

LETTER

Opportunistic attachment assembles plant–pollinator networks

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Abstract

Species and interactions are being lost at alarming rates and it is imperative to understand how communities assemble if we have to prevent their collapse and restore lost interactions. Using an 8-year dataset comprising nearly 20 000 pollinator visitation records, we explore the assembly of plant–pollinator communities at native plant restoration sites in an agricultural landscape. We find that species occupy highly dynamic network positions through time, causing the assembly process to be punctuated by major network reorganisations. The most persistent pollinator species are also the most variable in their network positions, contrary to what preferential attachment – the most widely studied theory of ecological network assembly – predicts. Instead, we suggest assembly occurs via an opportunistic attachment process. Our results contribute to our understanding of how communities assemble and how species interactions change through time while helping to inform efforts to reassemble robust communities.

Keywords

Change points, modularity, mutualism, nestedness, preferential attachment, restoration, robustness, community assembly.

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INTRODUCTION

When a species goes locally extinct, it threatens the loss of more than one species in the community. Species interact with many other species in their community in ways that likely support essential ecosystem functions such as pollination, nutrient flow, water storage and herbivore regulation (Cardinale *et al.* 2012; Kaiser-Bunbury *et al.* 2017). As the world continues to lose species locally and globally at an alarming rate (Ehrlich & Daily 1993; Dunn *et al.* 2009; Barnosky *et al.* 2011), anticipating a community's ability to maintain function and resist collapse will depend on the patterns of interaction between species (Memmott *et al.* 2004; Rezende *et al.* 2007; Bascompte & Stouffer 2009; Thébault & Fontaine 2010). Thus, to safeguard ecological function, it has become increasingly imperative to aid the recovery of lost interactions and component biodiversity by facilitating the assembly of robust interaction networks via ecological restoration (Menz *et al.* 2010; Kaiser-Bunbury *et al.* 2017). However, very little is known about how ecological networks assemble in general, often forcing efforts to restore interacting communities to proceed without a firm grounding in ecological theory.

Preferential attachment, the most widely explored mechanism of network assembly, predicts that species entering a network are more likely to interact with species that are already well-connected (the 'rich-get-richer' principle, Simon 1955; Barabasi and Albert 1999). In pollination systems, a particularly ubiquitous mutualism (Klein *et al.* 2007; Ollerton *et al.* 2011), some studies have found support for the preferential attachment assembly mechanism. Investigating the day-to-day,

temporal assembly of a plant–pollinator network within a season, Olesen *et al.* (2008) found that new plant and pollinator species entering the community tended to interact with already well-connected species, potentially because these species are either more abundant or temporally persistent. As specialist species attach to the well-connected, generalist core via preferential attachment, we expect network nestedness (i.e. a topology in which a core group of generalists interacts with both specialist and generalist species, Albrecht *et al.* 2010) and network-level specialisation to increase. Because nestedness is associated with resilience to species loss (e.g. Memmott *et al.* 2004), preferentially attaching communities would increase in robustness as they assembled. In addition, if as a community assembled via preferential attachment, multiple generalist cores emerged, the modularity of the network would increase though time.

Properties that enable a species to interact with a broad range of partners and thus serve as 'hubs' for preferential attachment (i.e. generalisation), will also enable them to switch partners depending on community context (Kaiser-Bunbury *et al.* 2010; Cuartas-Hernández & Medel 2015; MacLeod *et al.* 2016). According to the optimal foraging theory, for an individual to maximise the fitness benefit of an interaction, there must be a balance between specialising on a less abundant/lower quality resource or sharing an abundant/high quality resource with other species (e.g. Broshi 2016; Emlen 1968; Stephens & Krebs 1986). Thus, as a community assembles and the context changes, generalist species can switch their interaction partners to explore different, less competitive, resources – an 'opportunistic attachment' process.

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The signature of the opportunistic attachment process is that instead of being part of a persistent species core as with preferential attachment, generalist species continually adapt their interactions to exploit the most favourable resources (Valdovinos *et al.* 2016), leading to significant reorganisations of interactions, or change points (Peel & Clauset 2015). A change point is caused by a merge, split, fragmentation or formation of modules of interacting species within a network (Peel & Clauset 2015). In contrast, in communities assembling via preferential attachment, any change points would be driven primarily by changes in the interactions of peripheral, temporally variable species, while a stable, well-connected core of species remained stable in their interactions. Another indication of opportunistic attachment is that interaction patterns (e.g. nestedness) would not develop through time as might be expected with preferential attachment. With both assembly mechanisms, we might expect species entering the network to lead to higher rates of species and interaction turnover than in already assembled communities. However, with preferential attachment, the peripheral species that were turning over would essentially replace each other as they filled similar roles in the network, whereas in opportunistic attachment we might expect unique interactions to more continually form and then disappear. No studies, however, have examined how networks assemble across years to test whether network change points occur and/or how these changes relate to species behaviour.

Understanding network assembly is particularly relevant to ecological restoration, which is essentially ‘applied succession’ (e.g. Parker 1997). In pollination systems, the structure of networks in restored areas changes over time (Forup *et al.* 2008; Devoto *et al.* 2012), suggesting that interactions shift as a community develops. Facilitating network restoration is imperative in areas where species interactions provide essential ecosystem services, such as crop pollination in agricultural landscapes. To promote pollination services in agriculture (Garibaldi *et al.* 2014), some farmers plant strips of native vegetation along farm edges (hedgerows). By providing habitat, hedgerows augment the richness, abundance and trait diversity of pollinators in agricultural landscapes (Morandin & Kremen 2013; Kremen & M’Gonigle 2015; Ponisio *et al.* 2016), and promote the persistence and colonisation of floral resource specialists (M’Gonigle *et al.* 2015), while also enhancing adjacent pollination services (Morandin & Kremen 2013; Morandin *et al.* 2016) but see (Sardiñas & Kremen 2015). As the community assembles, it is important to understand how these new species are incorporated into the network as well as the consequences of adding species for network topology and robustness to species loss.

