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Major interaction reorganizations punctuate the assembly of pollination networks

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Abstract

The ability of communities to maintain function in the face of species extinction is related to the structure of networks. Understanding network structure and how it relates to network assembly, therefore, is a priority for conservation biology. Using a nine-year-dataset comprising nearly 20,000 pollinator visitation records, we explore the assembly of plant-pollinator communities at native plant restorations in the Central Valley of California. Across years, species are highly dynamic in their network position, causing community assembly to be punctuated by major interaction reorganizations. In contrast, the non-assembling networks did not restructure as frequently. Across all communities, pollinator species were opportunistic in the flowers they visited. The most persistent and generalized species were also the most variable in their network positions, contrary to what is expected through preferential attachment theory. High species and interaction turnover was ubiquitous across assembling and non-assembling communities, though unique interactions turned over at higher rates in assembling hedgerows as the networks continually reorganized. Nestedness of assembling networks also increased through time, but there was no increase in robustness to simulated plant extinctions. The sensitivity of networks to cascading perturbations, however, increased as the communities assembled, at least partially due to accumulating species richness. We elucidate some of the mechanisms underlying plant-pollinator network assembly and restoration, while providing further evidence that hedgerows are a valuable tool for promoting species conservation provision in agricultural areas.

²¹ community assembly, change points, specialization, nestedness, modularity, bipartite, preferential
²² attachment

²³ **Introduction**

²⁴ Global change has created a severe biodiversity crisis, and as species are lost, so are their inter-
²⁵ actions (Dunn *et al.*, 2009; Barnosky *et al.*, 2011). Because mutualistic interactions are essential
²⁶ for maintaining the diversity of their component guilds, these systems are particularly at risk from
²⁷ coextinction cascades. The nature of these cascades will depend on the interaction patterns within
²⁸ a community (Memmott *et al.*, 2004; Rezende *et al.*, 2007; Bascompte & Stouffer, 2009; Thébaud
²⁹ & Fontaine, 2010). To safeguard ecological function, it has become increasingly imperative to aid
³⁰ the recovery of lost interactions and component biodiversity through ecological restoration, and a
³¹ key restoration aim is to facilitate assembly of robust interaction networks (Menz *et al.*, 2010). We
³² know little, however, about how to re-assemble interacting communities through restoration, or the
³³ process of ecological network assembly more generally.

³⁴ Preferential attachment, the most widely explored mechanism of network assembly, (Barabási &
³⁵ Albert, 1999), predicts that species entering a network are more likely to interact with species that
³⁶ are already well-connected ("the rich-get-richer" principle, Barabási & Albert, 1999). In pollin-
³⁷ nation systems — a particularly ubiquitous mutualism (Ollerton *et al.*, 2011; Klein *et al.*, 2007)
³⁸ — some studies have found support for this assembly mechanism. Investigating the day-to-day,
³⁹ temporal assembly of a plant-pollinator network within a season, Olesen *et al.* (2008) found that
⁴⁰ phenologically new plant and pollinator species tended to interact with already well-connected
⁴¹ species, potentially because these species are either more abundant or more temporally persistent.
⁴² In addition, using a space-for-time substitution to study primary succession along a glacier fore-
⁴³ land, Albrecht *et al.* (2010) also found some evidence that assembly occurred through preferential
⁴⁴ attachment. Specifically, network nestedness (i.e, a core group of generalists interacts with both
⁴⁵ specialist and generalist species) increased as the community aged (Albrecht *et al.*, 2010). An in-
⁴⁶ crease in nestedness could result from the preferential attachment process where specialist species
⁴⁷ attach to the well-connected, generalist core.

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

58 Understanding network assembly is particularly relevant to ecological restoration, which is essen-
59 tially 'applied succession' (e.g., Parker, 1997). In pollination systems, the time since an area was
60 restored has been shown to affect the structure of networks (Forup *et al.*, 2008; Devoto *et al.*, 2012),
61 suggesting interactions are changing as the community develops. Understanding the mechanisms
62 of network assembly will help to guide community restoration. Facilitating network restoration
63 is especially imperative in areas where species interactions provide essential ecosystem services,
64 such as crop pollination. To ensure the continued provision of ecosystem services and curb bio-
65 diversity loss, it is critical to restore pollinators and their interactions in agricultural landscapes.
66 To promote pollinator services in agriculture, farmers may chose to plant strips of native plants
67 along farm edges (hedgerows) to help provide habitat for pollinators without removing arable land
68 from production. Hedgerows augment the richness, abundance and trait diversity of pollinators in
69 agricultural landscapes (Morandin & Kremen, 2013; Kremen & M'Gonigle, 2015; Ponisio *et al.*,
70 2016), and promote the persistence and colonization of floral resource specialists (M'Gonigle *et al.*,
71 2015). It is important to understand how these new species are being incorporated into the network
72 as the community assembles, and the consequences for interaction patterns and robustness.

73 We explore the process of network development using a nine year dataset of plant-pollinator com-
74 munity assembly following hedgerow restoration in the highly simplified and intensively managed
75 agricultural landscape of California's Central Valley. We first determine whether the mechanism
76 underlying network assembly is a build up of interactions as would be predicted by preferential
77 attachment, or instead is punctuated by significant reorganizations of interactions (i.e., network
78 changing points). Even with changing points in interaction organization, networks could still be
79 assembling via preferential attachment if the network reorganizations were primarily driven by pe-
80 ripheral, temporally variable species while a stable, well-connected core of species persist. We test
81 whether the species that are most variable in their network position — and thus important contrib-
82 utors to network reorganizations — are less persistent and connected species. To further explore
83 the mechanisms underlying the temporal dynamics of the networks, we examine patterns in the
84 species and interaction temporal turnover. Lastly, we investigate whether networks are assembling
85 toward predictable interaction patterns, and the ramifications for the robustness of the networks to
86 species extinction and cascading perturbations.

87 Materials & Methods

88 Study sites and collection methods

89 We surveyed plant-pollinator interaction networks of independent assembling hedgerows commu-
90 nities ($N=5$), and of two types of non-assembling communities to serve as controls: unrestored,
91 weedy field margins ($N=19$) and mature hedgerows (greater than 10 years since planting, $N=29$).
92 The sites were located in the Central Valley of California in Yolo, Colusa and Solano Counties.
93 This area is composed of intensively managed agriculture — primarily monocultures of conven-
94 tional row crops, vineyards and orchards. Hedgerows are ca. 3–6 m wide and approximately 350
95 m long, bordering large (ca. 30-hectare) crop fields. Hedgerows consist of native, perennial, shrub

96 and tree plantings including *Rosa californica*, *Cercis occidentalis*, *Ceanothus spp.*, *Heteromeles*
97 *arbutifolia*, *Sambucus mexicana*, *Eriogonum spp.*, *Baccharis spp.*, *Salvia spp.* and others (Fig. S1
98 Menz *et al.*, 2010; Kremen & M’Gonigle, 2015; M’Gonigle *et al.*, 2015). The mean distance be-
99 tween monitoring sites was 15 km, and the minimum distance between sites sampled in the same
100 year was 1 km. The entire area surveyed spanned almost 300 km². The crop fields adjacent to all
101 sites were similarly managed as intensive, high-input monoculture.

102 Monitoring of assembling hedgerows began in 2006 and continued through 2014. Surveys of
103 these sites began the year before the area was restored. For logistical reasons, no sampling of
104 assembling hedgerows was conducted in 2010. Sites were sampled between two and five times per
105 year (Tables S1-S3, mean 3.4 samples per year). In each round of sampling, the order in which
106 sites were sampled was randomized. Surveys were conducted under sunny conditions when the
107 temperature was above 21°C and wind speed was below 2.5 meters/second.

