

The temporal assembly of plant-pollinator networks following restoration

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Abstract

TO BE RE-WITTEN The structure of networks is related to ability of communities to maintain function in the face of species extinction. Understanding network structure and how it relates to network disassembly, therefore, is a priority for system-level conservation biology. We explore the assembly of plant-pollinator communities on native plant restorations in the Central Valley of California.

Keywords: changing points, temporal networks, hedgerows, species interactions, preferential attachment, mutualisms

9 Introduction

10 Global change has created a severe biodiversity crisis, and as species are lost, so are their inter-
11 actions (Dunn *et al.*, 2009; Barnosky *et al.*, 2011). Because mutualistic interactions are essential
12 for maintaining the diversity their component guilds of species, these systems are particularly at
13 risk from coextinction cascades. The nature of these coextinction cascades depends on the inter-
14 action patterns within a community (Memmott *et al.*, 2004; Rezende *et al.*, 2007; Bascompte &
15 Stouffer, 2009). Recovering the lost biodiversity and interactions through ecological restoration
16 has become increasingly imperative, and a key restoration aim is to facilitate assembly of robust
17 interaction networks (Menz *et al.*, 2010). We know little, however, about how to re-assemble in-
18 teracting communities through restoration, or the process of ecological network assembly more
19 generally.

20 The mostly widely explored mechanism of network assembly, preferential attachment (Barabási &
21 Albert, 1999), predicts that a new species is more likely to interact with species that are already
22 well-connected (“the rich-get-richer” principle, Barabási & Albert, 1999). In pollination systems
23 — a particularly ubiquitous mutualism (Ollerton *et al.*, 2011; Klein *et al.*, 2007) — some studies
24 have found support for this mechanism of assembly. Investigating the day-to-day, temporal as-
25 sembly of a plant-pollinator network within a season, Olesen *et al.* (2008) found that new species
26 tended to interact with already well-connected species, likely because these species are either more
27 abundant or more temporally persistent (Olesen *et al.*, 2008). In addition, using a space-for-time
28 substitution to study primary succession along a glacier foreland, Albrecht *et al.* (2010) found
29 some indication assembly was occurring through preferential attachment. Network nestedness, a
30 pattern of interactions where a generalist core interacts with both specialist and generalist species,
31 increased as the community aged (Albrecht *et al.*, 2010). Increasing nestedness could result from a
32 process like preferential attachment where specialist species attach to the well-connected, general-
33 ist core. In addition, non-successional temporal dynamics also suggest a stable core of generalists

persists despite high turnover of peripheral species (Fang & Huang, 2012; Díaz-Castelazo *et al.*, 2010; Alarcón *et al.*, 2008).

In contrast to the ordered network build-up described by preferential attachment, assembly can be punctuated by significant reorganizations of interactions (Peel & Clauset, 2014). Such significant reorganizations of interactions, or changing points, have been observed in social networks responding to abrupt shifts in the behavior of interactors (Peel & Clauset, 2014). In ecological communities, such shifts may occur if, as new species are added, resident species change their interaction partners to optimize their foraging effort. In plant-pollinator communities, theory predicts pollinators optimize their use of floral resources to reduce interspecific competition and improve resource-use efficiency (Pyke, 1984; Valdovinos *et al.*, 2010, 2013; Albrecht *et al.*, 2010; Blüthgen *et al.*, 2007). No studies, however, have examined whether changing points occur during ecological network assembly and how they relate to the behavior of the interactors.

Understanding network assembly is particularly relevant to ecological restoration, which is essentially 'applied succession' (Parker, 1997, e.g.). In pollination systems, the time since an area was restored has been shown to effect the structure of networks (Forup *et al.*, 2008a,b; Devoto *et al.*, 2012), suggesting interactions are evolving as the community develops. Understanding the mechanisms of network assembly will help to guide the restoration of particular communities.

Facilitating effective restoration of networks is especially imperative in areas where species interactions provide essential ecosystem services, such as crop pollination. In intensively managed agricultural landscapes, the demand for pollination services is the greatest (Kremen, 2008). However, honey bees, managed extensively around the world to provide crop pollination, are in global decline (Neumann & Carreck, 2010; van Engelsdorp *et al.*, 2009). In addition, native pollinators, which have the capacity to provide sufficient crop pollination (Kremen *et al.*, 2002; Winfree *et al.*, 2007; Kremen *et al.*, 2004), are in short supply because these landscapes make poor habitats for pollinator populations (Kremen *et al.*, 2002). To ensure provision the continued provision of

ecosystem services and curb biodiversity loss, effective restoration of pollinators and their interactions in agricultural landscapes is critical.

To promote pollinator services in agriculture, farmers are increasingly turning to the habitat restoration technique of planting strips of native plants along farm edges (hedgerows) to help provide habitat for pollinators without removing arable land from production. Hedgerows have been shown to augment the richness, abundance and trait diversity of pollinators in agricultural landscapes (Morandin & Kremen, 2013; M’Gonigle *et al.*, 2015; Kremen & M’Gonigle, 2015; Ponisio *et al.*, 2015). In addition, hedgerows promote the persistence and colonization of floral resource specialists (M’Gonigle *et al.*, 2015). Little is known however, about the assembly of the network following hedgerow restoration.

Using a long-term data-set of plant-pollinator communities assembling following hedgerow restoration in the highly simplified and intensively managed agricultural landscape of California’s Central Valley, we explore the process of network development. We first determine whether the mechanism underlying network assembly is a smooth build up of interactions as would be predicted by preferential attachment, or punctuated by significant reorganizations of interactions (i.e., changing points). Even with changing points in interaction organization, networks could still be assembling via preferential attachment if the network reorganizations were primarily driven by peripheral, temporally variable species while a stable, well-connected core of species still persists. We thus examine whether the species are most variable in their network position — and thus important contributors to network reorganizations — are less persistent and connected species. Lastly, we examine whether networks are assembling toward predictable interaction patterns, and the ramifications for the robustness of the networks to species extinction and cascading perturbations.