We explore the process of network development using 8 years of observations of plant–pollinator community assembly following hedgerow instalment in the highly simplified and intensively managed agricultural landscape of California’s Central Valley. We first test whether network assembly was punctuated by significant reorganisations of interactions. We next test whether the species that are most variable in their network position – and thus important contributors to network reorganisations – are the most persistent and connected species, as would be expected by opportunistic attachment, or

least persistent and peripheral species, as expected under preferential attachment. We also examined patterns of species and interaction temporal turnover to determine whether as species turnover, they replace each other (preferential attachment) or form novel interactions (opportunistic attachment). Finally, we investigated whether networks assemble towards specific network topologies (i.e. nestedness, specialisation and modularity) as expected under preferential attachment, and the ramifications for the robustness of the networks. Our results contribute to our understanding of how communities assemble while helping to inform efforts to reassemble robust communities through restoration.

MATERIALS AND METHODS

Study sites and collection methods

Study sites were located in the Central Valley of California in Yolo, Colusa and Solano Counties. This area is composed of intensively managed agriculture – primarily monocultures of conventional row crops, vineyards and orchards. Hedgerows border large (*c.* 30 ha) crop fields and measured between 3 and 6 m wide and *c.* 350 m long. Hedgerows consist of native, perennial, shrub and tree plantings (Fig. S1, Menz *et al.* 2010; Kremen & M’Gonigle 2015; M’Gonigle *et al.* 2015).

We selected five farm edges to be restored as hedgerows. We monitored these locations before the hedgerow was planted, and tracked the assembly of the community for up to 7 years after the hedgerow was planted (from 2006 to 2014). For controls, we concurrently monitored non-assembling communities within mature hedgerows (> 10 years since planting, $N = 29$) and unrestored, weedy field margins ($N = 19$). The mean distance between monitoring sites was 15 km, and the minimum distance between sites sampled in the same year was 1 km. The entire area surveyed spanned almost 300 km². The crop fields adjacent to all sites were similarly managed as intensive, high-input monoculture.

Sites were sampled between two and five times per year (Tables S1–S3, mean 3.4 samples per year). In each round of sampling, the order in which sites were sampled was randomised. Surveys were conducted under sunny conditions when the temperature was above 21 °C and wind speed was below 2.5 m s⁻¹.

During each sampling round, flower visitors to plants in assembling hedgerows and non-assembling controls were netted for 1 h of active search time (the timer was paused when handling specimens). The identity of the plant being visited was recorded for each floral visitor. Honey bees (*Apis mellifera*) were not collected because, as managed pollinators whose hives are placed near pollinator-dependent crops, they occur pervasively throughout this landscape in high abundances.

All other insect flower visitors that touched the reproductive parts of the flower were collected; however, here, we focus only on wild bees and syrphids – the most abundant and effective pollinators in the system (representing 49 and 19% of records, respectively, C. Kremen, A. Klein and L. Morandin, unpublished data). Bee and syrphid specimens were identified to species (or morphospecies for some bee specimens in the genera *Nomada* and *Sphecodes*) by expert taxonomists.

Quantitative networks were generated for each site through time. Because the number of sampling rounds varied between years (Tables S1–S3), we used the mean of the interactions between a pair of plants and pollinators within a year to represent interaction frequency.

Change point analysis

Identifying change points

We employed a change point detection method (Peel & Clauset 2015) to identify fundamental reorganisations in large-scale network topology. A change point could be the splitting, merging or formation of network modules or some combination therein (Peel & Clauset 2015). Change point detection methods are yet to be generalised to quantitative networks; hence, for this analysis, we focused on qualitative (binary) networks. To detect change points, we must first fit a model of the structure of the graph in each year. Following Peel & Clauset (2015), we fit a generalised hierarchical random graph model (GHRG). The GHRG model captures both assortative and disassortative structure at all scales in the network, and produces accurate fits to ecological networks (Peel & Clauset 2015). The GHRG model decomposes the vertices (species) of a network into a series of nested groups, the relationships among which are represented by a dendrogram. The GHRG model builds on the more classic hierarchical random graph model (HRG) (Clauset *et al.* 2007) but allows each node of the dendrogram to have any number of subbranches, instead of requiring a fully binary dendrogram. Relaxing the binary tree requirement allows the the GHRG model to capture more large scale patterns than the HRG model. The GHRG model is not designed specifically for bipartite networks, but is able to detect significant change points in the structure when fitted to simulated bipartite networks (Peel, pers. comm). The GHRG model is fit to the network using Bayesian posterior inference and techniques from phylogenetic tree reconstruction (Peel & Clauset 2015).

Once the GHRG model was fitted to the networks, whether a change point occurred between two time slices was determined. To detect a change point, we used Bayes factors to compare the fit of two models – one where a change point occurred between two time slices and one where no change occurred. We used sliding window of fixed length of 4 years to detect if any changes have occurred with respect to a GHRG model fitted over the window. Larger windows allowed for more gradual changes, and 4 was a balance between a window as large as possible and the constraint of 8 years of data. Lastly, to calculate *P*-values for the Bayes factors, we used parametric bootstrapping to numerically estimate the null distribution (100 000 samples, Peel & Clauset 2015). We modified the code published online by L. Peel for the change point analysis (<https://piratepeel.github.io/code.html>). We reran the change point detection algorithm 1000 times, and identified robust change points as those that were selected in 95% of iterations. Change points analyses were conducted in Python 2.7.10 and R 3.3.2 (R Core Team, 2015). The fully reproducible code and explanations for all analyses is available on GitHub at https://github.com/lponisio/hedgerow_assembly (Ponisio & Gariarsa 2017).

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We next tested whether the change points occurred at similar rates between the assembling and non-assembling communities. We modelled the number of change points as successes and the total number of sample years at each site as trials, and used a generalised linear model with binomial error to test whether the probability of a change point occurrence varied by site type. We used standard techniques to determine whether the assumptions of the models were met for this and all subsequent models. For the non-assembling controls, only sites with five or greater survey years were included in this analysis (field margins, $N = 11$, mature hedgerows, $N = 5$). All statistical analyses were conducted in R 3.3.2 (R Core Team, 2015).