108 Flower-visitors to plants in hedgerows and unrestored controls were netted for one hour of active
109 search time (the timer was paused when handling specimens). Honeybees (*Apis mellifera*) were
110 not collected because their abundance is determined largely by hive placement by bee-keepers.
111 All other insect flower visitors that touched the reproductive parts of the flower were collected;
112 however, here we focus only on wild bees and syrphids — the most abundant and effective polli-
113 nators in the system (representing 49 and 19 percent of records, respectively, C. Kremen, A. Klein
114 and L. Morandin, unpublished data). Bee and syrphid specimens were identified to species (or
115 morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*) by expert tax-
116 onomists.

117 Quantitative networks were generated for each site through time. To account for the unequal
118 number of surveys between years (Tables S1-S3), we use the mean of the interactions between a
119 pair of plants and pollinators across surveys within a year to represent interaction frequency.

120 **Change point analysis**

121 **Identifying change points**

122 We employed a change point detection method (Peel & Clauset, 2014) to identify fundamental
123 reorganizations in large-scale interaction patterns. A change point is caused by a merge, split, frag-
124 mentation or formation of modules (also called compartments). Change point detection methods
125 have yet to be generalized to quantitative networks, so for this analysis we focused on qualitative
126 (binary) networks. Following Peel & Clauset (2014), we first defined a probability distribution
127 over the networks using the generalized hierarchical random graph model (GHRG). The GHRG
128 model is able to capture both assortative and disassortative structure patterns at all scales in the
129 network (Peel & Clauset, 2014). A network G is composed of vertices V and edges E . The GHRG
130 model decomposes the N vertices into a series of nested groups, the relationships among which are
131 represented by the dendrogram T . The tips of T are the vertices of G , and the probability that two
132 vertices u and v connect is given by the parameter p_r . The probability distribution of the network
133 G is thus defined as:

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

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

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

¹⁴¹ Once the GHRG model has been fit to the networks, we determine whether a change point occurred
¹⁴² between two time slices. To detect a change point, we use Bayes factors to compare the fit of
¹⁴³ two models — one where a change point occurred between two networks, and one where no
¹⁴⁴ change occurred. We chose a sliding window of length, w , of four, within which to find change
¹⁴⁵ points. Larger windows allow for more gradual changes, and four was the maximum possible with
¹⁴⁶ our eight years of data. Lastly, to calculate a p -value for the Bayes factors, we use parametric
¹⁴⁷ bootstrapping to numerically estimate the null distribution (Peel & Clauset, 2014). We employed
¹⁴⁸ code published online by L. Peel for the change point analysis. Analyses were conducted in Python
¹⁴⁹ 3.4.

¹⁵⁰ We next test whether the change points occurring in maturing hedgerows were a component of
¹⁵¹ the assembly process or a product of environmental shifts that lead to network reorganizations
¹⁵² in all types of communities. We model the number of change points as successes and the total
¹⁵³ number of years each site was sampled as trials, and use a generalized linear model with Binomial
¹⁵⁴ error to test whether the probability of a change point occurring varied by site type. We used
¹⁵⁵ standard techniques to determine whether the assumptions of the models were met for this and all
¹⁵⁶ subsequent models. For the non-assembling hedgerows and weedy field margins, only sites with
¹⁵⁷ five or greater survey years were included in this analysis ($N=11$). All statistical analyses were
¹⁵⁸ conducted in R 3.2.3 (R Core Team, 2015).

¹⁵⁹ **Characteristics of species that contribute to change points**

¹⁶⁰ To further elucidate the nature of the change points, we examine the characteristics of the species
¹⁶¹ that contributed to interaction reorganization. Some species remain in relatively similar network
¹⁶² positions through time, whereas others are more variable in their position and thus contribute more
¹⁶³ strongly to network reorganization. We test whether the more persistent species with the highest
¹⁶⁴ degree (number of different interaction partners) are the most stable in their network positions, as

¹⁶⁵ would be expected if the networks were assembling via preferential attachment.

¹⁶⁶ We calculate species persistence as the proportion of surveys in which a plant or pollinator is ob-
¹⁶⁷ served. Species observed consistently within and between years are thus maximally persistent.
¹⁶⁸ Weighted species degree is calculated from interaction observations from an extensive dataset
¹⁶⁹ from Yolo County (approx. 18000 interaction records) that included both the data included in
¹⁷⁰ this study and additional data from sites where we collected flower visitors using the same meth-
¹⁷¹ ods (M'Gonigle *et al.*, 2015; Ponisio *et al.*, 2016). To represent network position variability, we
¹⁷² computed the coefficient of variation of weighted closeness centrality (Freeman, 1978) at each site
¹⁷³ through time. Closeness centrality represents the importance of a space by calculating the path
¹⁷⁴ lengths to other vertices (species) in the network (Freeman, 1978). The shorter the mean path
¹⁷⁵ length to other species, the higher is the closeness centrality. We use linear mixed models to test
¹⁷⁶ whether the species closeness variability (log) is related to the persistence or degree of that species
¹⁷⁷ (Bates *et al.*, 2014; Kuznetsova *et al.*, 2014). We included random effects for species and site.
¹⁷⁸ Because the degree and persistence of pollinators were strongly correlated, ($\rho = 0.84$, p -value <
¹⁷⁹ $2 * 10^{-16}$), we include each explanatory variable in separate models. Plant degree and persistence
¹⁸⁰ were not significantly correlated, but we use the same models as we did for the pollinators for
¹⁸¹ consistency. Because an approximately logarithmic increase in closeness centrality, as would be
¹⁸² expected with assembly by preferential attachment, would also lead to high variability in closeness
¹⁸³ scores, we also test whether log closeness centrality increases through time.

¹⁸⁴ Species and interaction turnover

¹⁸⁵ Reorganizations of network structure can be the result of species turnover or species changing
¹⁸⁶ their interaction partners (i.e., re-wiring). To better understand the mechanisms underlying the
¹⁸⁷ temporal dynamics of the assembling networks, we examined patterns of species and interac-
¹⁸⁸ tion turnover. For example, assembling networks may have higher rates of pollinator turnover

189 than non-assembling communities because new pollinator species are colonizing and establishing
190 themselves (M'Gonigle *et al.*, 2015). Similarly, because species are turning over and pollinators
191 are trying to maximize their foraging efficiency based on the species present, interactions may
192 turnover more quickly than in established communities. In addition, at assembling hedgerows,
193 plants that are unvisited in early years may appear to “colonize” the networks as they became more
194 attractive resources and establish new interactions with pollinators.

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

211 Though species may turnover across years, some groups of species may essentially replace each
212 other if they fill similar roles in the network, occupying the same network position and interact-
213 ing with similar species. At non-assembling communities, species turnover may overestimate the

214 temporal changes in the networks if the interactions occurring in one year are similar to those in
215 the next year when they are weighted by the similarity of their constituent species (Fig. S2). We
216 develop a method to examine the temporal turnover of interactions with weightings based on their
217 similarity. We followed the algorithm of Ahn *et al.* (2010) to cluster all the interactions (edges)
218 hierarchically across sites and years based on their similarity, and build a dendrogram. The interac-
219 tion similarity is based how many plants and pollinators (vertices) two edges share (Ahn *et al.*, 2010;
220 Kalinka & Tomancak, 2011). The more species edges shared in common, the shorter the branch
221 length between them on the dendrogram. We next calculated the temporal turnover of interactions
222 weighted by their similarity, as approximated by “phylogenetic” distance (Graham & Fine, 2008;
223 Kembel *et al.*, 2010). We then use linear models to test whether the weighted turnover of inter-
224 actions varied between assembling and non-assembling networks (Bates *et al.*, 2014; Kuznetsova
225 *et al.*, 2014).