Materials & Methods

Study sites and collection methods

We surveyed plant-pollinator interaction networks of assembling hedgerows (N=5), as well as in two types of non-assembling communities to serve as controls: unrestored, weedy field margins (N=19) and established hedgerows (greater than 10 years since planting, N=29). The sites were located in the Central Valley of California in Yolo, Colusa and Solano Counties. This area is comprised of intensively managed agriculture – primarily monocultures of conventional row crops, vineyards and orchards. Hedgerows we planted along field margins where they do not remove valuable land from production, and are ca. 3–6m wide and approximately 350m long and border large (ca. 30–hectare) crop fields. Hedgerows consist of native, perennial, shrub and tree plantings including *Rosa californica*, *Cercis occidentalis*, *Ceanothus spp.*, *Heteromeles arbutifolia*, *Sambucus mexicana*, *Eriogonum spp.*, *Baccharis spp.*, *Salvia spp.* and others (Kremen & M’Gonigle, 2015; M’Gonigle *et al.*, 2015). The mean distance between monitoring sites was 15 km, and the minimum distance between sites of the same type sampled in the same year was 2 km. The entire area surveyed spanned almost 300 km². The crop fields adjacent to all sites were similarly managed as intensive, high-input monoculture.

Monitoring began in 2006 and continued through 2015. Sampling of the assembling hedgerows began the year before the area was restored. For logistical reasons, no sampling of assembling hedgerows was conducted in 2010. Sites were sampled between two and five times per year (Tables S1-S3). In each round of sampling, the order in which sites were sampled was randomized. Surveys were conducted under sunny conditions when the temperature was above 21°C and wind speed was below 2.5 meters/second.

Flower-visitors to plants in hedgerows and unrestored controls were netted for one hour of active search time (the timer was paused when handling specimens). Honeybees (*Apis mellifera*) were

not collected because their abundance is determined largely by the placement of hives throughout the region by bee-keepers. 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 (representing 49 and 19 percent of records, respectively), the most abundant and effective pollinators in the system (C. Kremen, A. Klein and L. Morandin, unpublished data). Bee and syrphid specimens were identified to species (or morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*) by expert taxonomists.

Quantitative networks were generative for each site through time. To account for the unequal number of surveys between years, the mean of the interactions between a pair of plants and pollinators across surveys within a year was used as a representation of the frequency of interactions.

Change point analysis

Identifying change points

We employed a change point detection method (Peel & Clauset, 2014) to identify fundamental changes in large-scale pattern of interactions of plants and pollinators. A change point is caused by a merge, split, fragmentation or formation of communities (also called modules or compartments). Change point detection methods have yet to be generalized to quantitative networks, so for this analysis we focused on qualitative (binary) networks. Following Peel & Clauset (2014), we first defined a probability distribution over the networks using the generalized hierarchical random graph model (GHRG). The GHRG model is able to capture both assortative and disassortative community structure patterns at all scales in the network (Peel & Clauset, 2014). A network G is composed of vertices V and edges $E \subseteq VV$. The GHRG model decomposes the N vertices into a series of nested groups, the relationships among which are represented by the dendrogram T . The tips of T are the vertices of G , and the probability that two vertices u and v connect is given by the

parameter p_r . The probability distribution of the network G thus defined as:

$$P(G|T, p_r) = p_r^{E_r} (1 - p_r)^{N_r - E_r} \quad (1)$$

Where E_r is the observed number of edges between vertices with the common ancestor r , and N_r is the total possible edges.

Using Bayesian posterior inference and techniques from phylogenetic tree reconstruction, we fit the GHRG model to the networks (Peel & Clauset, 2014). This is accomplished by using a Markov Chain Monte Carlo (MCMC) procedure to first sample the posterior distribution of bipartitions, from which a consensus tree is derived (Peel & Clauset, 2014). We used β distributions with the hyperparameters $\alpha = \beta = 1$ to define priors for p_r .

Once the GHRG model has been fit to the networks, we determine whether a change point occurred between two time slices. To detect a change point, we compare the fit of two models – one where a change point had occurred between two networks, and one where no change occurred – using posterior Bayes factors. We chose a sliding window of length, w , of four, within which to find change points. Larger windows allow for more gradual changes, and four was the maximum possible with our maximum of nine years of data. Lastly, to calculate a p -value for the Bayes factors, we use parametric bootstrapping to numerically estimate the null distribution (Peel & Clauset, 2014). The change point analysis was carried out using code published online by L. Peel. Analyses we conducted in Python 3.4.

We next test whether the change points occurring in maturing hedgerows were a component of the assembly process or a product of environmental shifts that lead to network reorganizations in all types of communities. We model the number of change points as successes and the total number of years each site was sampled as trials, and use a generalized linear model with Binomial error to test whether the probability of a change point occurring varied by site type. For the non-assembling

hedgerows and weedy field margins, only sites with five or greater years of sampling was included in this analysis. All statistical analysis were conducted in R 3.2.3 (R Core Team, 2015).

Characteristics of species that contribute to change points

To further elucidate the nature of the change points, we examine the characteristics of the species that contributed the reorganization of interactions. Some species remain in relatively similar network positions through time, whereas others are more variable in their role and thus contribute more strongly to network reorganization. We test the that more persistent species with the highest degree are the most stable in their network position, as would be expected is the networks were assembling via preferential attachment.