Characteristics of species that contribute to change points

To further elucidate the nature of the change points, we examined the characteristics of the species that contributed to interaction reorganisation. We calculated species persistence as the proportion of surveys in which a plant or pollinator was observed. Species observed consistently within and between years were thus maximally persistent. Species degree was calculated from interaction observations from an extensive dataset from Yolo County (*c.* 18 000 interaction records) that included both the data included in this study and additional data from sites where we collected flower visitors using the same methods (M'Gonigle *et al.* 2015; Ponisio *et al.* 2016). Degree was estimated using the Chao2 estimator (Chao *et al.* 2009; Winfree *et al.* 2014), which approximates the number of plant species from which a given pollinator species would have been observed visiting, given sufficient sampling.

To represent network position variability, we computed the coefficient of variation of weighted closeness centrality (Freeman 1978) at each site through time. Zeros (the absence of the species in the network) were not included in the calculation of the coefficient of variation to avoid confounding persistence with variability in network position. Closeness centrality represents the importance of a species by calculating the path lengths to other vertices (species) in the network (Freeman 1978). The shorter the mean path length to other species, the higher the closeness centrality. We used linear mixed models to test whether the species closeness variability (log) is related to the persistence or degree of that species (Bates *et al.* 2014; Kuznetsova *et al.* 2014). We included random effects for species and site. *P*-values for mixed models were calculated based on Satterthwaite's approximations for degrees of freedom (Kuznetsova *et al.* 2014). We used variance inflation factors (VIF) to estimate the collinearity between explanatory variables (Zuur *et al.* 2010). Because variability in network position could be the result of log closeness centrality increasing through time – as would be expected with assembly by preferential attachment – we tested for this relationship as well.

Species and interaction turnover

To better understand the mechanisms underlying the temporal dynamics of the assembling networks, we examined patterns

of species and interaction turnover. To estimate the temporal species and interaction turnover, we used an approach similar to calculating spatial β -diversity. Instead of calculating the variation in community composition across sites within a year, we estimated turnover across years at a site. We first calculated the pairwise dissimilarity of plants, pollinators and interactions between years within each site using the Chao dissimilarity estimator that incorporates abundances, while also accounting for unobserved records (Chao *et al.* 2005). Dissimilarity estimates can be affected by the total number of species and individuals sampled at a site (e.g. Ponisio *et al.* 2016). For example, the probability that two sites do not share any species is higher when there are few individuals at those sites. Following Ponisio *et al.* (2016), we used null models that constrained species richness to estimate the deviation of the observed dissimilarity from that which would be expected under a random community assembly process. With the corrected dissimilarity values, we then calculated the multivariate dispersion of community composition across years (Anderson *et al.* 2011). In order to test whether assembling hedgerows had more species and interactions turnover than non-assembling communities, the species and interaction temporal turnover estimates were modelled as responses in a linear mixed model with site type as an explanatory variable and site as a random effect (Bates *et al.* 2014; Kuznetsova *et al.* 2014).

We developed a method to examine the temporal turnover of interactions with weightings based on their similarity (Fig. 1). We followed the algorithm of Ahn *et al.* (2010) to cluster all the interactions (edges) hierarchically across sites and years based on their similarity, and built a dendrogram. The interaction similarity is based on how many vertex neighbours (plants and pollinators) two edges share (Ahn *et al.* 2010; Kalinka & Tomancak 2011). The more neighbours edges shared in common, the shorter the branch length between them on the dendrogram. We next calculated the temporal turnover of interactions weighted by their similarity, as approximated by cophenetic distance (Graham & Fine 2008; Kembel *et al.* 2010). We then used linear mixed models to test whether the weighted turnover of interactions varied between assembling and non-assembling networks, including

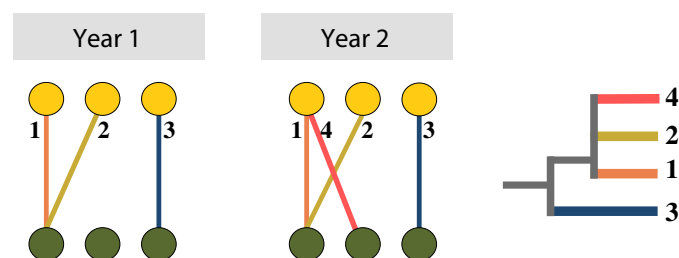


Figure 1 Diagram illustrating the weights used to examine the temporal turnover of interactions based on their similarity. Light colored nodes represent animal species and dark colored nodes represent plant species. Interactions between species (edges) are numbered. The dendrogram depicts the similarity of the edges based on their shared neighbour species (animals and plants), across years. Edge 4 is gained between year one and two, while edges 1, 2 and 3 remain the same. Since edge 4 shares an interaction partner with edge 1, edge 4 appears in the same cluster as edges 1 and 2 in the dendrogram.

site as a random effect (Bates *et al.* 2014; Kuznetsova *et al.* 2014).

Temporal changes in interaction patterns

Network structure

To evaluate network nestedness, we used the estimator weighted NODF (nestedness overlap and decreasing fills) (Almeida-neto *et al.* 2008). NODF evaluates whether species with fewer partners interact with subsets of partners with which more connected species interact (Almeida-neto *et al.* 2008). To estimate modularity, we used an approach based on edge betweenness (Newman & Girvan 2004; Csardi & Nepusz 2006). This hierarchical clustering algorithm generates a dendrogram based on potential modules, and selects the partition that maximises modularity (Newman & Girvan 2004; Csardi & Nepusz 2006). We evaluated network specialisation with the metric H2, which estimates the deviation of the observed interaction frequency between plants and pollinators from a null expectation where all partners interact in proportion to their abundances (Blüthgen *et al.* 2006, 2008). H2 describes specialisation in terms of exclusiveness (or reciprocal specialisation). We also included another measure of specialisation, connectance, calculated as the proportion of observed out of possible interactions. Connectance measures the degree of generalisation or redundancy in a system (Blüthgen *et al.* 2008). We calculated standardised *z*-scores so that nestedness, modularity and specialisation metrics could be compared across communities. The *z*-scores were calculated by generating an ensemble of 999 null assembled communities, subtracting the mean of the statistic calculated across these communities from the observed value, and then dividing by the standard deviation. To assemble null communities, we reshuffled the interactions between species but fixed the total number of interactions, species and interaction frequency distributions (Galeano *et al.* 2009).

