

**Running head:** PLANT-POLLINATOR NETWORK ASSEMBLY

# Major network reorganizations punctuate the assembly of plant-pollinator communities

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## Abstract

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

<sup>13</sup> community assembly, change points, robustness, nestedness, modularity, restoration, mutualism,  
<sup>14</sup> preferential attachment

## <sup>15</sup> Introduction

<sup>16</sup> Species in ecological communities are linked through ecological interactions. As the world contin-  
<sup>17</sup> ues to lose species at an alarming rate [22, 6], anticipating a community’s ability to resist collapse  
<sup>18</sup> will depend on the strength of each interaction network and the species within it [40, 57, 9, 61].  
<sup>19</sup> Furthermore, it has been show that biodiversity has a pivotal role in maintaining ecosystems ser-  
<sup>20</sup> vices [15]. Thus, to safeguard ecological function, it has become increasingly imperative to aid  
<sup>21</sup> the recovery of lost interactions and component biodiversity and by facilitating the assembly of ro-  
<sup>22</sup> bust interaction networks via ecological restoration [41]. However, we know very little about how  
<sup>23</sup> ecological networks assemble in general, rendering restoration of interacting communities quite  
<sup>24</sup> difficult.

<sup>25</sup> Preferential attachment, the most widely explored mechanism of network assembly, predicts that  
<sup>26</sup> species entering a network are more likely to interact with species that are already well-connected  
<sup>27</sup> [the “rich-get-richer” principle, 5]. In pollination systems — a particularly ubiquitous mutual-  
<sup>28</sup>ism [49, 36] — some studies have found support for this assembly mechanism. Investigating the  
<sup>29</sup> day-to-day, temporal assembly of a plant-pollinator network within a season, [48] found that phe-  
<sup>30</sup>nologically new plant and pollinator species tended to interact with already well-connected species,  
<sup>31</sup> potentially because these species are either more abundant or temporally persistent. Using a space-  
<sup>32</sup>for-time substitution to study primary succession, [2] also found evidence that assembly along a  
<sup>33</sup>glacier foreland occurred through preferential attachment. Specifically, network nestedness (i.e.,  
<sup>34</sup>a core group of generalists interacts with both specialist and generalist species) increased as the  
<sup>35</sup>community aged [2]. An increase in nestedness could have occurred via the preferential attachment  
<sup>36</sup>process, whereby specialist species attach to the well-connected, generalist core.

<sup>37</sup> Significant reorganizations of interactions — change points — can also punctuate assembly [51]. A  
<sup>38</sup>change point is caused by a merge, split, fragmentation or formation of modules within a network.  
<sup>39</sup> Such interaction reorganizations are observed in social networks responding to abrupt shifts in

40 the behavior of interactors [51]. In ecological communities, such shifts may occur if, as new  
41 species colonize, resident species change their interaction partners to optimize their foraging effort  
42 [54, 12, 63, 2, 62]. For preferential attachment to be at play, change points would need to be  
43 driven primarily by peripheral, temporally variable species while a stable, well-connected core  
44 of species remained stable in their interactions. No studies, however, have examined if network  
45 changing points occur during ecological network assembly and/or how these changes relate to  
46 species behavior.

47 Understanding network assembly is particularly relevant to ecological restoration, which is es-  
48 sentially “applied succession” [e.g., 50]. In pollination systems, time has been shown to affect the  
49 structure of networks in restored areas [25, 19], suggesting that interactions change as a community  
50 develops. Facilitating network restoration is especially imperative in areas where species interac-  
51 tions provide essential ecosystem services, such as crop pollination in agricultural landscapes. To  
52 promote pollinator services in agriculture, some farmers plant strips of native plants along farm  
53 edges (hedgerows). By providing habitat, hedgerows augment the richness, abundance and trait  
54 diversity of pollinators in agricultural landscapes [44, 37, 53], and promote the persistence and  
55 colonization of floral resource specialists [42]. As the community assembles, it is important to  
56 understand how these new species are incorporated into the network as well as the consequences  
57 of adding species for interaction patterns and robustness.