We calculate species persistence as the proportion of the surveys a pollinator was observed. Species observed consistently within and between years are thus maximally persistent. Weighted species degree is calculated from interaction observations observed in more extensive data-set from Yolo County (approx. 18000 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.*, 2015). To represent the the variability of species within networks, we computed the coefficient of variation of weighted closeness at each site through time. Closeness describes the centrality of a species in the network by calculating path lengths to other vertices (species) in the graph. We used linear mixed models to test whether the variability of species closeness values was related to the persistence or degree of that species (Bates *et al.*, 2014; Kuznetsova *et al.*, 2014). We included random effects for species, as well as site. We focused on the pollinator species because the hedgerow flowers are planted and thus are not directly assembling. Because degree and persistence were strongly correlated, ($\rho = 0.84$, $p\text{-value} < 2 * 10^{-16}$), each explanatory variable was included in the model separately. Because a linear increase in closeness, as might be expected with assembly by preferential attachment, would lead to a high variability in closeness

scores, we also test whether closeness increases through time.

Temporal changes in interaction patterns

Network structure

Any changing points in network structure may contribute to the reorganization of the assembling networks into predictable interaction patterns. Pollination networks exhibit two main structural patterns — modularity (e.g., Olesen *et al.*, 2007) and nestedness (e.g., Bascompte *et al.*, 2006, 2003). In modular networks, interactions are insular, occurring within separate groups or “modules” more often than between modules. Communities in the network may fragment as the network assembles, enhancing modularity. Conversely, nested networks are like pyramid of interactions, where there are some species that interact with many species, other species that interact with a subset of those species, and so on. If species entering the network tend to interact with the generalist base of the network pyramid (i.e., via preferential attachment), nestedness would increase through time. Lastly, if the network is accumulating specialist species or species are beginning to limit their interaction niche breadth as the network assembles, this would lead to an increase in the network-level specialization (Blüthgen *et al.*, 2006). To test whether network modularity, nestedness or specialization 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.

We use NODF (weighted or unweighted) to evaluate network nestedness (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 use a hierarchical clustering algorithm (Newman & Girvan, 2004; Csardi & Nepusz, 2006). We

calculated standardized z-scores so that nestedness and modularity metrics could be compared between communities. The z-scores were calculated by generating an ensemble of 999 randomly 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 random communities, we reshuffled the interactions between species but fixed the total number of interactions, species and the distribution of the interaction frequencies (Galeano *et al.*, 2009). Lastly, Network specialization was measured using H2, which estimate 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). It ranges from 0 for generalized networks to 1 for specialized networks.

Network robustness

Lastly, we test the changes in interaction patterns associated with network assembly affect the robustness of the network to species loss and to cascading effects. Following Memmott *et al.* (2004), we simulate the extinction of plant species the subsequent extinction cascades of pollinator species. Because the reproduction of plant species if facilitated by active restoration efforts, it is unlikely the extinction of pollinators 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. Plants species were eliminated based on their degree or abundance, and the number of pollinators that secondarily went extinct is calculated. The area below the extinction curve is used as a measure of network robustness (Dormann *et al.*, 2008).

We also explored how the robustness to cascading effects changed as community assembled, using algebraic connectivity — the second smallest eigenvalue of the Laplacian matrix (Fiedler, 1973) — as a proxy for network robustness (Gaiarsa *et al.*, submitted). Algebraic connectivity is related to the mean diameter of a graph and to how difficult it is to turn a network into completely dis-

connected groups of nodes, or species (Costa *et al.*, 2007) — the larger the algebraic connectivity, the more robust a network is to cascading effects (Gaiarsa et al., submitted), and the harder it is to break the community into isolated groups of species.

Results

Over eight years and 747 samples, we collected and identified 19,547 wild bees and syrphids comprising 173 species from 50 genera. We observed 1,521 unique interactions between plants and pollinators.

Change point analysis

Identifying change points

The majority (76%) of the sites tests underwent at least one significant reorganization of interactions (Fig. 1). All five of the assembling hedgerows experienced changing points, whereas only 40% and 81% of non-assembling hedgerows and field margins, respectively, underwent significant interaction reorganizations. Assembling hedgerows experienced significantly more changing points than the non-assembling networks (difference in the odds ratios between assembling and non-assembling networks, 3.316, 95% CI [1.314, 8.572], p -value= 0.0117). Network assembly following restoration is thus punctuated by more interaction reorganizations than would be expected by environmental shifts that would effect assembling and non-assembling networks equally.