To test whether network modularity, nestedness, connectance or specialisation changed linearly with assembly, we used linear mixed models with the descriptive network metrics as the response variable, year of assembly as the explanatory variable, and random effects of site and year. The number of species in a network affects the network topologies possible, so we also examined the change in plant and pollinator species richness through time. We employed generalised linear mixed models with Poisson error to model richness (Bates *et al.* 2014). We scaled all continuous explanatory variables.

Network robustness

Finally, we tested whether the changes in network topology associated with network assembly affect the robustness of the network to species loss and cascading perturbations. Following Memmott *et al.* (2004), we simulated plant species extinction and the subsequent extinction cascades of pollinator species. Because the reproduction of plant species is facilitated by active restoration efforts, it is unlikely the extinction of pollinator species would affect plant populations in the hedgerows. However, plants ceasing to bloom, for example, in response to drought, will likely affect the pollinators that

depend on them. We eliminated plants species based on their degree or abundance, and then calculated the number of pollinators that secondarily went extinct. The area below the extinction curve is an estimate of network robustness (Memmott *et al.* 2004; Burgos *et al.* 2007; Dormann *et al.* 2008).

We also explored how the robustness to cascading perturbations changed as the community assembled, using algebraic connectivity – the second smallest eigenvalue of the Laplacian matrix (Fiedler 1973) – as a proxy for network robustness. Algebraic connectivity relates to how difficult it is to turn a network into completely disconnected groups of species (Costa *et al.* 2007; Gibert *et al.* 2013). The larger the algebraic connectivity, the more sensitive a network is to cascading perturbations. Perturbations, such as the decrease in abundance of a plant or pollinator, can have negative consequences for the species in the network. For example, a decrease in abundance of a pollinator will diminish the pollination services it provides to plants. The affected plants would set less seeds, and decrease in abundance the subsequent year. Consequently, other pollinators that depend on those plant species would also be affected, and the effects of this perturbation would continue to propagate throughout the network. Alternatively, perturbations could also have a positive effect if, for example, the increase in the abundance of a plant species lead to an increase in resource availability for pollinators. The examples of negative perturbations (e.g. resource collapse, disease spreading, parasites), however, outnumber possible positive perturbations. It is important to note that both robustness and algebraic connectivity assume that the network is static – they do not account for the ability of species to alter their interaction depending on circumstances and the resource availability.

In order to test whether hedgerows changed in robustness as the communities assembled, the three measures of robustness were modelled as responses in a linear mixed model with site type as an explanatory variable and site as a random effect (Bates *et al.* 2014; Kuznetsova *et al.* 2014).

RESULTS

Over 8 years and from 747 samples, we collected and identified 19 547 wild bees and syrphids comprising 173 species from 50 genera. We observed 1521 unique interactions between plants and pollinators.

Change point analysis

Identifying change points

Four of the five of assembling hedgerows underwent at least one significant interaction reorganisation (Figs 2 and 3, Table S2–S4), while only 20% of non-assembling communities experienced a change point (one field margin and two non-assembling hedgerows each underwent one change point). The proportion of years with change points in assembling hedgerows was 21.2%, whereas only 8.6% of years in non-assembling hedgerows and 1.3% of years in field margins were changing points. Assembling hedgerows had significantly more changing points than the non-assembling field margin networks (difference in the odds ratios estimate between

assembling and non-assembling networks, 0.057, 95% CI [0.003, 0.34], z -value = -2.6216 , P -value = 0.0089), but not significantly more than the non-assembling (mature) hedgerows. Because the sample sizes are small and unbalanced ($N = 33$ for assembling hedgerows, 23 for non-assembling hedgerows, and 66 for non-assembling field margins, where N is the number of consecutive years assessed totalled over all sites within a site type, Table S4), this may induce bias which may skew the odds ratios away from one.

Characteristics of species that contribute to change points

Inconsistent with the predictions of assembly by preferential attachment, degree and persistence were not negatively related to variability in network position. Instead, pollinator persistence was significantly positively related to network position variability (Fig. 4, estimate of the slope of closeness centrality variability and persistence \pm SE of the estimate, 0.742 ± 0.246 , t -value = $3.01215.42$, P -value = 0.0086), although degree was not. The slope of persistence and closeness centrality remained significant when the species with the top 10 persistence scores were dropped. Plant persistence and degree were not significantly related to network position variability (Fig. 4). In both models, we tested collinearity in degree and persistence using variance inflation factors (VIF), and did not find strong evidence for collinearity (all VIF < 2, Zuur *et al.* 2010). The variability of species network position was not the result of closeness linearly increasing through time, and, in fact, plant and pollinator closeness decreased slightly through time (Fig. S5, estimate of the slope of closeness through time \pm SE, pollinators: -0.082 ± 0.021 , t -value = $-3.879_{44.66}$; plants -0.089 ± 0.044 , t -value = $-2.026_{610.2}$).

Species and interaction turnover

Contrary to expectations, the rates of plant, pollinator and interaction temporal turnover were similar across assembling hedgerows, non-assembling mature hedgerows and field margins, although mature hedgerows had significantly less pollinator turnover than field margins (Fig. 5, estimate \pm SE of the difference in turnover between field margins and mature hedgerows, -0.051 ± 0.026 , t -value = -1.979_{195} , P -value = 0.0493). When interactions were weighted by their similarity, both assembling and mature hedgerows had higher rates of turnover than field margins (Fig. 5, estimate \pm SE of the difference in turnover between field margins and assembling hedgerows, 0.115 ± 0.027 , t -value = $4.216_{31.12}$, P -value = 0.0002; field margins and mature hedgerows, 0.082 ± 0.024 , t -value = $3.4_{35.13}$, P -value = 0.002). The weighted interaction turnover at assembling hedgerows, however, was not significantly higher than in non-assembling, mature hedgerows.