58 We explore the process of network development using a eight-year dataset of plant-pollinator com-  
59 munity assembly following hedgerow installment in the highly simplified and intensively managed  
60 agricultural landscape of California’s Central Valley. We first determine whether network assembly  
61 was punctuated by significant reorganizations of interactions. We next tested whether the species  
62 that are most variable in their network position — and thus important contributors to network re-  
63 organizations — are less persistent and connected species, as would be expected by preferential  
64 attachment. To further explore the mechanisms underlying the temporal dynamics of the networks,

65 also we examine patterns in the species and interaction temporal turnover. Finally, we investigate  
66 whether networks assemble toward predictable interaction patterns, and the ramifications for the  
67 robustness of the networks.

## 68 Materials & Methods

### 69 Study sites and collection methods

70 Study sites were located in the Central Valley of California in Yolo, Colusa and Solano Counties.  
71 This area is composed of intensively managed agriculture — primarily monocultures of conven-  
72 tional row crops, vineyards and orchards. Hedgerows border large (ca. 30-hectare) crop fields and  
73 measured between 3 – 6 m wide and approximately 350 m long. Hedgerows consist of native,  
74 perennial, shrub and tree plantings [Fig. S1, 41, 37, 42].

75 We selected five farm edges to be restored as hedgerows. We monitored those locations before  
76 the hedgerow was planted, and tracked the assembly of the community for up to seven years  
77 as the hedgerow matured (from 2006 – 2014). For controls, we concurrently monitored non-  
78 assembling communities within mature hedgerows (greater than 10 years since planting,  $N = 29$ )  
79 and unrestored, weedy field margins ( $N = 19$ ). The mean distance between monitoring sites  
80 was 15 km, and the minimum distance between sites sampled in the same year was 1 km. The  
81 entire area surveyed spanned almost 300  $km^2$ . The crop fields adjacent to all sites were similarly  
82 managed as intensive, high-input monoculture.

83 Sites were sampled between two and five times per year (Tables S1-S3, mean 3.4 samples per  
84 year). In each round of sampling, the order in which sites were sampled was randomized. Surveys  
85 were conducted under sunny conditions when the temperature was above 21°C and wind speed  
86 was below 2.5 meters/second.

87 During each sampling round, flower-visitors to plants in assembling hedgerows and non-assembling  
88 controls were netted for one hour of active search time (the timer was paused when handling spec-  
89 imens). The identify of the plant being visited was recorded for each floral visitor. Honeybees  
90 (*Apis mellifera*) were not collected because their abundance is determined largely by hive place-  
91 ment by bee-keepers. All other insect flower visitors that touched the reproductive parts of the  
92 flower were collected; however, here we focus only on wild bees and syrphids — the most abun-  
93 dant and effective pollinators in the system (representing 49 and 19 percent of records, respectively,  
94 C. Kremen, A. Klein and L. Morandin, unpublished data). Bee and syrphid specimens were identi-  
95 fied to species (or morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*)  
96 by expert taxonomists.

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

## 100 Change point analysis

### 101 Identifying change points

102 We employed a change point detection method [51] to identify fundamental reorganizations in  
103 large-scale interaction patterns. Change point detection methods have yet to be generalized to  
104 quantitative networks, so for this analysis we focused on qualitative (binary) networks. Following  
105 [51], we first defined a probability distribution over the networks using the generalized hierarchi-  
106 cal random graph model (GHRG). The GHRG model captures both assortative and disassortative  
107 structure patterns at all scales in the network [51]. A network  $G$  is composed of vertices  $V$  and  
108 edges  $E$ . The GHRG model decomposes the  $N$  vertices into a series of nested groups, the rela-  
109 tionships among which are represented by the dendrogram  $T$ . The tips of  $T$  are the vertices of  $G$ ,

110 and the probability that two vertices  $u$  and  $v$  connect is given by the parameter  $p_r$ . The probability  
111 distribution of the network  $G$  is thus defined as:

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

112 Where  $E_r$  is the observed number of edges between vertices with the common ancestor  $r$ , and  $N_r$   
113 is the total possible edges, and the rest of the notation is described above.