226 **Temporal changes in interaction patterns**

227 **Network structure**

228 Any changing points in network structure may contribute to the reorganization of the assembling
229 networks into predictable interaction patterns. Pollination networks exhibit two main structural
230 patterns — modularity (e.g., Olesen *et al.*, 2007) and nestedness (e.g., Bascompte *et al.*, 2006,
231 2003). In modular networks, interactions are insular, occurring within separate groups or “mod-
232 ules” more often than between modules. Modules in the network may fragment as the network
233 assembles, enhancing modularity. Conversely, nested networks are like a pyramid of interactions,
234 where there are some species that interact with many species, other species that interact with a
235 subset of those species, and so on. If species entering the network tend to interact with the gener-
236 alist base of the network pyramid as would be expected with preferential attachment, nestedness

would increase through time. The connectance — the proportion of observed out of possible interactions — would decrease as new, specialist species, preferentially attach to the core. Lastly, the overall level of network specialization may change as the community assembles. Network-level specialization will increase if specialist species colonize the network or species begin to limit their interaction niche breadth as the network assembles (Blüthgen *et al.*, 2006).

To evaluate network nestedness, we used the estimator weighted NODF (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 evaluate network specialization 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). It ranges from zero for generalized networks to one for specialized networks. We calculated standardized z-scores so that nestedness, modularity and specialization metrics could be compared across 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 interaction frequency distributions (Galeano *et al.*, 2009).

To test whether network modularity, nestedness, connectance 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. The number of species in a network affects the patterns of interaction possible, so we also examined the change in plant and pollinator species richness through time. We employ generalized linear mixed models with Poisson error to model richness. We scaled explanatory variables.

262 **Network robustness**

263 Lastly, we tested whether the changes in interaction patterns associated with network assembly
264 affect the robustness of the network to species loss and cascading perturbations. Following Mem-
265 mott *et al.* (2004), we simulated plant species extinction and the subsequent extinction cascades
266 of pollinator species. Because the reproduction of plant species is facilitated by active restora-
267 tion efforts, it is unlikely the extinction of pollinator species would affect plant populations in the
268 hedgerows. However, plants ceasing to bloom, for example in response to drought, will likely
269 affect the pollinators that depend on them. We eliminated plants species based on their degree or
270 abundance, and then calculated the number of pollinators that secondarily went extinct. The area
271 below the extinction curve is an estimate of network robustness (Memmott *et al.*, 2004; Dormann
272 *et al.*, 2008).

273 We also explored how the robustness to cascading perturbations changed as the community as-
274 sembled, using algebraic connectivity — the second smallest eigenvalue of the Laplacian matrix
275 (Fiedler, 1973) — as a proxy for network robustness (Gaiarsa *et al.*, in prep). Algebraic connec-
276 tivity relates to how difficult it is to turn a network into completely disconnected groups of species
277 (Costa *et al.*, 2007; Gibert *et al.*, 2013). The larger the algebraic connectivity, the more sensitive
278 a network is to cascading perturbations. Perturbations, such as the decrease in abundance of a
279 plant or pollinator, can have negative consequences for the species in the network. For example,
280 a decrease in abundance of a pollinator will diminish the pollination services it provides to plants.
281 The affected plants would set less seeds, and decrease in abundance the subsequent year. Con-
282 sequently, other pollinators that depended on those plant species would also be affected, and the
283 effects of this perturbation would continue to propagate throughout the network. Alternatively,
284 perturbations could also have a positive effect. For example, the increase in abundance of a plant
285 species would lead to an increase in resource availability for the pollinators. The examples of
286 negative perturbations (e.g., resource collapse, disease spreading, parasites), however, outnumber

287 possible positive perturbations. It is important to note that both robustness and algebraic connec-
288 tivity assume that the network is static. They do not account for the ability of species to alter their
289 interaction depending on circumstances and the resource availability.

290 **Results**

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

294 **Change point analysis**

295 **Identifying change points**

296 The majority (76%) of the sites underwent at least one significant interaction reorganization (Fig. 1,
297 2). All five of the assembling hedgerows experienced network changing points, whereas only 40%
298 and 81% of non-assembling hedgerows and field margins, respectively, underwent significant in-
299 teraction reorganizations. Assembling hedgerows had significantly more changing points than the
300 non-assembling networks (estimate of the difference in the odds ratios between assembling and
301 non-assembling networks, 3.316, 95% CI [1.314, 8.572], p -value= 0.0117). Network assembly
302 following restoration is thus punctuated by more interaction reorganizations than would be ex-
303 pected by environmental shifts alone that would effect all networks similarly.

304 **Characteristics of species that contribute to change points**

305 In contradiction to the predictions of assembly by preferential attachment, both pollinator per-
306 sistence and degree were positively related to network position variability (Fig. 3, estimate of
307 the slope of closeness centrality variability and persistence \pm standard error of the estimate,
308 0.653 ± 0.225 , $p\text{-value}=0.009$; slope of closeness centrality variability and degree, 0.008 ± 0.002 ,
309 $p\text{-value}=0.002$). The slope of these relationships remained significant when the species with the
310 top 10 persistence and degree scores were dropped. In addition, plant persistence and degree were
311 not significantly related to network position variability (Fig. 3). The variability of species net-
312 work position was not the result of closeness linearly increasing through time, and, in fact, plant
313 and pollinator closeness decreased slightly through time (Fig. S2, estimate of the slope of closeness
314 through time \pm SE, pollinators: -0.0003 ± 0.00005 , $p\text{-value}=2.7 * 10^{-12}$; plants -0.007 ± 0.001 ,
315 $p\text{-value}=1.4 * 10^{-6}$). Through statistically significant, the slopes are so slight they may not be bi-
316 ologically significant.

317 **Species and interaction turnover**

318 The rates of plant, pollinator and interaction temporal turnover were similar across assembling
319 hedgerows, non-assembling hedgerows and field margins, though mature hedgerows has marginally
320 significantly less pollinator turnover than field margins (Fig. 4, estimate \pm SE of the difference
321 in turnover between field margins and mature hedgerows, -0.0498 ± 0.026 , $p\text{-value}=0.058$).
322 When interactions where weighted by their similarity, both assembling and mature hedgerows had
323 higher rates of turnover than field margins (Fig. 4, estimate \pm SE of the difference in turnover
324 between field margins and assembling hedgerows, 0.115 ± 0.027 , $p\text{-value}=0.0002$; field mar-
325 gins and mature hedgerows, 0.082 ± 0.024 , $p\text{-value}=0.002$). The weighted interaction turnover
326 at assembling hedgerows, however, was not significantly higher than in non-assembling, mature

327 hedgerows.

328 **Temporal changes in interaction patterns**

329 **Network structure**

330 Network nestedness significantly increased with assembly (Fig. 5, estimate of the slope of nest-
331 edness through time \pm SE, 1.834 ± 0.6142 , p -value=0.022). All of the networks were signifi-
332 cantly nested (z -scores > 2 , Fig. 5). Modularity decreased (Fig. 5), though the slope was not
333 significantly different from zero. In addition, none of the networks were significantly modular
334 (z -scores < 2 , Fig. 5). Connectance decreased as the community assembled (Fig. 5, estimate of
335 the slope of connectance through time \pm standard error of the estimate, -0.0434 ± 0.0152 , p -
336 value=0.03). Specialization also decreased, though the slope was only marginally significantly
337 different from zero (estimate of the slope of specialization through time \pm SE, -0.926 ± 0.450 ,
338 p -value=0.078). Most communities were more generalized than expected when interactions were
339 randomized (Fig. 5).

340 Both plant and pollinator species richness increased through time (Fig. 5, estimate of the slope
341 of richness through time \pm SE, pollinators: 0.193 ± 0.0729 , p -value=0.008; plants: $0.212 \pm$
342 0.0653 , p -value=0.001). Unsurprisingly, pollinator species are colonizing and persisting at the
343 assembling hedgerows. Plant species richness in the networks is based on the flowers actually
344 visited by pollinators and not the presence of a particular plant species at a site. Thus, though
345 some new plant species may establish themselves in the hedgerows, the increase in plant richness
346 in the networks is likely due to previously unvisited plants attracting visitors as they mature and
347 offer better rewards.