Temporal changes in interaction patterns

Network structure

As predicted by opportunistic attachment, nestedness, modularity and specialisation did not increase linearly with assembly (Fig. 6). All the networks were significantly nested (z -scores > 1.96 assuming a Gaussian distribution of null community network metrics), but not modular (z -scores

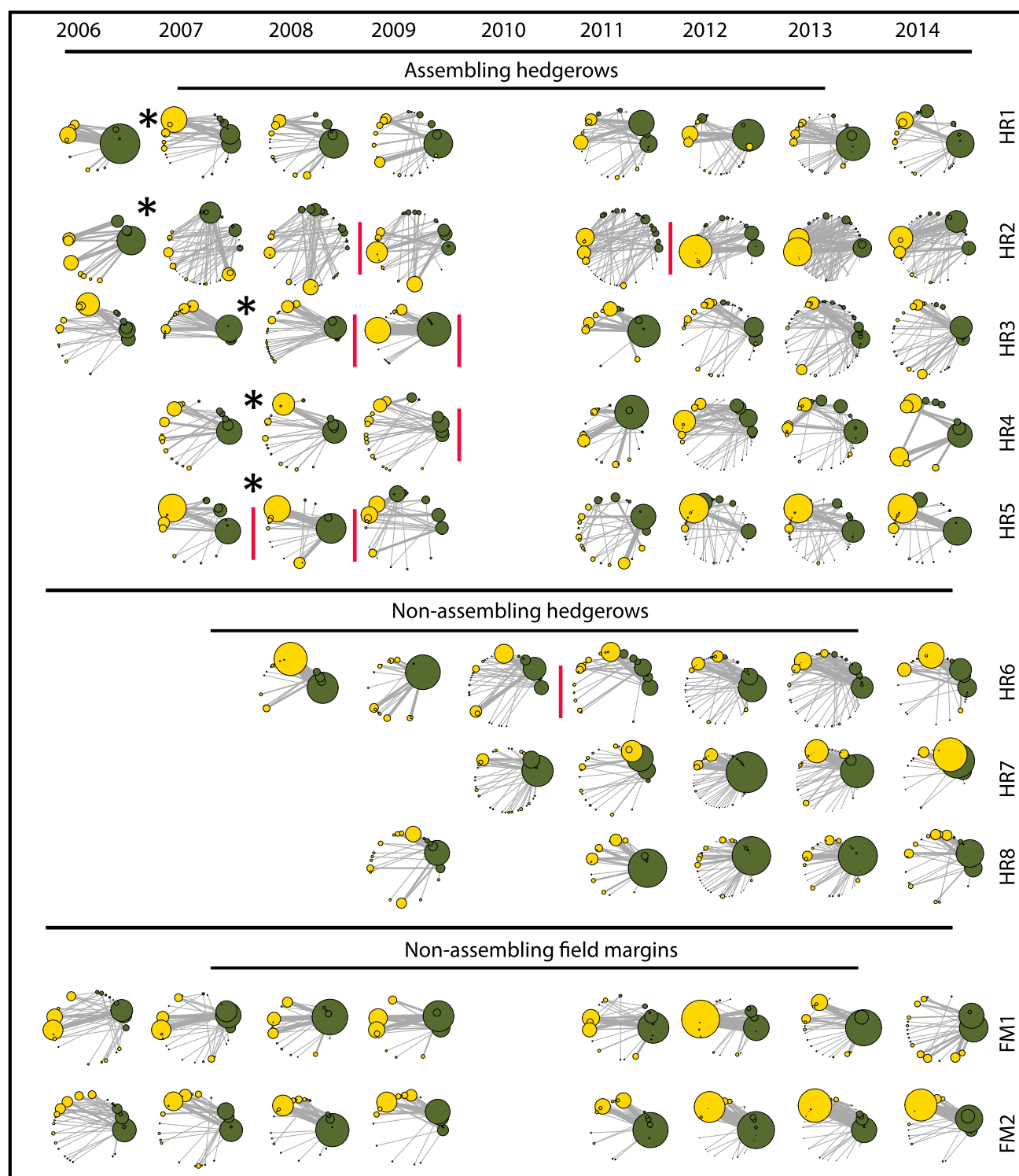


Figure 2 Assembling hedgerow networks had more changing points (vertical lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here, the time series for all survey sites are represented in Figs S2–S4). In each network, plants and pollinators are represented by dark and light circles, respectively, weighted by their degree. Each species has a consistent position in the perimeter of the network across years and survey sites. Asterisks indicate the year the hedgerow was planted. Before that, the sites were weedy field margins.

< 1.96, Fig. 6). Most communities were more generalised than expected when interactions were reshuffled between species (z -scores < 1.96, Fig. 6). Connectance decreased as the community assembled (Fig. 6, estimate of the slope of

connectance through time \pm SE of the estimate, -0.023 ± 0.008 , t -value = $-2.78_{30.733}$, P -value = 0.007).

Both plant and pollinator species richness increased through time (Fig. 6, estimate of the slope of richness through