114 Using Bayesian posterior inference and techniques from phylogenetic tree reconstruction, we fit  
115 the GHRG model to the networks [51]. We used a Markov chain Monte Carlo (MCMC) procedure  
116 to first sample the posterior distribution of bipartitions, from which a consensus tree was derived  
117 [51]. We used  $\beta$  distributions with the hyperparameters  $\alpha = \beta = 1$  to define priors for  $p_r$ .

118 Once the GHRG model was fit to the networks, we determined whether a change point occurred  
119 between two time slices. To detect a change point, we used Bayes factors to compare the fit of two  
120 models — one where a change point occurred between two networks, and one where no change  
121 occurred. We chose a sliding window of length,  $w$ , of four years to detect change points. Larger  
122 windows allow for more gradual changes, and four was the maximum possible with our eight years  
123 of data. Lastly, to calculate a  $p$ -value for the Bayes factors, we used parametric bootstrapping to  
124 numerically estimate the null distribution [51]. We employed code published online by L. Peel for  
125 the change point analysis. Analyses were conducted in Python 3.4.

126 We next tested whether the change points occurring in maturing hedgerows were a component of  
127 the assembly process or a product of environmental shifts that lead to network reorganizations in  
128 all types of communities. We modeled the number of change points as successes and the total  
129 number of sample years at each site as trials, and used a generalized linear model with Binomial  
130 error to test whether the probability of a change point occurrence varied by site type. We used  
131 standard techniques to determine whether the assumptions of the models were met for this and all  
132 subsequent models. For the non-assembling controls, only sites with five or greater survey years

133 were included in this analysis ( $N = 11$ ). All statistical analyses were conducted in R 3.2.3 [55].

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

135 To further elucidate the nature of the change points, we examined the characteristics of the species  
136 that contributed to interaction reorganization. We tested whether the more persistent species with  
137 the highest degree (number of different interaction partners) were the most stable in their network  
138 positions, as would be expected if the networks were assembling via preferential attachment.

139 We calculated species persistence as the proportion of surveys in which a plant or pollinator is  
140 observed. Species observed consistently within and between years were thus maximally persistent.

141 Species degree was calculated from interaction observations from an extensive dataset from Yolo  
142 County (approx. 18000 interaction records) that included both the data included in this study and  
143 additional data from sites where we collected flower visitors using the same methods [42, 53].

144 To represent network position variability, we computed the coefficient of variation of weighted  
145 closeness centrality [26] at each site through time. Closeness centrality represents the importance  
146 of a species by calculating the path lengths to other vertices (species) in the network [26]. The  
147 shorter the mean path length to other species, the higher the closeness centrality. We used linear  
148 mixed models to test whether the species closeness variability (log) is related to the persistence  
149 or degree of that species [10, 38]. We included random effects for species and site. Because  
150 the degree and persistence of pollinators were strongly correlated, ( $\rho = 0.071$ ,  $p$ -value  $< 2 * 10^{-16}$ ), we included each explanatory variable in separate models. Plant degree and persistence  
152 were not significantly correlated, but we used the same models as we did for the pollinators for  
153 consistency. Because an approximately logarithmic increase in closeness centrality — as would  
154 be expected with assembly by preferential attachment — we also tested whether log closeness  
155 centrality increased through time.

156 **Species and interaction turnover**

157 Reorganizations of network structure can be the result of species turnover or species changing  
158 their interaction partners (i.e., re-wiring). To better understand the mechanisms underlying the  
159 temporal dynamics of the assembling networks, we examined patterns of species and interac-  
160 tion turnover. For example, assembling networks may have higher rates of pollinator turnover  
161 than non-assembling communities because new pollinator species are colonizing and establishing  
162 themselves [42]. Similarly, because species are turning over and pollinators are trying to maximize  
163 their foraging efficiency based on the species present, interactions may turnover more quickly than  
164 in established communities. In addition, at assembling hedgerows, plants that are unvisited in  
165 early years may appear to “colonize” the networks as they became more attractive resources and  
166 establish new interactions with pollinators.