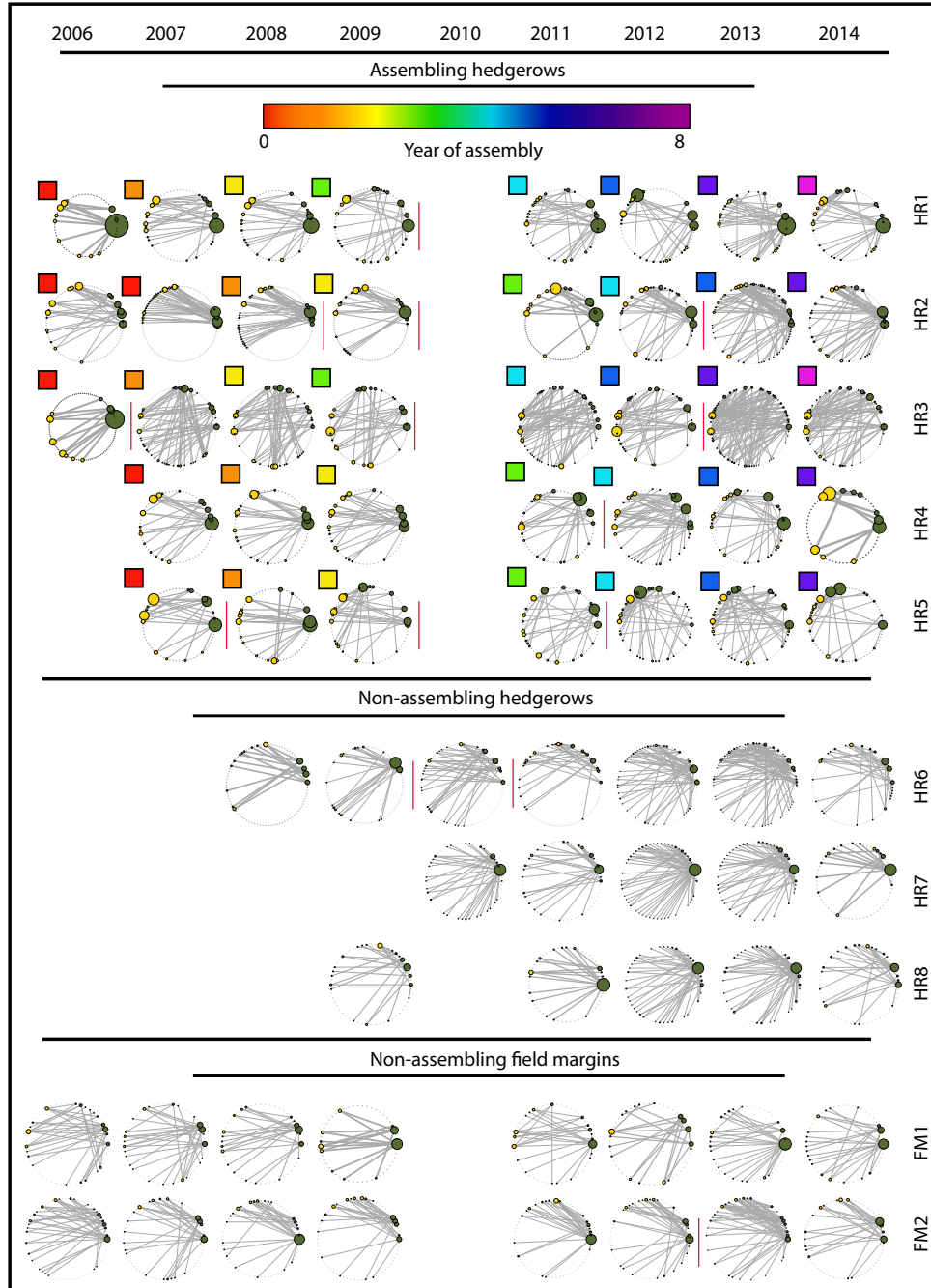


Figure 1: The network structure and changing points (vertical red lines) in assembling hedgerows and a representative sample of non-assembling hedgerows and weedy field margins. In each network, plants and pollinators are represented by green and yellow circles, respectively, weighted by their degree. Each species has a consistent position in the network across years. In the assembling hedgerows, colored squares in the corner of each network represent the years post restoration.

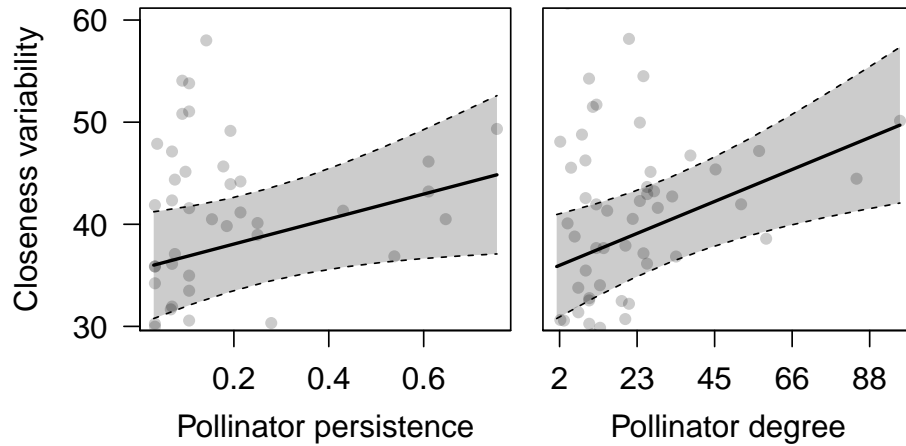


Figure 2: The coefficient of variation of network position, as represented by closeness, plotted against pollinator persistence and degree. Points represents means for each species across sites. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

Characteristics of species that contribute to change points

In contradiction to the predictions of assembly by preferential attachment, both pollinator persistence and degree were positively related to network position variability. (ADD STATS IF KEEP-ING RESULT).

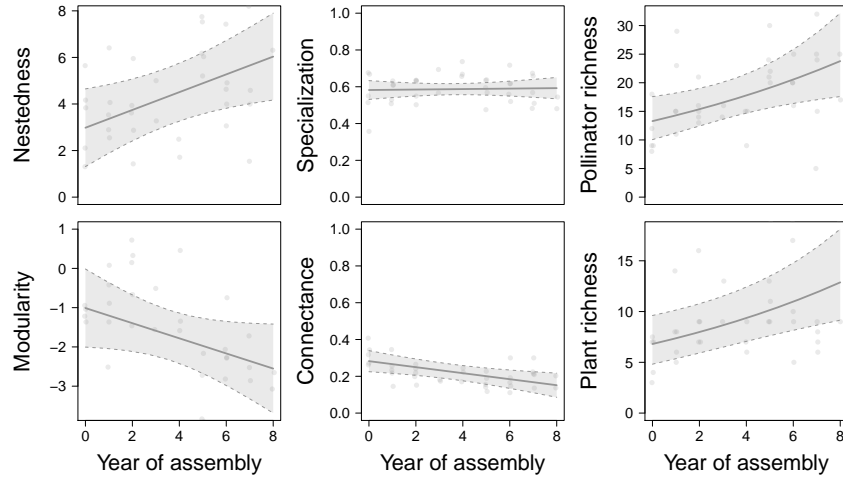


Figure 3: The change in nestedness, modularity, specialization and connectance as the networks assemble. The left panels represent z-scores. Scores greater than ~ 2 or less than ~ -2 are significantly more or less structured than randomly assembled networks. Points are the value for each site at each year of assembly. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