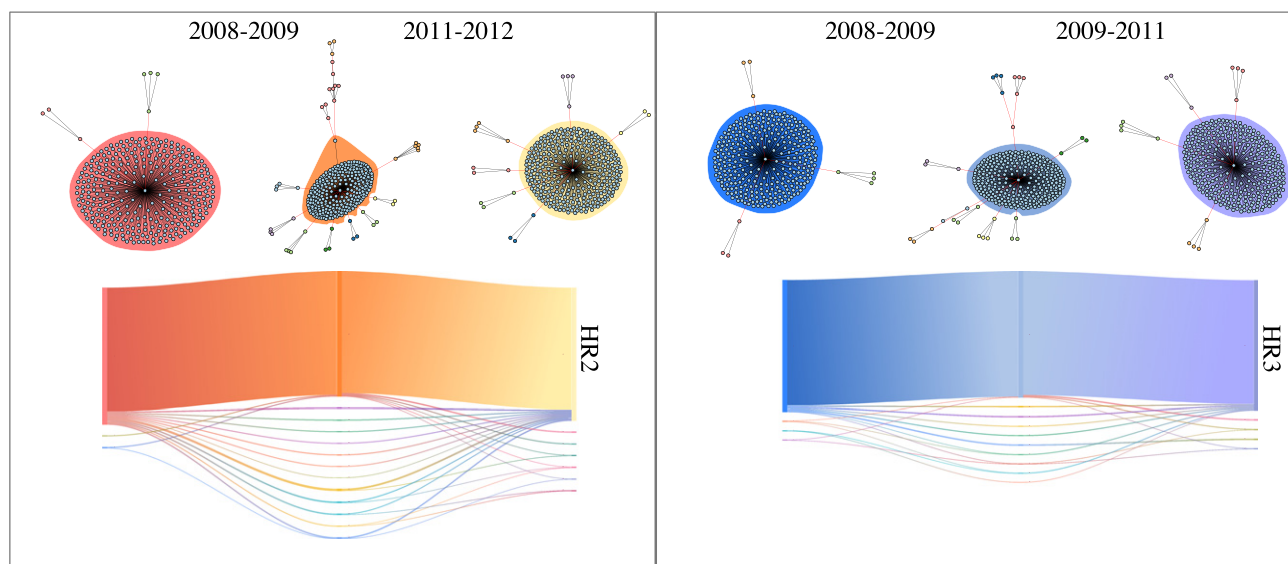


Figure 3 The species module membership between network changing points as fit by the GHRG model. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species to different modules between change points. Time progresses from the left to the right of the figure. Within a time slice modules are colored according to the module membership representation above. The thicker the line, the more species that belong to that module. Between change points, some species move between modules, represented by the change in the grouping and color of the lines through time.

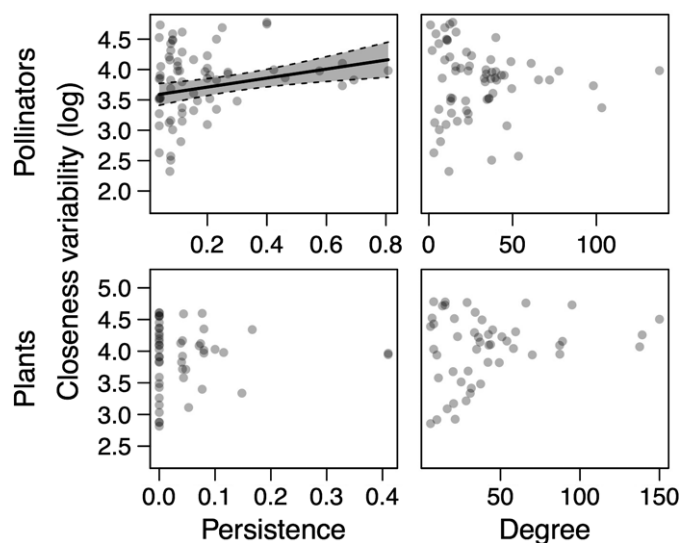


Figure 4 The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Only persistence was positively related to network position variability in pollinators. Points represent means for each species across sites. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

time \pm SE, pollinators: 0.136 ± 0.064 , z -value = 2.12, P -value = 0.034; plants: 0.140 ± 0.060 , z -value = 2.519, P -value = 0.012). Unsurprisingly, pollinator species are colonising and persisting at the assembling hedgerows. Plant species richness in the networks is based on the flowers actually visited by pollinators and not the presence of a particular plant species at a site. Thus, although some new plant species may establish themselves in the hedgerows, the increase in plant richness in the networks is likely

due to previously unvisited plants attracting visitors as they mature and offer better rewards.

Network robustness

Assembly did not affect network robustness to species extinction when species were removed incrementally by degree or abundance (Fig. S6). Similarly, the sensitivity of networks to cascading perturbations, as measured by the algebraic connectivity of the network, did not change linearly as the community assembled (Fig. S6).

DISCUSSION

We show that the temporal assembly of plant–pollinator networks following restoration is a highly dynamic process punctuated by change points, indicating that interactions undergo significant reorganisations. Degree and persistence were not negatively related to network position variability as might be expected if the network was assembling by preferential attachment, and, in pollinators, persistence and network variability were in fact positively related. Finally, of the descriptive metrics of network topology, only connectance showed a significant linear relationship with assembly. Together, these results suggest an opportunistic attachment process.

Change points did not occur consistently across all sites in specific years (Fig. 2), suggesting that community-specific biotic factors such as the abundance and identity of species present in each year – likely in addition to abiotic drivers such as rainfall – contribute to interaction reorganisations. Most assembling hedgerows did not undergo a significant interaction reorganisation immediately after planting (i.e. the transition from weedy field margin to hedgerow). This result is