167 To estimate the temporal species and interaction turnover, we used an approach similar to calcu-  
168 lating spatial  $\beta$ -diversity. Instead of calculating the variation in community composition across  
169 sites within a year, we estimated turnover across years at a site. We first calculated the pairwise  
170 dissimilarity of plants, pollinators and interactions between years within each site using the Chao  
171 dissimilarity estimator that incorporates abundances, while also accounting for unobserved records  
172 [16]. Dissimilarity estimates can be affected by the total number of species and individuals sam-  
173 pled at a site [e.g., 53]. For example, the probability that two sites do not share any species is  
174 higher when there are few individuals at those sites. Following [53], we used null models that con-  
175 strained species richness to estimate the deviation of the observed dissimilarity from that which  
176 would be expected under a random community assembly process. With the corrected dissimilarity  
177 values, we then calculated the multivariate dispersion of community composition across years [4].  
178 In order to test whether assembling hedgerows had more species and interactions turnover than  
179 non-assembling communities, the species and interaction temporal turnover estimates were mod-  
180 eled as responses in a linear mixed model with site type as an explanatory variable and site as a

181 random effect [10, 38].

182 Though species may turnover across years, some groups of species may essentially replace each  
183 other if they fill similar roles in the network, occupying the same network position and interact-  
184 ing with similar species. At non-assembling communities, species turnover may overestimate the  
185 temporal changes in the networks if the interactions occurring in one year are similar to those in  
186 the next year when they are weighted by the similarity of their constituent species (Fig. 1). We de-  
187 veloped a method to examine the temporal turnover of interactions with weightings based on their  
188 similarity. We followed the algorithm of [1] to cluster all the interactions (edges) hierarchically  
189 across sites and years based on their similarity, and built a dendrogram. The interaction similarity  
190 is based how many plants and pollinators (vertices) two edges share [1, 34]. The more species  
191 edges shared in common, the shorter the branch length between them on the dendrogram. We next  
192 calculated the temporal turnover of interactions weighted by their similarity, as approximated by  
193 “phylogenetic” distance [30, 35]. We then used linear mixed models to test whether the weighted  
194 turnover of interactions varied between assembling and non-assembling networks, including site  
195 as a random effect [10, 38].

## 196 **Temporal changes in interaction patterns**

### 197 **Network structure**

198 Any changing points in network structure may contribute to the reorganization of the assembling  
199 networks into predictable interaction patterns. Pollination networks exhibit two main structural  
200 patterns — modularity [e.g., 47] and nestedness [e.g., 8, 7]. In modular networks, interactions are  
201 insular, occurring within separate groups or “modules” more often than between modules. Mod-  
202 ules in the network may fragment as the network assembles, enhancing modularity. Conversely,  
203 nested networks are like a 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 as would be expected with preferential attachment, nestedness would increase through time. The connectance — the proportion of observed out of possible interactions — would also decrease as new, specialist species, preferentially attach to the core. Finally, network-level specialization will increase if specialist species colonize the network or species begin to limit their interaction niche breadth as the network assembles [11].

To evaluate network nestedness, we used the estimator weighted NODF [3]. NODF evaluates whether species with fewer partners interact with subsets of partners with which more connected species interact [3]. To estimate modularity, we used a hierarchical clustering algorithm [45, 18]. We evaluated 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 [11]. 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 [27].

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 employed generalized linear

229 mixed models with Poisson error to model richness [10]. We scaled explanatory variables.

230 **Network robustness**

231 Finally, we tested whether the changes in interaction patterns associated with network assembly  
232 affect the robustness of the network to species loss and cascading perturbations. Following [40],  
233 we simulated plant species extinction and the subsequent extinction cascades of pollinator species.  
234 Because the reproduction of plant species is facilitated by active restoration efforts, it is unlikely the  
235 extinction of pollinator species would affect plant populations in the hedgerows. However, plants  
236 ceasing to bloom, for example in response to drought, will likely affect the pollinators that depend  
237 on them. We eliminated plants species based on their degree or abundance, and then calculated  
238 the number of pollinators that secondarily went extinct. The area below the extinction curve is an  
239 estimate of network robustness [40, 13, 21].