Temporal changes in interaction patterns

Network structure

Network nestedness significantly increased with assembly (estimate of the slope of nestedness through time \pm standard error of the estimate, 1.834 ± 0.6142 , p -value=0.022, Fig. 3). Modularity decreased (Fig. 3), though the slope was not significantly different from zero (estimate of the slope of modularity through time \pm standard error of the estimate, -0.524 ± 0.295 , p -value=0.124). Specialization remained relatively constant (estimate of the slope of specialization through time \pm standard error of the estimate, 0.003 ± 0.015 , p -value=0.827).

Network robustness

Assembly did not effect the robustness of the networks to species extinction when species where removed incrementally by degree (estimate of the slope of robustness through time \pm standard error of the estimate, $6 * 10^{-5} \pm 4 * 10^{-3}$, p -value=0.987) or abundance (0.001 ± 0.003 , p -value=0.65, Fig. 4).

In contrast, the robustness of networks to cascading perturbations, as measured by the algebraic connectivity of the network, increased as the network assembled (estimate of the slope of robustness through time \pm standard error of the estimate, 0.6814 ± 0.272 , p -value=0.042, Fig. 4).

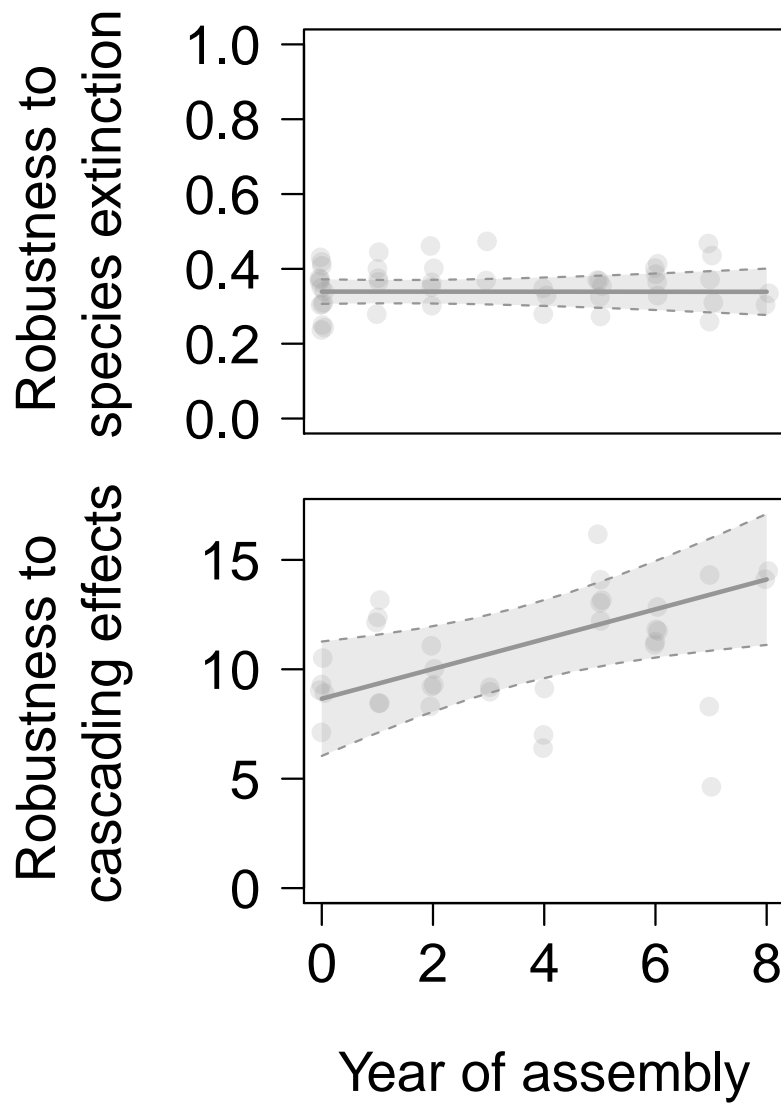


Figure 4: The robustness of networks to species extinction and to cascading effects. The robustness to species extinction is measured by incrementally removing species by degree, through removing species by abundance did not yield qualitatively different results. The robustness of networks to cascading effects is measured as the algebraic connectivity, the second smallest eigenvalue of the Laplacian matrix. Points are the value for each site at each year of assembly. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

Discussion

We show that the temporal assembly of plant-pollinator networks following restoration is a highly dynamic process where interactions often undergo significant reorganizations. These network organizations are unlikely to be a product of environmental forces alone because the network changing points in non-assembling communities are less frequent, and there are few consistent trends in when change points occurred across all sites. Several sites had changing points between year 2009 and 2011 (Fig. 1). In California, 2011 marked the beginning of a multi-year drought. In the assembling hedgerows were not sampled in 2010, so disentangling whether the changing points are due to skipping a year of assembly or the drought is not possible. Interestingly, most of the assembling hedgerows did not undergo a significant reorganization of interactions immediately the hedgerow was planted (i.e., the transition from weedy field margin to hedgerow). This result is consistent with the finding that in our study system, hedgerow restoration takes several years to have a significant impact on the plant-pollinator communities (Kremen and M’Gonigle, in prep).