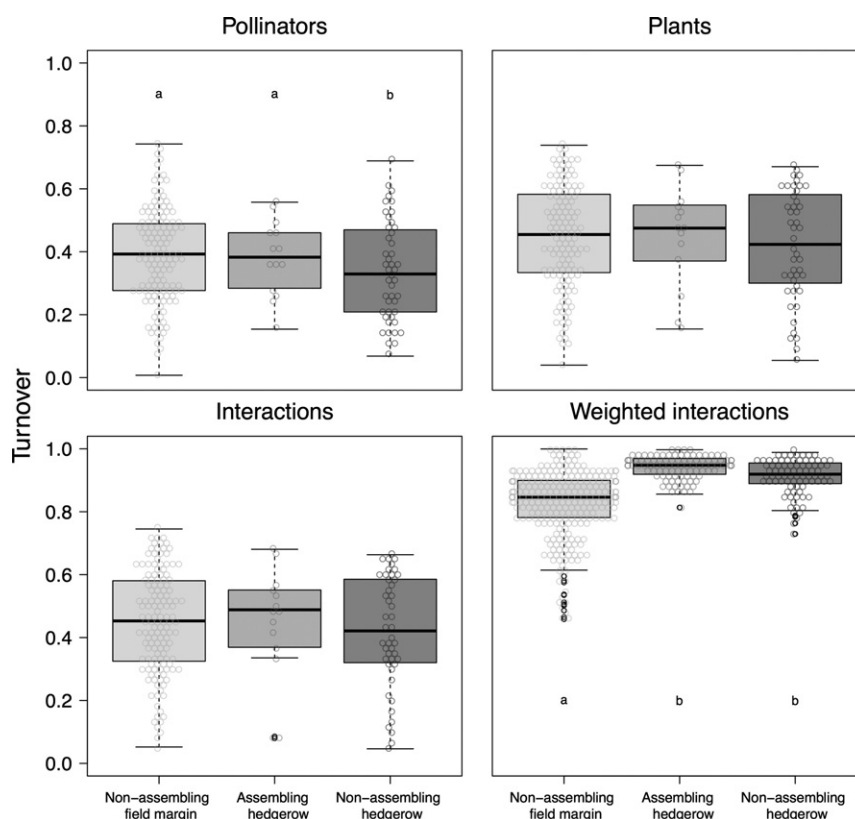


Figure 5 Species interaction and weighted interactions turnover of plant–pollinator networks at non-assembling field margins sites ($N = 138$, across 29 sites), assembling hedgerows ($N = 14$, across five sites) and non-assembling, mature hedgerows ($N = 46$, across 19 sites). Rates of species and interaction turnover were similar between site types, though mature hedgerows had significantly less pollinator turnover. However, when interactions were weighted by their similarity, both hedgerow types had higher turnover than unrestored field margins. Boxplots represent medians (black horizontal line) first and third quartiles (box perimeter) and extremes (whiskers).

consistent with the finding that hedgerow restoration takes several years to have an impact on the plant–pollinator communities in our study system, as well as with the observation that hedgerows do not begin to produce many flowers until 3–5 years following planting (Kremen & M’Gonigle 2015).

The change point analysis we employed is only able to detect large-scale changes in network structure (Peel & Clauset 2015), and does not consider interaction weights. Pollinators can adapt to changing context by shifting their interaction partners, the frequency with which they visit them, or both (Valdovinos *et al.* 2016), and the method currently does not detect such interaction frequency-driven change points. Methods to directly model entire time-varying graphs and compare networks more generally are an active area of research, and thus in the future, we may be able to describe more subtle changes in network structure that may build our understanding of how communities respond to change (Jacobs & Clauset 2014). Even so, much of network science is concerned with modelling in data-rich fields with large networks and long time series and minimal observation error, unlike what is currently available in ecology. To our knowledge, the interaction data from this study represents the longest continuous sampling of multiple, species-level ecological networks to date. However, due to the constraints of funding, human effort and working on private land, our sample size is unbalanced and relatively small in comparison to the networks for

which graph comparison methods are developed. In order to gain insights into how ecological networks change, ecology must match the data needs of network methods through innovations that will facilitate more efficient collection of data (e.g. image recognition, Hall 2011) along with efforts to tailor the methods themselves through interdisciplinary collaborations between ecologists and researchers developing network methods.

Interestingly, although assembling hedgerows generally had more network reorganisations than non-assembling communities, pollinator species and interaction turnover occurred at similar rates across site types. Assembling hedgerows have higher turnover than non-assembling field margins only when interactions were weighted by their similarity. This is likely because although species and interactions are turning over at the unrestored field margins, species and interactions that fill similar roles in the network are replacing each other as would be expected with opportunistic attachment. In contrast, at the assembling hedgerows, unique interactions are turning over as the networks continually reorganise and community richness increases (M’Gonigle *et al.* 2015). Non-assembling mature hedgerow communities had not only similar rates of weighted interaction turnover as assembling hedgerows but also the lowest pollinator turnover. Pollinators at mature hedgerows may generally be more persistent, and rare and/or specialised pollinators could generate this pattern they formed unique but