³⁴⁸ **Network robustness**

³⁴⁹ Assembly did not effect the robustness of the networks to species extinction when species were re-
³⁵⁰ moved incrementally by degree or abundance. In contrast, the sensitivity of networks to cascading
³⁵¹ perturbations, as measured by the algebraic connectivity of the network, increased as the network
³⁵² assembled (Fig. 6, estimate of the slope of sensitivity to cascading perturbations through time \pm
³⁵³ SE, 0.6814 ± 0.272 , $p\text{-value}=0.042$).

³⁵⁴ **Discussion**

³⁵⁵ We show that the temporal assembly of plant-pollinator networks following restoration is a highly
³⁵⁶ dynamic process where interactions often undergo significant reorganizations, the so called chang-
³⁵⁷ ing points. If these network reorganizations were a product of environmental forces alone, we
³⁵⁸ would expect to observe the same changing points at the same periods, consistently across all
³⁵⁹ sites. However, network changing points in non-assembling communities are less frequent, and
³⁶⁰ there are few consistent trends in when change points occurred across all sites. Several sites had
³⁶¹ network changing points between years 2009 and 2011 (Fig. 1). In California, 2011 marked the
³⁶² beginning of a multi-year drought. The assembling hedgerows were not sampled in 2010, so dis-
³⁶³ entangling whether the changing points are due to skipping a year of monitoring the assembly
³⁶⁴ process or the drought is not possible. Interestingly, most assembling hedgerows did not undergo
³⁶⁵ a significant interaction reorganization immediately after a hedgerow was planted (i.e., the transi-
³⁶⁶ tion from weedy field margin to hedgerow). This result is consistent with the finding that in our
³⁶⁷ study system, hedgerow restoration takes several years to have an impact on the plant-pollinator
³⁶⁸ communities, and with the observation that hedgerows do not begin to produce many flowers until
³⁶⁹ 3–5 years following planting (Kremen and M’Gonigle, in prep).

³⁷⁰ In addition to finding multiple network organization changing points during assembly, the way in

which these reorganizations occur was different from what would be expected from preferential attachment. With a preferential attachment process, we expect that the most persistent and high degree species would remain stable in the network core during assembly (Barabási & Albert, 1999). Surprisingly, however, we encountered the opposite pattern. For example, the four most ubiquitous species in our study landscape — *Halictus ligatus*, *Halictus tripartitus*, *Lasioglossum (Dialictus) incompletum*, and *Toxomerus marginatus* — were the only species that changed which module they were a member in across years in all 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 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). More persistent species usually have longer phenologies, so they can visit many different flowers, resulting in a higher degree (Vázquez *et al.*, 2009; Fort *et al.*, 2016). 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 both the other pollinator species that are present and the state of the plant community (MacLeod *et al.*, 2016; Gómez & Zamora, 2006; Waser *et al.*, 1996). Thus given the opportunity and ability to use different resources, species will often change their network positions (MacLeod *et al.*, 2016).

Interestingly, though assembling hedgerows had more network reorganizations 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 though species and interactions are turning over at the field margins, species and interactions that fill similar roles in the network are replacing each other. In contrast, at the assembling hedgerows, unique interactions are turning over as the networks continually reorganize. Non-assembling mature hedgerow communities, however, had similar rates of weighted interaction turnover as assembling hedgerows but also the

397 lowest pollinator turnover. Pollinator communities at mature hedgerows may be generally more
398 stable, but rare and/or specialized pollinators could generate this pattern if they entered a commu-
399 nity, formed unique interactions with plants that did not previously share pollinators, but did not
400 persist in the networks. These species would not contribute strongly to network reorganization or
401 species turnover, but would enhance weighted interaction turnover. Mature hedgerows may thus
402 both support more stable pollinator communities, while also providing resources for rare and/or
403 specialized species (Kremen & M'Gonigle, 2015; M'Gonigle *et al.*, 2015).

404 When we explore the how network-level interaction patterns changed through time, we found that
405 nestedness did increase as the community assembled, as would be expected if colonizing, specialist
406 species preferentially attached to a central, generalist core (Albrecht *et al.*, 2010). In addition,
407 connectance decreased, as would be expected if the network is being colonized by specialist species
408 and the overall mean number of interactions per species did not change. However, the frequent
409 changing points in network organization, dynamic nature of species positions in the networks, and
410 turnover of species and interactions all point to an assembly mechanism other than preferential
411 attachment. The stable level of network-level specialization through the assembly process may be
412 due to the increased colonization of specialized species (M'Gonigle *et al.*, 2015) accompanied by
413 an increase in the diet breath of resident species. This would be expected if resident species were
414 able to minimize their foraging time by expanding their diet breath as plant diversity increases
415 with hedgerow maturation (Waser *et al.*, 1996; Pyke, 1984; Blüthgen *et al.*, 2007; Albrecht *et al.*,
416 2010). Such a change in pollinator behavior would also explain the increase in network nestedness.
417 Because so many mechanisms give rise to the same patterns of interaction, additional tests are
418 necessary to assess the contribution of different mechanisms to community assembly.

419 Interestingly, however, the changes in network patterns associated with assembly did not effect
420 the robustness of hedgerow communities to species loss. This is particularly surprising given the
421 observed increase in nestedness, which is often associated with an enhanced in robustness to ex-

422 tinction (Memmott *et al.*, 2004). Perhaps assembling hedgerows have yet to reach sufficient levels
423 of nestedness to realize the benefits nestedness confers. Nestedness of the assembling hedgerows,
424 however, did not asymptote within the eight years following restoration that the sites were sur-
425 veyed, so hedgerow networks may eventually reach sufficient levels of nestedness to gain the ro-
426 bustness advantage.

427 Contrary to the general restoration goals, the susceptibility of the networks to cascading pertur-
428 bations increased as the communities assembled. Because network vulnerability to cascading
429 perturbations, as measured by algebraic connectivity, is correlated with species richness, the in-
430 crease in and plant and pollinator richness following restoration is at least partially responsible for
431 the increase in response to cascading effects. Connectance is also positively related to algebraic
432 connectivity (Gibert *et al.*, 2013), but because we observed a decrease in connectance, topological
433 characteristics of the networks beyond species richness and connectance are needed to explain the
434 increased sensitivity to perturbations spreading. These hedgerows were designed to provide flo-
435 ral resources to the largest number of pollinators across the growing season (Menz *et al.*, 2010).
436 The generalized nature of the floral community may explain why the networks tended to be more
437 generalized than expected if interactions were randomly distributed across species (Fig. 5). In ad-
438 dition, the design of the hedgerow plantings may have facilitated the emergence of a single, highly
439 connected module in all of the networks (see 2 for examples). This network configuration results
440 in short path lengths (the distance between species in a network based on their shared partners),
441 and thus, a perturbation in one species can more easily spread to other species. In order to promote
442 more resilient communities, future restoration efforts should explore designing floral communi-
443 ties to promote more interaction partitioning using, for example, algorithms to optimize different
444 network properties based on prior knowledge of pollinator floral preferences (M’Gonigle *et al.*,
445 2016), and on desired network architectures that renders them more robust both to species loss and
446 to cascading effects.

447 Plant-pollinator networks, in general, are highly dynamic, with high turnover of species and inter-
448 actions both within and between seasons (Burkle & Alarcón, 2011). Though our non-assembling
449 communities experience fewer network reorganizations than the assembling hedgerows, 82% of
450 field margins and 40% of mature hedgerows underwent at least one changing point in network
451 structure. Pollinators are also highly opportunistic (Petanidou *et al.*, 2008; Vázquez, 2005; Al-
452 brecht *et al.*, 2010), though trait complementarity such as tongue length and corolla depth impose
453 some biophysical limits to the interactions between plants and pollinators (Vázquez *et al.*, 2009;
454 Vázquez *et al.*, 2009; Stang *et al.*, 2009, 2006; Santamaría & Rodríguez-Gironés, 2007). Such
455 opportunism may buffer plant-pollinator communities from global change (e.g., Ramos-Jiliberto
456 *et al.*, 2012; Kaiser-Bunbury *et al.*, 2010), but our limited understanding of the assembly of these
457 communities impedes making such predictions (Vázquez *et al.*, 2009; Burkle & Alarcón, 2011).
458 Unlike in the broader food web literature, we have few assembly models of mutualistic network as-
459 sembly (Valdovinos *et al.*, 2013; Nuismer *et al.*, 2013; Guimarães *et al.*, 2011). In addition, the few
460 developed models often borrow their mechanisms from competitive interactions, leading to inac-
461 curate biological assumptions (Holland *et al.*, 2006). We need further development of mechanistic
462 models of mutualistic systems to generate testable predictions, along with empirical exploration
463 of network assembly. Plant-pollinator communities and mutualisms broadly are vital for biodi-
464 versity maintenance and essential ecosystem service provision. We must therefore understand the
465 processes underlying their assembly to facilitate restoration and conservation.