Given that several changing points in network organization occurred during assembling, we next explored the species most likely responsible for the observed shifts in interaction patterns. Based on a preferential attachment-like mechanism, we expect that the most persistent and high degree species would remain stable in the network core during assembly, and would thus contribute the least to the changing points in network organization. Surprisingly however, we encountered the opposite: the species that were most variable in their network position and thus contributed most to network reorganizations were species with the highest degrees (i.e., most generalized) and persistence. For example, the five most ubiquitous species in our study landscape — *Halictus ligatus*, *Halictus tripartitus*, *Lasioglossum (Dialictus) incompletum*, and *Toxomerus marginatus* — were the only species that changed what module (i.e., community), and they were also present in across years in all of the assembling hedgerows. Because species degree and persistence were strongly correlated, it is difficult to disentangle the causal mechanism for why species with those

characteristics are so variable in their network position. Generalized species may be able to better exploit the limited floral resources the intensively managed agriculture landscape, and thus also most persistent. More persistent species also have longer phenologies, so they have the opportunity to visit many different flowers, resulting in a higher degree. Either way, our result suggests that adaptable species can change their network position to utilize the most advantageous floral resources available, which may depend on the other pollinator species that are present and the state of the floral resource. Thus given the opportunity and ability to use different resources, species will often change their network positions.

Given the regional species pool it is possible that specialization might be constant either because species are not changing through time, or because there is a species turnover, but new species have the same role/position as the species there are absent in the following time step. We found that node turnover was higher in assembling and non-assembling hedgerows when compared to field margin, but there was no difference between them. Thus, maybe looking just at network level metrics, such as nestedness and modularity, when exploring the temporal assembly of ecological networks might be misleading, given that there is a node turnover happening at the species level.

The frequent changing points in network organization, dynamic nature of the location of species in networks, and turnover of species and nodes all point to an assembly mechanism other than preferential attachment. Nestedness did increase with years post restoration, as would be expected if colonizing, specialist species attached to a central, generalist core Albrecht *et al.* (2010). With preferential attachment, however, we would also expect connectance and specialization to increase, and we found no such trends. The stable level of network-level specialization through the assembly process may be due to the increased colonization of specialized species (M'Gonigle *et al.*, 2015) accompanied by an increase in the diet breadth of resident species. This would be expected if resident species were able to minimize their foraging time by expanding their diet breadth as plant

diversity increases with hedgerow maturation (Waser *et al.*, 1996; Pyke, 1984; Blüthgen *et al.*, 2007; Albrecht *et al.*, 2010). Such a change in pollinator behavior would also explain the increase in network nestedness.

The changes in network patterns with assembly also increased the robustness of the networks to cascading perturbations – providing further evidence that hedgerows are valuable tool for promoting species conservation and ecosystem provision in agricultural areas (M’Gonigle *et al.*, 2015; Ponisio *et al.*, 2015; Kremen & M’Gonigle, 2015). Because the vulnerability of the network to cascading effects, as measured by algebraic connectivity, is correlated with species richness, the increase in plant and pollinator richness following restoration is at least partially responsible for enhancing network robustness to cascading effects. The relationship between diversity and stability in networks has been the subject of considerable debate (e.g., May, 1972; Pimm, 1984; Montoya *et al.*, 2006). Our results provides one of the few empirical examples of how restoring species diversity contributes to enhancing network stability. Through these hedgerows were designed to promote floral resources across the growing season and not specifically to promote any specific network properties (Menz *et al.*, 2010), the pollinators assembled into resilient interaction patterns. With prior knowledge of the floral preferences of pollinators, future restoration efforts may also be able to incorporate promoting network stability into planning efforts (?)

Interestingly, however, the robustness of hedgerow communities to species loss did not change with assembly. This is particularly surprising given the observed increase in nestedness, which is often associated with an enhanced robustness to extinction (Memmott *et al.*, 2004). It may be that assembling hedgerows have not yet reached a sufficient level of nestedness to realize its benefits. Nestedness of the assembling hedgerows, however, did not asymptote within the eight years following restoration that the sites were surveyed, so hedgerow networks may eventually reach sufficient levels of nestedness to gain the robustness advantage.

Plant-pollinator networks in general are highly dynamic, with high turnover of species and inter-

actions both within and between seasons (Burkle & Alarcón, 2011). Though our non-assembling communities experience fewer network reorganizations than the assembling hedgerows, 82% of field margins and 40% of mature hedgerows underwent at least one changing point in network structure. Pollinators are also highly opportunistic (Petanidou *et al.*, 2008; Vázquez, 2005; Albrecht *et al.*, 2010), though trait complementarity such as tongue length and corolla depth impose some biophysical limits to the interactions between plants and pollinators (Vázquez *et al.*, 2009; Vázquez *et al.*, 2009; Stang *et al.*, 2009, 2006; Santamaría & Rodríguez-Gironés, 2007). Such opportunism may buffer plant-pollinator communities from global change (e.g., Ramos-Jiliberto *et al.*, 2012; Kaiser-Bunbury *et al.*, 2010), but our limited understanding of the assembly of these communities impedes making such predictions (Vázquez *et al.*, 2009; Burkle & Alarcón, 2011). Unlike in the broader food web literature, we have few mechanistic models of mutualistic network assembly (Valdovinos *et al.*, 2013). In addition, the few that have been developed often borrow their mechanisms from competitive interactions, leading to inaccurate biological assumptions (Holland *et al.*, 2006). We need further development of mechanistic models of mutualistic system to generate testable predictions, along with empirical exploration of network assembly. Plant-pollinator communities and mutualisms in general are vital for the maintenance of biodiversity and the provision of essential ecosystem services. We must therefore understand the processes underlying their assembly to facilitate restoration and conservation.