240 We also explored how the robustness to cascading perturbations changed as the community as-  
241 sembled, using algebraic connectivity — the second smallest eigenvalue of the Laplacian matrix  
242 [23] — as a proxy for network robustness. Algebraic connectivity relates to how difficult it is to  
243 turn a network into completely disconnected groups of species [17, 28]. The larger the algebraic  
244 connectivity, the more sensitive a network is to cascading perturbations. Perturbations, such as the  
245 decrease in abundance of a plant or pollinator, can have negative consequences for the species in  
246 the network. For example, a decrease in abundance of a pollinator will diminish the pollination  
247 services it provides to plants. The affected plants would set less seeds, and decrease in abundance  
248 the subsequent year. Consequently, other pollinators that depended on those plant species would  
249 also be affected, and the effects of this perturbation would continue to propagate throughout the  
250 network. Alternatively, perturbations could also have a positive effect if, for example, the increase  
251 in the abundance of a plant species lead to an increase in resource availability for pollinators. The  
252 examples of negative perturbations (e.g., resource collapse, disease spreading, parasites), however,

253 outnumber possible positive perturbations. It is important to note that both robustness and alge-  
254 braic connectivity assume that the network is static — they do not account for the ability of species  
255 to alter their interaction depending on circumstances and the resource availability.

256 In order to test whether hedgerows changed in robustness as the communities assembled, the three  
257 measures of robustness were modeled as responses in a linear mixed model with site type as an  
258 explanatory variable and site as a random effect [10, 38].

## 259 **Results**

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

## 263 **Change point analysis**

### 264 **Identifying change points**

265 The majority (76%) of the sites underwent at least one significant interaction reorganization (Fig. 2,  
266 3). All five of the assembling hedgerows experienced network changing points, whereas only 40%  
267 and 81% of non-assembling hedgerows and field margins, respectively, underwent significant in-  
268 teraction reorganizations. Assembling hedgerows had significantly more changing points than the  
269 non-assembling networks (estimate of the difference in the odds ratios between assembling and  
270 non-assembling networks, 3.316, 95% CI [1.314, 8.572],  $p$ -value= 0.0117). Network assembly fol-  
271 lowing restoration is thus punctuated by more interaction reorganizations than would be expected  
272 by external factors such as environmental shifts that would have affected all networks (assembling  
273 or non-assembling) similarly.

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

275 In contradiction to the predictions of assembly by preferential attachment, both pollinator per-  
276 sistence and degree were positively related to network position variability (Fig. 4, estimate of  
277 the slope of closeness centrality variability and persistence  $\pm$  standard error of the estimate,  
278  $0.496 \pm 0.182$ ,  $p\text{-value}=0.016$ ; slope of closeness centrality variability and degree,  $0.004 \pm 0.002$ ,  
279  $p\text{-value}=0.056$ ). The slope of these relationships remained significant when the species with the  
280 top 10 persistence and degree scores were dropped. In addition, plant persistence and degree were  
281 not significantly related to network position variability (Fig. 4). The variability of species net-  
282 work position was not the result of closeness linearly increasing through time, and, in fact, plant  
283 and pollinator closeness decreased slightly through time (Fig. S2, estimate of the slope of close-  
284 ness through time  $\pm$  SE, pollinators:  $-0.082 \pm 0.021$ ,  $p\text{-value}=0.003$ ; plants  $-0.089 \pm 0.044$ ,  
285  $p\text{-value}=0.04$ ).

286 **Species and interaction turnover**

287 The rates of plant, pollinator and interaction temporal turnover were similar across assembling  
288 hedgerows, non-assembling hedgerows and field margins, though mature hedgerows had marginally  
289 less pollinator turnover than field margins (Fig. 5, estimate  $\pm$  SE of the difference in turnover be-  
290 tween field margins and mature hedgerows,  $-0.051 \pm 0.026$ ,  $p\text{-value}=0.049$ ). The turnover of  
291 plants and interactions was not significantly different between site types. When interactions were  
292 weighted by their similarity, both assembling and mature hedgerows had higher rates of turnover  
293 than field margins (Fig. 5, estimate  $\pm$  SE of the difference in turnover between field margins  
294 and assembling hedgerows,  $0.115 \pm 0.027$ ,  $p\text{-value}=0.0002$ ; field margins and mature hedgerows,  
295  $0.082 \pm 0.024$ ,  $p\text{-value}=0.002$ ). The weighted interaction turnover at assembling hedgerows, how-  
296 ever, was not significantly higher than in non-assembling, mature hedgerows.