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References

- Ahn, Y.Y., Bagrow, J.P. & Lehmann, S. (2010). Link communities reveal multiscale complexity in networks. *Nature*, 466, 761–764.
- 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., Guimaraes, P., Guimaraes, P., Loyola, R. & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117, 1227–1239.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F. *et al.* (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.*, 14, 19–28.

- 491 Barabási, A.L. & Albert, R. (1999). Emergence of scaling in random networks. *Science*, 286,
- 492 509–512.
- 493 Barnosky, A.D., Matzke, N., Tomaia, S., Wogan, G.O., Swartz, B., Quental, T.B., Marshall, C.,
- 494 McGuire, J.L., Lindsey, E.L., Maguire, K.C. *et al.* (2011). Has the earth's sixth mass extinction
- 495 already arrived? *Nature*, 471, 51–57.
- 496 Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). The nested assembly of plant-
- 497 animal mutualistic networks. *Proc. Natl. Acad. Sci. USA*, 100, 9383–9387.
- 498 Bascompte, J., Jordano, P. & Olesen, J.M. (2006). Asymmetric coevolutionary networks facilitate
- 499 biodiversity maintenance. *Science*, 312, 431–433.
- 500 Bascompte, J. & Stouffer, D.B. (2009). The assembly and disassembly of ecological networks.
- 501 *Phil. Trans. R. Soc. B*, 364, 1781.
- 502 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). *lme4: Linear mixed-effects models using*
- 503 *Eigen and S4*. R package version 1.1-7.
- 504 Blüthgen, N., Menzel, F. & Blüthgen, N. (2006). Measuring specialization in species interaction
- 505 networks. *BMC Ecol.*, 6, 9.
- 506 Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B. & Blüthgen, N. (2007). Specialization, con-
- 507 straints, and conflicting interests in mutualistic networks. *Curr. Biol.*, 17, 341–346.
- 508 Burkle, L.A. & Alarcón, R. (2011). The future of plant-pollinator diversity: Understanding inter-
- 509 action networks across time, space, and global change. *Am. J. Bot.*, 98, 528.
- 510 Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.J. (2005). A new statistical approach for
- 511 assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.*, 8,
- 512 148–159.

- 513 Costa, L.d.F., Rodrigues, F.A., Travieso, G. & Villas Boas, P.R. (2007). Characterization of com-
plex networks: A survey of measurements. *Adv. Phys.*, 56, 167–242.
- 515 Csardi, G. & Nepusz, T. (2006). The igraph software package for complex network research.
516 *InterJournal*, p. 1695.
- 517 Devoto, M., Bailey, S., Craze, P. & Memmott, J. (2012). Understanding and planning ecological
518 restoration of plant–pollinator networks. *Ecol. Lett.*, 15, 319–328.
- 519 Díaz-Castelazo, C., Guimarães Jr, P.R., Jordano, P., Thompson, J.N., Marquis, R.J. & Rico-Gray,
520 V. (2010). Changes of a mutualistic network over time: reanalysis over a 10-year period. *Ecol-*
521 *ogy*, 91, 793–801.
- 522 Dormann, C., Gruber, B. & Fründ, J. (2008). Introducing the bipartite package: analysing ecolog-
523 ical networks. *R News*, 8, 8.
- 524 Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P. & Sodhi, N.S. (2009). The sixth mass coex-
525 tinction: are most endangered species parasites and mutualists? *Proc. R. Soc. Lond. B*, 276,
526 3037–3045.
- 527 Fiedler, M. (1973). Algebraic connectivity of graphs. *Czech. Math. J.*, 23, 298–305.
- 528 Fort, H., Vázquez, D.P. & Lan, B.L. (2016). Abundance and generalisation in mutualistic networks:
529 solving the chicken-and-egg dilemma. *Ecol. Lett.*, 19, 4–11.
- 530 Forup, M., Henson, K., Craze, P. & Memmott, J. (2008). The restoration of ecological interactions:
531 plant-pollinator networks on ancient and restored heathlands. *J. Appl. Ecol.*, 45, 742–752.
- 532 Freeman, L.C. (1978). Centrality in social networks conceptual clarification. *Soc. Networks*, 1,
533 215–239.

- 534 Galeano, J., Pastor, J.M. & Iriondo, J.M. (2009). Weighted-interaction nestedness estimator (wine):
535 a new estimator to calculate over frequency matrices. *Environ. Model. Softw.*, 24, 1342–1346.
- 536 Gibert, J.P., Pires, M.M., Thompson, J.N. & Guimarães Jr, P.R. (2013). The spatial structure of
537 antagonistic species affects coevolution in predictable ways. *Am. Nat.*, 182, 578–591.
- 538 Gómez, J.M. & Zamora, R. (2006). Ecological factors that promote the evolution of generaliza-
539 tion in pollination systems. *Plant-pollinator interactions*, NM Waser, J. Ollerton (eds.). *The*
540 *University of Chicago Press, Chicago*, pp. 145–166.
- 541 Graham, C.H. & Fine, P.V. (2008). Phylogenetic beta diversity: linking ecological and evolutionary
542 processes across space in time. *Ecol. Lett.*, 11, 1265–1277.
- 543 Guimarães, P.R., Jordano, P. & Thompson, J.N. (2011). Evolution and coevolution in mutualistic
544 networks. *Ecol. Lett.*, 14, 877–885.
- 545 Holland, J.N., Okuyama, T. & DeAngelis, D.L. (2006). Comment on “asymmetric coevolutionary
546 networks facilitate biodiversity maintenance”. *Science*, 313, 1887b–1887b.
- 547 Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B. & Caflisch, A. (2010). The robustness
548 of pollination networks to the loss of species and interactions: a quantitative approach incorpo-
549 rating pollinator behaviour. *Ecol. Lett.*, 13, 442–452.
- 550 Kalinka, A.T. & Tomancak, P. (2011). linkcomm: an r package for the generation, visualization,
551 and analysis of link communities in networks of arbitrary size and type. *Bioinformatics*, 27.
- 552 Kembel, S., Cowan, P., Helmus, M., Cornwell, W., Morlon, H., Ackerly, D., Blomberg, S. &
553 Webb, C. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26,
554 1463–1464.

- 555 Klein, A., Vaissière, B., Cane, J., Steffan-Dewenter, I., Cunningham, S., Kremen, C. & Tscharntke,
556 T. (2007). Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B*,
557 274, 303–313.
- 558 Kremen, C. & M'Gonigle, L.K. (2015). Small-scale restoration in intensive agricultural landscapes
559 supports more specialized and less mobile pollinator species. *J. Appl. Ecol.*, 52, 602–610.
- 560 Kuznetsova, A., Bruun Brockhoff, P. & Haubo Bojesen Christensen, R. (2014). *lmerTest: Tests*
561 *for random and fixed effects for linear mixed effect models (lmer objects of lme4 package)*. R
562 package version 2.0-11.
- 563 MacLeod, M., Genung, M.A., Ascher, J.S. & Winfree, R. (2016). Measuring partner choice in
564 plant–pollinator networks: Using null models to separate rewiring and fidelity from chance.
565 *Ecology*.
- 566 Memmott, J., Waser, N.M. & Price, M.V. (2004). Tolerance of pollination networks to species
567 extinctions. *Proc. R. Soc. Lond. B*, 271, 2605–2611.
- 568 Menz, M., Phillips, R., Winfree, R., Kremen, C., Aizen, M., Johnson, S. & Dixon, K. (2010).
569 Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms.
570 *Trends Plant Sci.*, 16, 4–12.
- 571 M'Gonigle, L., Ponisio, L., Cutler, K. & Kremen, C. (2015). Habitat restoration promotes pollina-
572 tor persistence and colonization in intensively-managed agriculture. *Ecol. Appl.*, 25, 1557–1565.
- 573 M'Gonigle, L.K., Williams, N.M., Lonsdorf, E. & Kremen, C. (2016). A tool for selecting plants
574 when restoring habitat for pollinators. *Conserv. Lett.*
- 575 Morandin, L. & Kremen, C. (2013). Hedgerow restoration promotes pollinator populations and
576 exports native bees to adjacent fields. *Ecol. Appl.*, 23, 829–839.