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References

- Alarcón, R., Waser, N.M. & Ollerton, J. (2008). Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos*, 117, 1796–1807.
- Albrecht, M., Riesen, M. & Schmid, B. (2010). Plant–pollinator network assembly along the chronosequence of a glacier foreland. *Oikos*, 119, 1610–1624.
- Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Loyola, R.D. & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117, 1227–1239.
- Barabási, A.L. & Albert, R. (1999). Emergence of scaling in random networks. *science*, 286, 509–512.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C. *et al.* (2011). Has the earth’s sixth mass extinction already arrived? *Nature*, 471, 51–57.
- Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci. USA*, 100, 9383–9387.

- 377 Bascompte, J., Jordano, P. & Olesen, J.M. (2006). Asymmetric coevolutionary networks facilitate
378 biodiversity maintenance. *Science*, 312, 431–433.
- 379 Bascompte, J. & Stouffer, D.B. (2009). The assembly and disassembly of ecological networks.
380 *Phil. Trans. R. Soc. B*, 364, 1781.
- 381 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). *lme4: Linear mixed-effects models using*
382 *Eigen and S4*. R package version 1.1-7.
- 383 Blüthgen, N., Menzel, F. & Blüthgen, N. (2006). Measuring specialization in species interaction
384 networks. *BMC Ecol.*, 6, 9.
- 385 Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B. & Blüthgen, N. (2007). Specialization, con-
386 straints, and conflicting interests in mutualistic networks. *Curr. Biol.*, 17, 341–346.
- 387 Burkle, L.A. & Alarcón, R. (2011). The future of plant-pollinator diversity: Understanding in-
388 teraction networks across time, space, and global change. *American Journal of Botany*, 98,
389 528.
- 390 Costa, L.d.F., Rodrigues, F.A., Travieso, G. & Villas Boas, P.R. (2007). Characterization of com-
391 plex networks: A survey of measurements. *Advances in physics*, 56, 167–242.
- 392 Csardi, G. & Nepusz, T. (2006). The igraph software package for complex network research.
393 *InterJournal, Complex Systems*, 1695.
- 394 De Abreu, N.M.M. (2007). Old and new results on algebraic connectivity of graphs. *Linear*
395 *algebra and its applications*, 423, 53–73.
- 396 Devoto, M., Bailey, S., Craze, P. & Memmott, J. (2012). Understanding and planning ecological
397 restoration of plant–pollinator networks. *Ecology letters*, 15, 319–328.

- Díaz-Castelazo, C., Guimaraes Jr, P.R., Jordano, P., Thompson, J.N., Marquis, R.J. & Rico-Gray, V. (2010). Changes of a mutualistic network over time: reanalysis over a 10-year period. *Ecology*, 91, 793–801.
- Dormann, C., Gruber, B. & Fründ, J. (2008). Introducing the bipartite package: analysing ecological networks. *R News*, 8, 8.
- Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P. & Sodhi, N.S. (2009). The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society of London B: Biological Sciences*, 276, 3037–3045.
- van Engelsdorp, D., Evans, J., Saegerman, C., Mullin, C., Haubruge, E., Nguyen, B., Frazier, M., Frazier, J., Cox-Foster, D., Chen, Y., Underwood, R., Tarpy, D. & Pettis, J. (2009). Colony collapse disorder: A descriptive study. *Plos One*, 4, 1–17.
- Fang, Q. & Huang, S.Q. (2012). Relative stability of core groups in pollination networks in a biodiversity hotspot over four years. *PloS one*, 7, e32663.
- Fiedler, M. (1973). Algebraic connectivity of graphs. *Czechoslovak mathematical journal*, 23, 298–305.
- Forup, M., Henson, K., Craze, P. & Memmott, J. (2008a). The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. *J. Appl. Ecol.*, 45, 742–752.
- Forup, M.L., Henson, K.S., Craze, P.G. & Memmott, J. (2008b). The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. *Journal of Applied Ecology*, 45, 742–752.
- Galeano, J., Pastor, J.M. & Iriando, J.M. (2009). Weighted-interaction nestedness estimator (wine): a new estimator to calculate over frequency matrices. *Environmental Modeling & Software*, 24, 1342–1346.

421 Holland, J.N., Okuyama, T. & DeAngelis, D.L. (2006). Comment on asymmetric coevolutionary
 422 networks facilitate biodiversity maintenance. *Science*, 313, 1887b–1887b.

423 Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B. & Caflisch, A. (2010). The robustness
 424 of pollination networks to the loss of species and interactions: a quantitative approach incorpo-
 425 rating pollinator behaviour. *Ecology Letters*, 13, 442–452.

426 Klein, A., Vaissière, B., Cane, J., Steffan-Dewenter, I., Cunningham, S., Kremen, C. & Tscharntke,
 427 T. (2007). Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B*,
 428 274, 303–313.

429 Kremen, C. (2008). *Bee Pollinators in Agricultural Ecosystems*, New York: Oxford University
 430 Press, chap. Crop Pollination Services From Wild Bees, pp. 10–26.

431 Kremen, C. & M’Gonigle, L.K. (2015). Small-scale restoration in intensive agricultural landscapes
 432 supports more specialized and less mobile pollinator species. *J. Appl. Ecol.*, 52, 602–610.

433 Kremen, C., Williams, N., Bugg, R., Fay, J. & Thorp, R. (2004). The area requirements of an
 434 ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.*, 7,
 435 1109–1119.

436 Kremen, C., Williams, N. & Thorp, R. (2002). Crop pollination from native bees at risk from
 437 agricultural intensification. *Proc. Natl. Acad. Sci. U.S.A.*, 99, 16812–16816.

438 Kuznetsova, A., Bruun Brockhoff, P. & Haubo Bojesen Christensen, R. (2014). *lmerTest: Tests*
 439 *for random and fixed effects for linear mixed effect models (lmer objects of lme4 package)*. R
 440 package version 2.0-11.