297 **Temporal changes in interaction patterns**

298 **Network structure**

299 Nestedness, modularity and specialization did not change predictably assembly (Fig. 6). All of the  
300 networks were significantly nested ( $z$ -scores  $> 2$ ), but not modular ( $z$ -scores  $< 2$ , Fig. 6). Most  
301 communities were more generalized than expected when interactions were randomized (Fig. 6).  
302 Connectance decreased as the community assembled (Fig. 6, estimate of the slope of connectance  
303 through time  $\pm$  standard error of the estimate,  $-0.023 \pm 0.008$ ,  $p$ -value=0.007).

304 Both plant and pollinator species richness increased through time (Fig. 6, estimate of the slope of  
305 richness through time  $\pm$  SE, pollinators:  $0.136 \pm 0.064$ ,  $p$ -value=0.034; plants:  $0.140 \pm 0.060$ ,  
306  $p$ -value=0.012). Unsurprisingly, pollinator species are colonizing and persisting at the assembling  
307 hedgerows. Plant species richness in the networks is based on the flowers actually visited by  
308 pollinators and not the presence of a particular plant species at a site. Thus, though some new plant  
309 species may establish themselves in the hedgerows, the increase in plant richness in the networks is  
310 likely due to previously unvisited plants attracting visitors as they mature and offer better rewards.

311 **Network robustness**

312 Assembly did not affect network robustness to species extinction when species were removed  
313 incrementally by degree or abundance (Fig. S3). Similarly, the sensitivity of networks to cascading  
314 perturbations, as measured by the algebraic connectivity of the network, did not change predictably  
315 as the community assembled (Fig. S3).

316 **Discussion**

317 We show that the temporal assembly of plant-pollinator networks following restoration is a highly  
318 dynamic process in which interactions often undergo significant reorganizations, or changing points.  
319 If these network reorganizations were a product of environmental forces alone, we would expect to  
320 observe the same changing points at the same time periods, consistently across all sites. However,  
321 network changing points in non-assembling communities are less frequent, and there are few con-  
322 sistent trends in the years when change points occurred across all sites. Several sites had network  
323 changing points between years 2009 and 2011 (Fig. 2). In California, 2011 marked the begin-  
324 ning of a multi-year drought. The assembling hedgerows were not sampled in 2010, so we cannot  
325 disentangle whether the point changes are due to skipping a year of monitoring or the drought.  
326 Interestingly, most assembling hedgerows did not undergo a significant interaction reorganization  
327 immediately after planting (i.e., the transition from weedy field margin to hedgerow). This result  
328 is consistent with the finding that hedgerow restoration takes several years to have an impact on the  
329 plant-pollinator communities in our study system, as well as with the observation that hedgerows  
330 do not begin to produce many flowers until 3 – 5 years following planting [37].

331 In a preferential attachment process, we expect that the most persistent and high degree species (the  
332 species with the most unique interaction partners) would remain stable in the network core during  
333 assembly [5]. Surprisingly, however, we encountered the opposite pattern. For example, the four  
334 most ubiquitous species in our study landscape — *Halictus ligatus*, *Halictus tripartitus*, *Lasioglos-*  
335 *um (Dialictus) incompletum*, and *Toxomerus marginatus* — were the only species that changed  
336 which module they were a member in across years in all the assembling hedgerows. Because  
337 species degree and persistence were strongly correlated, it is difficult to disentangle the causal  
338 mechanism for why species with those characteristics are so variable in their network position.  
339 Species that can interact with a relatively high number of partners may be better able to exploit the  
340 limited floral resources in the intensively managed agriculture landscape, and thus also be the most

341 persistent [in ant-plant mutualisms, 20]. More persistent species usually have longer phenologies,  
342 so they can visit many different flowers, resulting in a higher degree [65, 24]. Either way, our result  
343 suggests that adaptable species can change their network position to utilize the most advantageous  
344 floral resources available, which may depend on both the other pollinator species that are present  
345 and the state of the plant community [67, 29, 39]. Thus given the opportunity and ability to use  
346 different resources, species will often change their network positions [39].