- 577 Newman, M.E.J. & Girvan, M. (2004). Finding and evaluating community structure in networks.
- 578 *Phys. Rev. E*, 69, 026113.
- 579 Nuismer, S.L., Jordano, P. & Bascompte, J. (2013). Coevolution and the architecture of mutualistic
- 580 networks. *Evolution*, 67, 338–354.
- 581 Olesen, J.M., Bascompte, J., Dupont, Y. & Jordano, P. (2007). The modularity of pollination
- 582 networks. *Proc. Natl. Acad. Sci. USA*, 104, 19891–19896.
- 583 Olesen, J.M., Bascompte, J., Elberling, H. & Jordano, P. (2008). Temporal dynamics in a pollina-
- 584 tion network. *Ecology*, 89, 1573.
- 585 Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants are pollinated by
- 586 animals? *Oikos*, 120, 321–326.
- 587 Parker, V.T. (1997). The scale of successional models and restoration objectives. *Restor. Ecol.*, 5,
- 588 301–306.
- 589 Peel, L. & Clauset, A. (2014). Detecting change points in the large-scale structure of evolving
- 590 networks. *arXiv preprint arXiv:1403.0989*.
- 591 Petanidou, T., Kallimanis, S., Tzanopoulos, J., Sgardelis, S. & Pantis, J. (2008). Long-term ob-
- 592 servation of a pollination network: fluctuation in species and interactions, relative invariance of
- 593 network structure and implications for estimates of specialization. *Ecol. Lett.*, 11, 564–575.
- 594 Ponisio, L.C., M’Gonigle, L.K. & Kremen, C. (2016). On-farm habitat restoration counters biotic
- 595 homogenization in intensively managed agriculture. *Global Change Biol.*, 22, 704–715.
- 596 Pyke, G.H. (1984). Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Evol. Syst.*, pp.
- 597 523–575.

- 598 R Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation
599 for Statistical Computing, Vienna, Austria.
- 600 Ramos-Jiliberto, R., Valdovinos, F.S., Moisset de Espanés, P. & Flores, J.D. (2012). Topological
601 plasticity increases robustness of mutualistic networks. *J. Anim. Ecol.*, 81, 896–904.
- 602 Rezende, E.L., Lavabre, J.E., Guimarães, P.R., Jordano, P. & Bascompte, J. (2007). Non-random
603 coextinctions in phylogenetically structured mutualistic networks. *Nature*, 448, 925–928.
- 604 Santamaría, L. & Rodríguez-Gironés, M.A. (2007). Linkage rules for plant–pollinator networks:
605 Trait complementarity or exploitation barriers? *PLoS Biol.*, 5, e31.
- 606 Stang, M., Klinkhamer, P., Waser, N.M., Stang, I. & van der, M.E. (2009). Size-specific interaction
607 patterns and size matching in a plant-pollinator interaction web. *Ann. Bot.*, 103.
- 608 Stang, M., Klinkhamer, P.G. & Van Der Meijden, E. (2006). Size constraints and flower abundance
609 determine the number of interactions in a plant–flower visitor web. *Oikos*, 112, 111–121.
- 610 Thébault, E. & Fontaine, C. (2010). Stability of ecological communities and the architecture of
611 mutualistic and trophic networks. *Science*, 329, 853–856.
- 612 Valdovinos, F.S., Moisset de Espanés, P., Flores, J.D. & Ramos-Jiliberto, R. (2013). Adaptive
613 foraging allows the maintenance of biodiversity of pollination networks. *Oikos*, 122, 907–917.
- 614 Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P. & Dunne, J.A. (2010). Con-
615 sequences of adaptive behaviour for the structure and dynamics of food webs. *Ecol. Lett.*, 13,
616 1546–1559.
- 617 Vázquez, D.P. (2005). Degree distribution in plant-animal mutualistic networks: forbidden links
618 or random interactions? *Oikos*, 108, 421–426.

- 619 Vázquez, D.P., Blüthgen, N., Cagnolo, L. & Chacoff, N.P. (2009). Uniting pattern and process in
620 plant-animal mutualistic networks: a review. *Ann. of Bot.*, 103, 1445–1457.
- 621 Vázquez, D.P., Chacoff, N.P. & Cagnolo, L. (2009). Evaluating multiple determinants of the
622 structure of plant-animal mutualistic networks. *Ecology*, 90, 2039–2046.
- 623 Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. (1996). Generalization in
624 pollination systems, and why it matters. *Ecology*, 77, 1043.