441 May, R.M. (1972). Will a large complex system be stable? *Nature*, 238, 413–414.

442 Memmott, J., Waser, N.M. & Price, M.V. (2004). Tolerance of pollination networks to species
 443 extinctions. *Proc. R. Soc. Lond. B*, 271, 2605–2611.

444 Menz, M., Phillips, R., Winfree, R., Kremen, C., Aizen, M., Johnson, S. & Dixon, K. (2010).
 445 Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms.
 446 *Trends Plant Sci.*, 16, 4–12.

447 M’Gonigle, L., Ponisio, L., Cutler, K. & Kremen, C. (2015). Habitat restoration promotes pollina-
 448 tor persistence and colonization in intensively-managed agriculture. *Ecol. Appl.*, 25, 1557–1565.

449 Mohar, B., Alavi, Y., Chartrand, G. & Oellermann, O. (1991). The laplacian spectrum of graphs.
 450 *Graph theory, combinatorics, and applications*, 2, 12.

451 Montoya, J.M., Pimm, S.L. & Solé, R.V. (2006). Ecological networks and their fragility. *Nature*,
 452 442, 259–264.

453 Morandin, L. & Kremen, C. (2013). Hedgerow restoration promotes pollinator populations and
 454 exports native bees to adjacent fields. *Ecol. Appl.*, 23, 829–839.

455 Neumann, P. & Carreck, N.L. (2010). Honey bee colony losses. *J. Api. Res.*, 49, 1–6.

456 Newman, M.E.J. & Girvan, M. (2004). Finding and evaluating community structure in networks.
 457 *Phys. Rev. E*, 69, 026113.

458 Olesen, J.M., Bascompte, J., Dupont, Y. & Jordano, P. (2007). The modularity of pollination
 459 networks. *Proc. Natl. Acad. Sci. USA*, 104, 19891–19896.

460 Olesen, J.M., Bascompte, J., Elberling, H. & Jordano, P. (2008). Temporal dynamics in a pollina-
 461 tion network. *Ecology*, 89, 1573.

462 Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants are pollinated by
 463 animals? *Oikos*, 120, 321–326.

464 Parker, V.T. (1997). The scale of successional models and restoration objectives. *Restoration*
 465 *ecology*, 5, 301–306.

466 Peel, L. & Clauset, A. (2014). Detecting change points in the large-scale structure of evolving
 467 networks. *arXiv preprint arXiv:1403.0989*.

468 Petanidou, T., Kallimanis, S., Tzanopoulos, J., Sgardelis, S. & Pantis, J. (2008). Long-term ob-
 469 servation of a pollination network: fluctuation in species and interactions, relative invariance of
 470 network structure and implications for estimates of specialization. *Ecol. Lett.*, 11, 564–575.

471 Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326.

472 Ponisio, L.C., M’Gonigle, L.K. & Kremen, C. (2015). On-farm habitat restoration counters biotic
 473 homogenization in intensively managed agriculture. *Global change biology*.

474 Pyke, G.H. (1984). Optimal foraging theory: a critical review. *Annual review of ecology and*
 475 *systematics*, pp. 523–575.

476 R Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation
 477 for Statistical Computing, Vienna, Austria.

478 Ramos-Jiliberto, R., Valdovinos, F.S., Moisset de Espanés, P. & Flores, J.D. (2012). Topological
 479 plasticity increases robustness of mutualistic networks. *Journal of Animal Ecology*, 81, 896–
 480 904.

481 Rezende, E.L., Lavabre, J.E., Guimarães, P.R., Jordano, P. & Bascompte, J. (2007). Non-random
 482 coextinctions in phylogenetically structured mutualistic networks. *Nature*, 448, 925–928.

483 Santamaría, L. & Rodríguez-Gironés, M.A. (2007). Linkage rules for plant–pollinator networks:
 484 Trait complementarity or exploitation barriers? *PLoS Biol.*, 5, e31.

485 Stang, M., Klinkhamer, P., Waser, N.M., Stang, I. & van der, M.E. (2009). Size-specific interaction
 486 patterns and size matching in a plant-pollinator interaction web. *Ann. Bot.*, 103.

- 487 Stang, M., Klinkhamer, P.G. & Van Der Meijden, E. (2006). Size constraints and flower abundance
488 determine the number of interactions in a plant–flower visitor web. *Oikos*, 112, 111–121.
- 489 Valdovinos, F.S., Moisset de Espanés, P., Flores, J.D. & Ramos-Jiliberto, R. (2013). Adaptive
490 foraging allows the maintenance of biodiversity of pollination networks. *Oikos*, 122, 907–917.
- 491 Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P. & Dunne, J.A. (2010). Con-
492 sequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology Letters*,
493 13, 1546–1559.
- 494 Vázquez, D.P. (2005). Degree distribution in plant-animal mutualistic networks: forbidden links
495 or random interactions? *Oikos*, 108, 421–426.
- 496 Vázquez, D.P., Blüthgen, N., Cagnolo, L. & Chacoff, N.P. (2009). Uniting pattern and process in
497 plant-animal mutualistic networks: a review. *Annals of Botany*, 103, 1445–1457.
- 498 Vázquez, D.P., Chacoff, N.P. & Cagnolo, L. (2009). Evaluating multiple determinants of the
499 structure of plant-animal mutualistic networks. *Ecology*, 90, 2039–2046.
- 500 Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. (1996). Generalization in
501 pollination systems, and why it matters. *Ecology*, 77, 1043.
- 502 Winfree, R., Williams, N., Dushoff, J. & Kremen, C. (2007). Native bees provide insurance against
503 ongoing honey bee losses. *Ecol. Lett.*, 10, 1105–1113.