influence long-term metacommunity dynamics. Our findings contribute to the growing evidence that restoration of hedgerows in intensive agricultural landscapes positively influence long-term population dynamics of wild bees, as opposed to simply redistributing individuals across the landscape (Kremen *et al.* 2019). Further, our results show for the first time that establishing networks of florally-diverse hedgerows and other habitat across the landscape maintains a wild bee metacommunity across space and time. While metacommunity dynamics have been posited to play an important role in restoration ecology, this has been a notable research gap (Montoya *et al.* 2012).

Examining each component of occupancy in turn, across the landscape, bees with wider floral diet breadths colonised sites at a higher rate, likely because they were more able to find their preferred floral interaction partners at any given site. As a result, generalist bees were more likely than specialists to serve as hubs connecting the metacommunity network through both space and time. Local floral diversity also augmented colonisation rates, suggesting that bees select high diversity sites. These florally diverse sites were also most important for maintaining metacommunity connectivity, aligning with other studies showing that spatial hubs have high habitat quality (Bodin & Norberg 2007; Estrada & Bodin 2008; Urban *et al.* 2009). The positive effect of bee generalisation and floral diversity on colonisation point to the importance of habitat selection, or species tracking the abiotic and biotic conditions to which they are adapted (Vellend 2010), in structuring metacommunity dynamics (Ponisio *et al.* 2016). The importance of habitat selection was reinforced by the negative relationship between body size and both colonisation and metacommunity connectivity. Though bee body size scales with movement potential (Greenleaf *et al.* 2007), for wild bees it can also scale with resource needs, with larger bodied bees needing more floral resources to support their populations (Cresswell *et al.* 2000). Some of the largest bees in this community also require more specialized nesting materials, such as dead wood to build nests (*Megachile parallela*, *M. coquilletti* and *Xylocopa tabaniformis orpifex*) and above/below ground cavities (*Bombus melanopygus*, *B. californicus*). In such a resource-poor landscape, it is therefore likely that the floral and nesting requirements of large bees (i.e. habitat selection characteristics) limit their colonisation more than does their dispersal potential.

Hedgerow proximity increased colonisation rates, which combined with previous work showing hedgerows have higher species persistence than field margin controls, [48] suggests hedgerows are acting as source populations exporting bees to other sites (Hanski 1999; Gilpin 2012; Kremen *et al.* 2019). In addition, the best-fitting model steeply down-weighted the area of distant hedgerows (> 1 km), adding to evidence that dispersal limitation structures bee communities in this landscape (Ponisio *et al.* 2016) and suggesting hedgerows that are closer to each other are more ecologically useful to bees (Williams & Kremen 2007). Some of the effects of habitat

selection on colonisation patterns are masked when super-generalists were included as part of the metacommunity, likely because their highly generalised resource requirements may shift the balance between species habitat selection and random dispersal in determining their spatial distribution. When we excluded the super-generalist species, hedgerow proximity also increased colonisation rates of more specialised bees, as well as colonisation to the most florally diverse sites, reinforcing evidence for species selecting high diversity sites, rather than dispersing at random.

The best-fitting model had a shallow down-weighting of remnant habitat area as the distance from the focal site increased, implying that more distant, large patches of annual grassland and oak woodlands (e.g. the Central Coast Range) are as important as closer, smaller patches intermixed within the agricultural landscape (Fig. 1, Fig. S3). Many studies have shown remnant, or 'natural' habitat in agricultural landscapes increases the richness and abundance of pollinators in this (Kremen *et al.* 2002) and other landscapes (Garibaldi *et al.* 2011), increasing the pollination services provided (Kremen *et al.* 2004; Klein *et al.* 2012). Interestingly, however, the negative main effect of remnant habitat and negative interaction with body size on colonisation suggests that large bees resident in remnant habitat do not often leave to successfully colonise other sites, possibly due to their large and/or specialised resource needs (Cresswell *et al.* 2000; Jha & Kremen 2013). In addition, removal of super-generalists revealed an interaction between remnant proximity and floral diversity, suggesting that remnant habitat may intercept colonists even from florally diverse restored habitats. However, unlike hedgerows, we do not have information on the local bee persistence in these habitats, so we cannot infer whether they support stable populations or whether they are population sinks.

Once bees colonise a site, the local floral diversity and the bee species' floral generalisation determined persistence probability, and these characteristics interacted with hedgerow proximity. Reinforcing the role of habitat selection in shaping metacommunity dynamics, the persistence of bees at the most florally diverse sites (> *c.* 11 flowering plant species, and a Shannon's diversity of 0.78) increased with higher hedgerow proximity, suggesting source populations from nearby hedgerows rescue populations at focal florally diverse sites at a higher rate than more depauperate sites. In addition, as we predicted, the persistence of the most generalised bees (having diet breadth > *c.* 20 plant species) increased with higher hedgerow proximity, suggesting these generalist populations may wink out but are more likely to be rescued by populations at nearby hedgerows. Similarly, the positive interaction between body size and remnant habitat proximity on persistence suggests that larger species that wink out are more likely to be rescued by nearby populations found in remnants. Although we found that hedgerows promote persistence locally, particularly of specialist pollinators (M'Gonigle *et al.* 2015), in contrast we find that the main effect of hedgerow proximity on bee persistence is negative. It may be that most of the surveyed sites in this intensively-managed landscape do not provide adequate and/or preferred floral resources (especially the unrestored field margins), so bees quickly move on

to another site, and will do this more readily if there are nearby, attractive hedgerows.

While a number of results did not match our original predictions, the observed interactions between local and landscape characteristics, habitat selection and dispersal provide insights into the complex population dynamics characterising fragmented landscapes. Our results thus support emerging consensus in ecology that a metacommunity approach provides a useful perspective when considering the effect of restoration on population dynamics (Montoya *et al.* 2012; Burkle *et al.* 2017). We find that hedgerow restorations are important contributors to bee metacommunity dynamics, providing further evidence for their utility in conserving pollinator populations in agricultural landscapes (Kremen & M'Gonigle 2015; M'Gonigle *et al.* 2015; Ponisio *et al.* 2016). Dispersal and habitat selection – which can be influenced by plant composition (M'Gonigle *et al.* 2017) and placement of hedgerows in the landscape – were important in shaping species colonisation and persistence at hedgerows, suggesting that through careful planning, restoration ecologists can build persistent metacommunities, even in intensely inhospitable landscapes. Remnant habitat and hedgerows contribute uniquely to metacommunity dynamics. In particular, hedgerows increase the proportion of high floral diversity sites occupied at equilibrium, whereas may be preferred by floral specialists and large bees. Thus, in combination, the installation of hedgerows and conservation of remnant patches is needed to support the complex metacommunity dynamics of populations in intensively managed and altered agricultural landscapes.

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AUTHOR CONTRIBUTIONS

CK and LCP designed the study, LCP performed the analyses with the input of all authors. PD helped to debug and increase the sampling efficiency of models. LCP wrote the

first draft of the manuscript. All authors contributed to revisions.

DATA ACCESSIBILITY STATEMENT

Data is deposited in github/Zenodo with the analysis code at <https://doi.org/10.5281/zenodo.2575861> or https://github.com/lponisio/hedgerow_metacom.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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