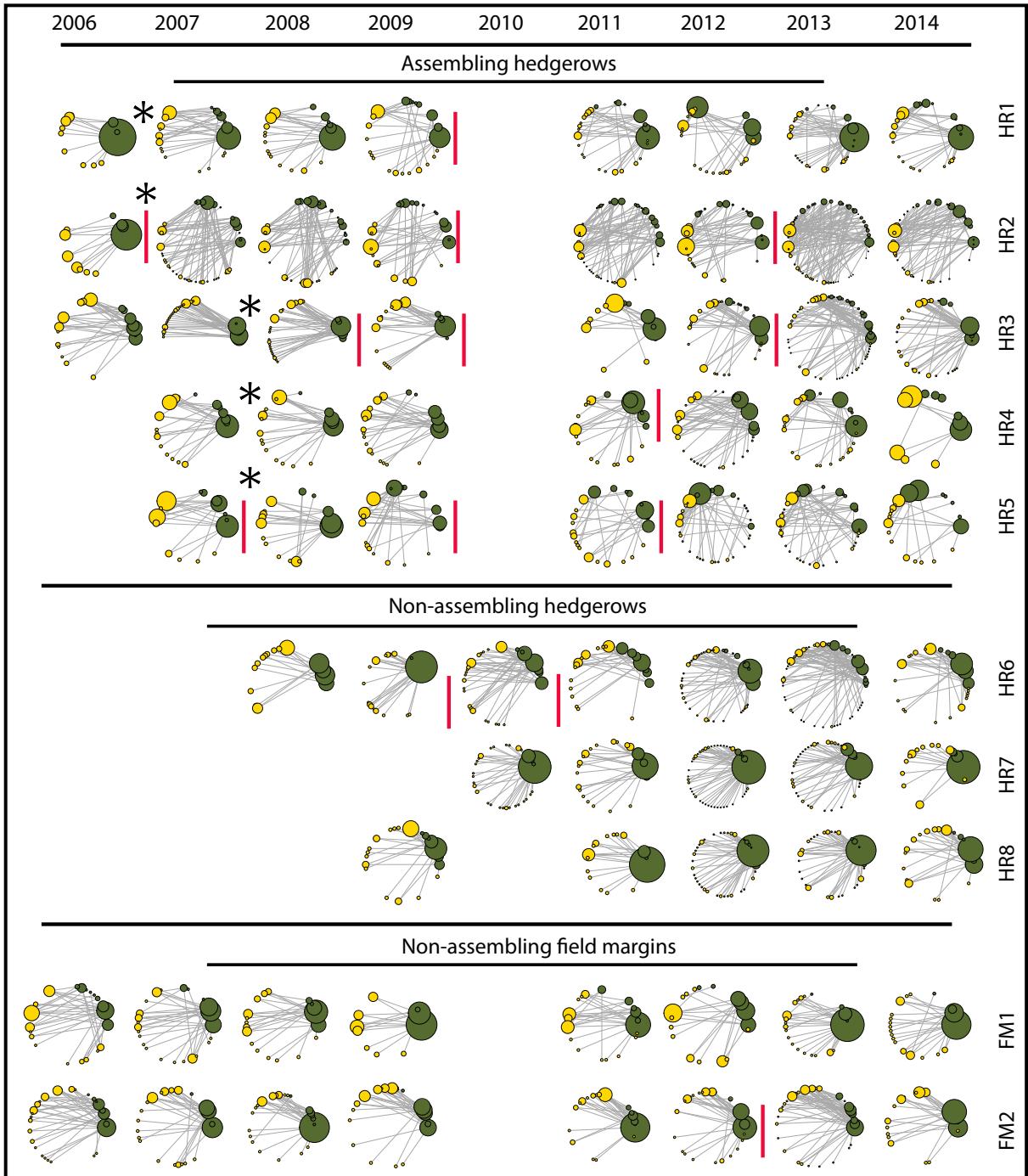


Figure 1: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, respectively, weighted by their degree. Each species has a consistent position in the perimeter of the network across years. In the assembling hedgerows, colored squares in the corner of each network represent the year of assembly. Asterisks indicate the year the hedge was planted. Before that, the sites were weedy field margins. 30

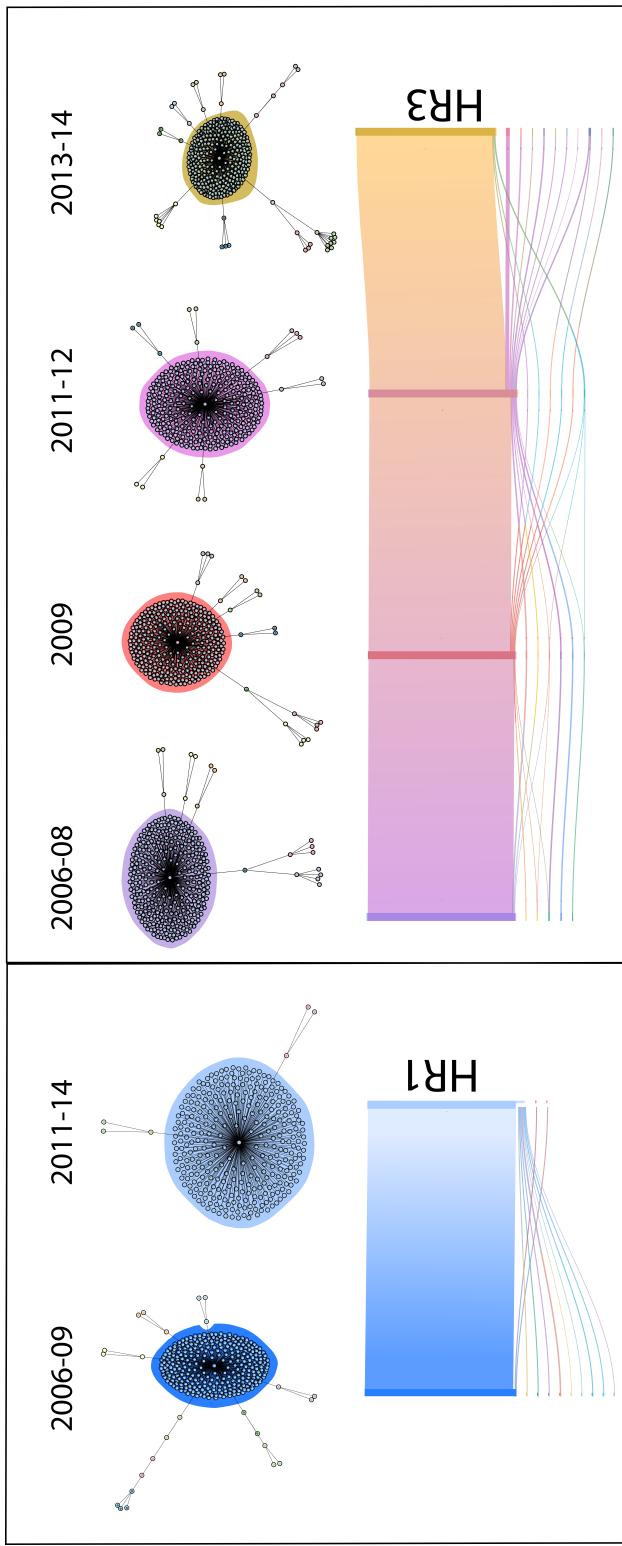


Figure 2: The module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species between modules between changing points.

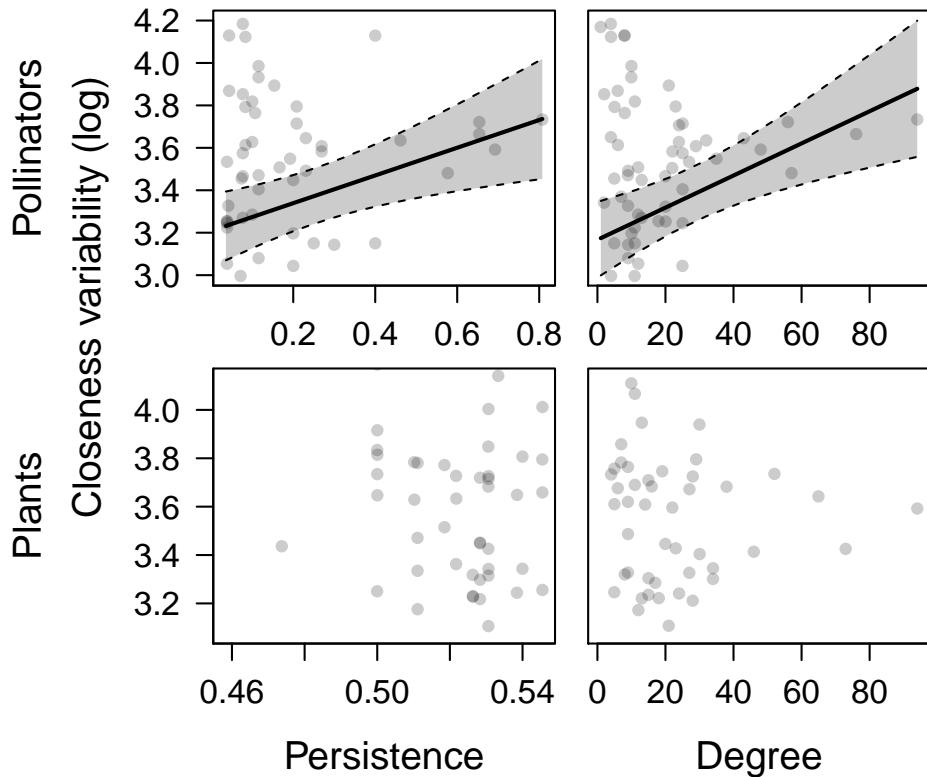


Figure 3: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across sites. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