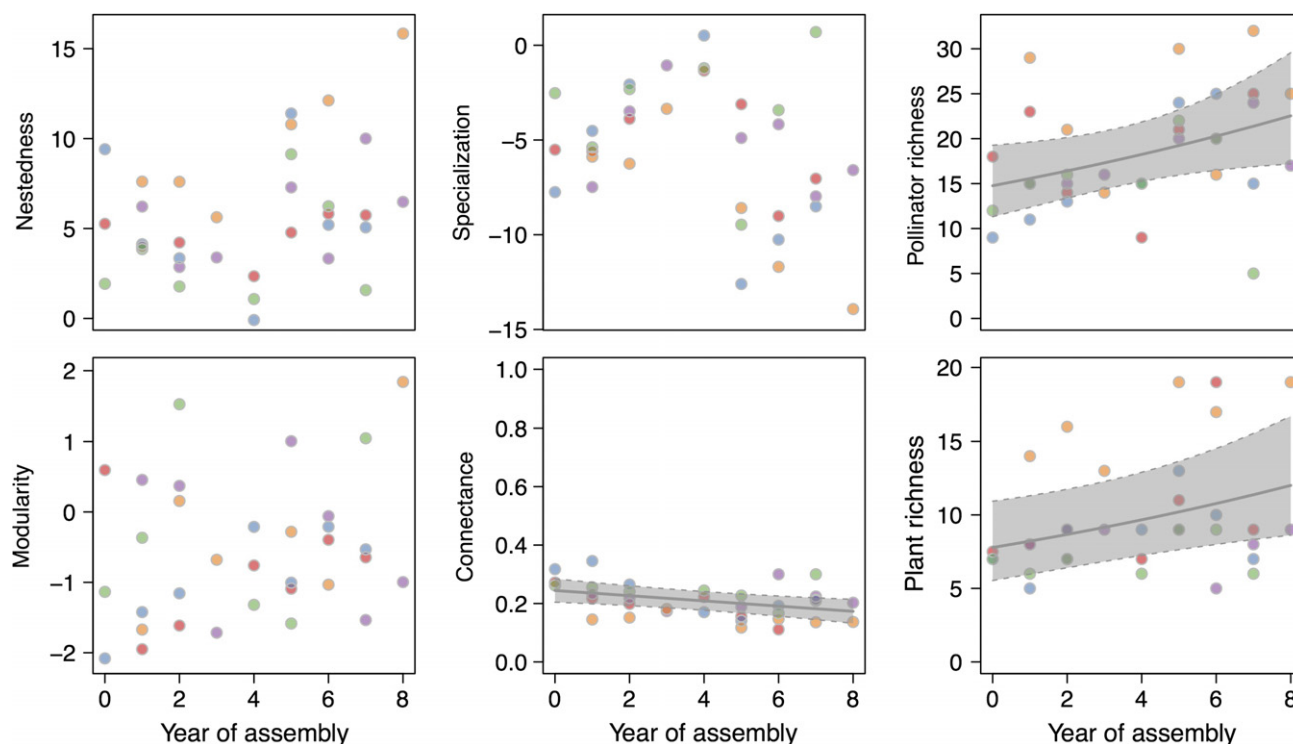


Figure 6 Plant richness and pollinator richness increased through time in the assembling hedgerows. Nestedness, modularity and specialisation did not change linearly across years, while connectance decreased. The nestedness, modularity and specialisation scores represent z -scores. Scores $> c. 1.96$ or $< c. -1.96$ are significantly more or less structured than randomly assembled networks. Points are the metric value for each site at each year of assembly, and the colours indicate the different survey sites. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

transient interactions with plants that did not previously share pollinators. These species would not contribute strongly to network reorganisation or species turnover, but would enhance weighted interaction turnover. Mature hedgerows, therefore, support more persistent pollinator communities, while also providing resources for rare and/or specialised species (Kremen & M'Gonigle 2015; M'Gonigle *et al.* 2015).

Although persistence and not degree was significantly related to network position variability, because degree and persistence are traits that are often related in pollinator species, it is difficult to disentangle the causal mechanism for why persistent pollinators tended to be more variable in their network positions. The most persistent bee species in our landscape (*Halictus ligatus*, *Halictus tripartitus* and *Lasioglossum incompletum*) have multiple generations within a year enabling them to have long phenologies and high abundances. These species can then visit many different flowers over the season, resulting in a higher degree (Vázquez *et al.* 2009; Fort *et al.* 2016). Species that can interact with a relatively high number of partners may be better able to exploit the limited floral resources in the intensively managed agriculture landscape, and thus also be the most persistent (in ant-plant mutualisms, Díaz-Castelazo *et al.* 2010). Either way, our results suggest that given the opportunity and ability to use different resources, pollinator species will often change their network positions, likely to utilise the most advantageous floral resources available which will depend on both the other pollinator species that are present and the state of the

plant community (Waser *et al.* 1996; Gómez & Zamora 2006; Cuartas-Hernández & Medel 2015; MacLeod *et al.* 2016).

When we explored how network topology changed through time, we found few trends. Connectance decreased, as would be expected if the network is being colonised by specialist species (M'Gonigle *et al.* 2015). However, network specialisation, as measured by the degree to which species deviate from interacting with partners in proportion to their abundances, did not change linearly with assembly. Decreasing connectance without an accompanying increase in specialisation would be possible if the increased colonisation of specialised species was accompanied by an increase in the diet breadth of resident species. This would be expected if resident species were able to minimise their foraging time by expanding their diet breadth as plant diversity and/or intraspecific competition increases with hedgerow maturation (Pyke 1984; Waser *et al.* 1996; Blüthgen *et al.* 2007; Albrecht *et al.* 2010; Brosi 2016). Connectance may also decrease simply because as species richness increases, the number of potential links grows exponentially (Kay & Schemske 2004).

Hedgerow network resilience as measured by robustness to species extinction or susceptibility to cascading perturbations also did not increase linearly with assembly. While these results differ with other studies that have found network robustness increases after restoration (Forup *et al.* 2008; Kaiser-Bunbury *et al.* 2017), such studies either used space for time substitution to compare sites over a much longer time

sequence (> 250 years, Forup *et al.* 2008) or examined restoration processes based on non-native species removal (Kaiser-Bunbury *et al.* 2017). Our study looks at species addition and rapid assembly. Although both community assembly and non-native species removal (Kaiser-Bunbury *et al.* 2017) can contribute and are often needed to restore communities, these processes are not necessarily opposites that mirror each other in their effects on network properties. The process of network disassembly may be related to the process of network build-up, but little is known about either process and even less about their relationship (Bascompte & Stouffer 2009).

We show rapid assembling and successional communities assemble opportunistically such that species continually change their positions in the network in response to shifting biotic and abiotic contexts. If opportunistic assembly, or 'rewiring', also occurs as a habitat degrades or is destroyed, then species in each time slice will reorganise their interactions based on the species remaining, and novel interactions may compensate for function lost from species extinction (Kaiser-Bunbury *et al.* 2010). Such reorganisations within networks would be likely to provide substantial buffering capacity to maintain plant–pollinator interactions, since it is the generalised and abundant species that are most prone to reorganising their interactions, and least likely to be lost first with habitat loss (Aizen *et al.* 2012; Winfree *et al.* 2014). For example, in an experiment where the most abundant bumble bee species was removed from sub-alpine meadows, the remaining bumble bees shifted their interactions by expanding the diversity of plant species they visited during a foraging bout (Brosi & Briggs 2013). However, the only empirical study examining the disassembly of both species and interactions in habitat fragments of different sizes within an agricultural matrix, found that the interactions present in each fragment tended to be proper subsets of those in the next, larger fragment (Aizen *et al.* 2012). This work suggests a more ordered progression of network disassembly where there is minimal interaction reorganisation to compensate for the lost species; however, we do not know if this is a common pattern, or one that is tied to the specific ecology and evolutionary history of the species in those communities. Further, the pathway of disassembly may differ from reassembly (hysteresis, Suding & Hobbs 2009). Understanding under what ecological circumstances species rewire will also be important for developing new methods for estimating a community's robustness to species extinction or susceptibility to cascading perturbations, which is currently based on static networks. In order to facilitate management, restoration and conservation, future studies should explore the prevalence of opportunistic attachment in both network assembly and disassembly, and the species life histories and biological contexts that enable it to occur.

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AUTHOR CONTRIBUTIONS

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

DATA ACCESSIBILITY STATEMENT

Data is deposited in GitHub/Zenodo with the analysis code (Ponisio & Gariarsa 2017)

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