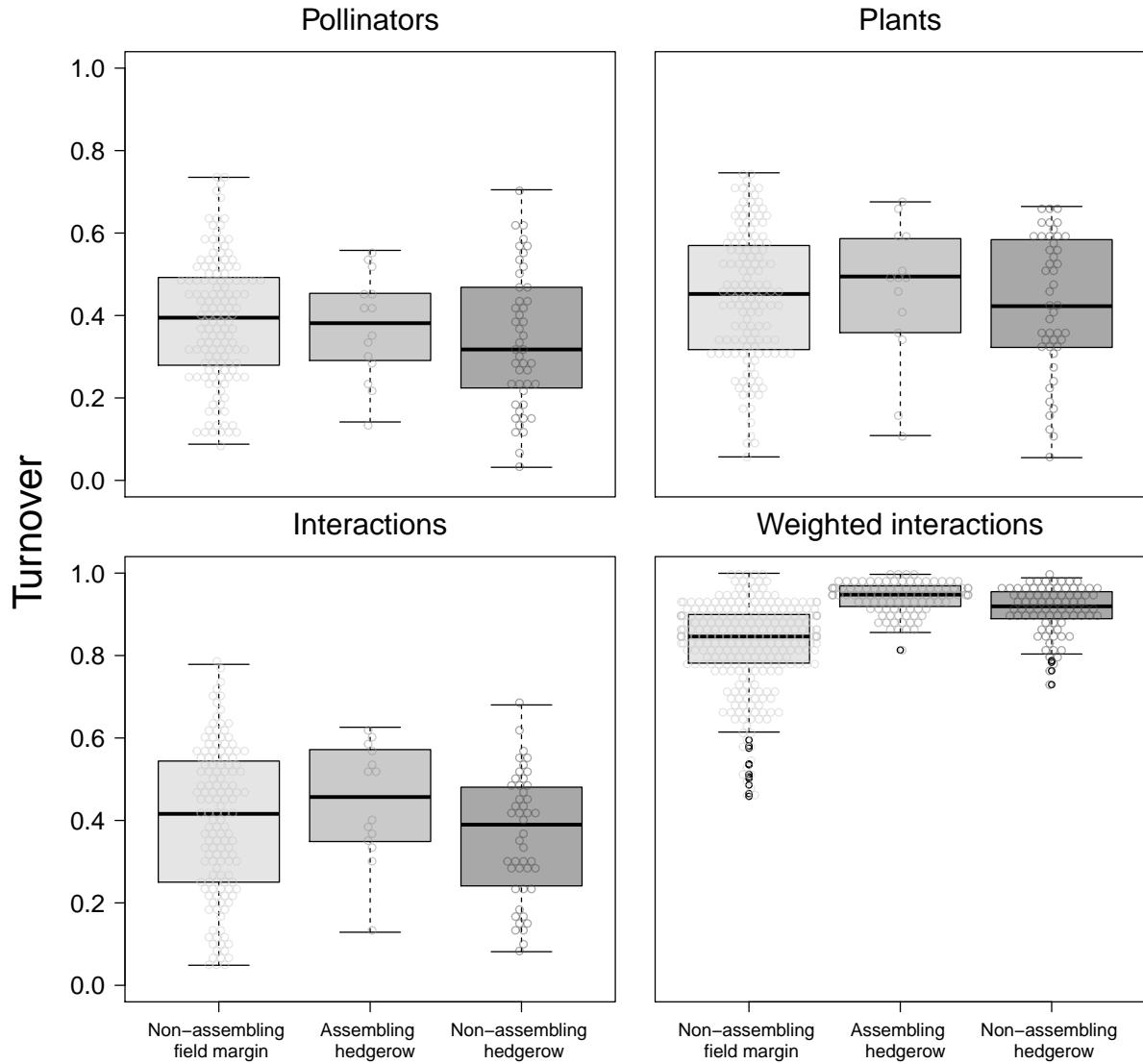


Figure 4: The species, interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally significantly less pollinator turnover. However, when interactions where 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).

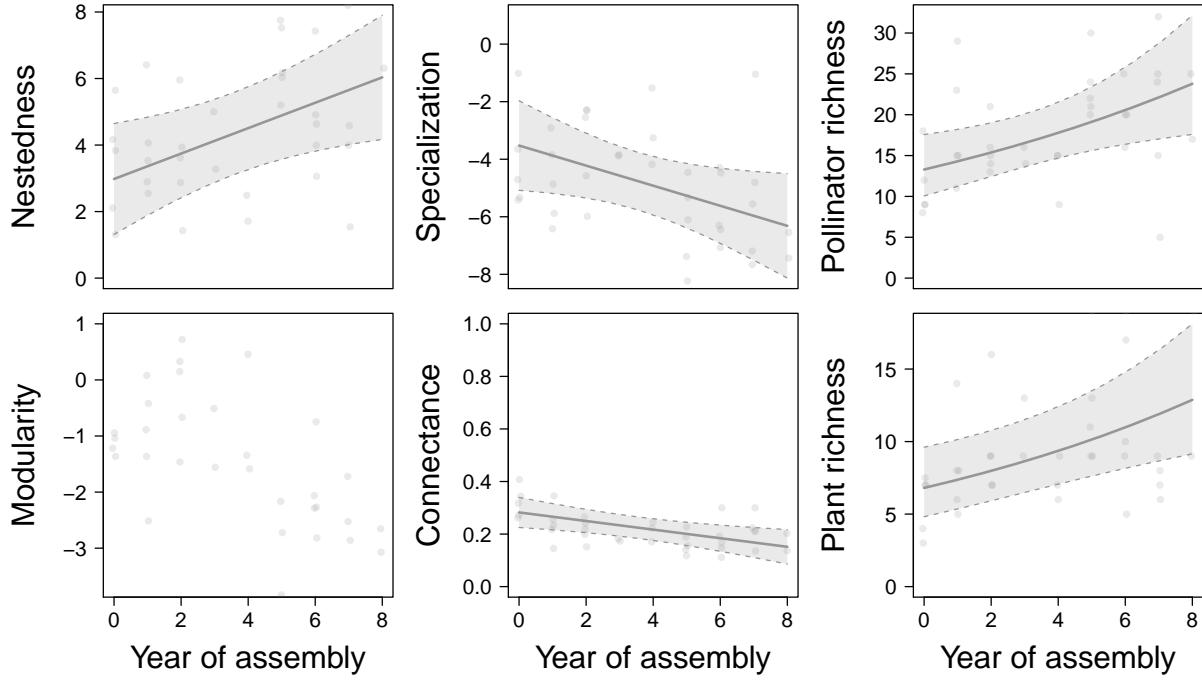


Figure 5: Nestedness, plant richness and pollinator richness increased as the networks assembled. Specialization and modularity remained consistent across years, while connectance decreased. The nestedness, modularity and specialization scores represent z-scores. Scores greater than ~ 2 or less than ~ -2 are significantly more or less structured than randomly assembled networks. Points are the metric 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.

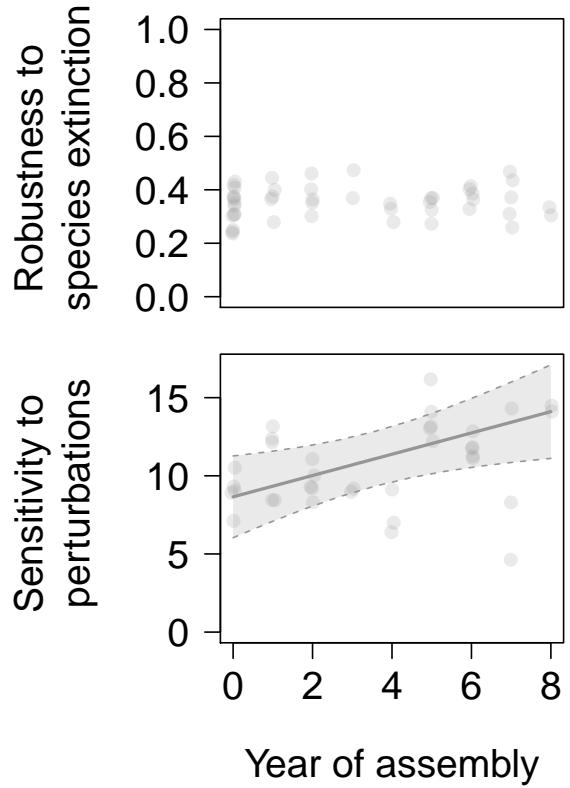


Figure 6: The robustness of networks to species extinction did not change with network assembly, but the sensitivity to cascading perturbations increased. The robustness to species extinction is measured by incrementally removing species by degree, though removing species by abundance did not yield qualitatively different results. The robustness of networks to cascading perturbations 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.