347 Interestingly, though assembling hedgerows had more network reorganizations than non-assembling  
348 communities, pollinator species and interaction turnover occurred at similar rates across site types.  
349 Assembling hedgerows have higher turnover than non-assembling field margins only when inter-  
350 actions were weighted by their similarity. This is likely because though species and interactions  
351 are turning over at the field margins, species and interactions that fill similar roles in the network  
352 are replacing each other. In contrast, at the assembling hedgerows, unique interactions are turn-  
353 ing over as the networks continually reorganize. Non-assembling mature hedgerow communities,  
354 however, had similar rates of weighted interaction turnover as assembling hedgerows but also the  
355 lowest pollinator turnover. Pollinator communities at mature hedgerows may generally be more  
356 stable, but rare and/or specialized pollinators could generate this pattern if they entered a commu-  
357 nity, formed unique interactions with plants that did not previously share pollinators, but did not  
358 persist in the networks. These species would not contribute strongly to network reorganization or  
359 species turnover, but would enhance weighted interaction turnover. Mature hedgerows therefore  
360 both support more stable pollinator communities, while also providing resources for rare and/or  
361 specialized species [37, 42].

362 When we explored how network-level interaction patterns changed through time, we found few  
363 patterns. The connectance decreased, as would be expected if the network is being colonized by  
364 specialist species [42]. Network specialization, however, did not change predictably with assembly.  
365 Decreasing connectance without an accompanying increase in specialization would be possible

366 if the increased colonization of specialized species was accompanied by an increase in the diet  
367 breath of resident species. This would be expected if resident species were able to minimize their  
368 foraging time by expanding their diet breath as plant diversity increases with hedgerow maturation  
369 [54, 67, 12, 2].

370 Interestingly, however, the changes in network patterns associated with assembly did not affect  
371 the hedgerow network robustness to species extinction or susceptibility to cascading perturbations.  
372 The hedgerows were designed to provide floral resources for the largest number of pollinators  
373 across the growing season [41]. The generalized nature of the floral community may explain why  
374 the networks tended to be more generalized than expected if interactions were randomly distributed  
375 across species (Fig. 6). In addition, the design of the hedgerow plantings may have facilitated the  
376 emergence of a single, highly connected module in all of the networks (see 3 for examples). This  
377 network configuration results in short path lengths (the distance between species in a network  
378 based on their shared partners), and thus, a perturbation in one species can more easily spread to  
379 other species. These networks are also vulnerable to the extinction of highly connected species  
380 [13]. In order to promote more resilient communities, future restoration efforts should explore de-  
381 signing floral communities to promote more interaction partitioning using, for example, algorithms  
382 to optimize different network properties based on prior knowledge of pollinator floral preferences  
383 [43], and on desired network architectures that renders them more robust both to species loss and  
384 to cascading effects.

385 In general, plant-pollinator networks are highly dynamic, with high turnover of species and in-  
386 teractions both within and between seasons [14]. Though our non-assembling communities ex-  
387 perienced fewer network reorganizations than the assembling hedgerows, 82% of field margins  
388 and 40% of mature hedgerows underwent at least one changing point in network structure. Pol-  
389 linators are highly opportunistic [52, 64, 2], though trait complementarity such as tongue length  
390 and corolla depth impose some biophysical limits to the interactions between plants and pollina-

tors [60, 58, 66, 65, 59]. Such opportunism may buffer plant-pollinator communities from global change [e.g., 56, 33], but our limited understanding of the assembly of these communities impedes making such predictions [65, 14]. Unlike in the broader food web literature, we have few assembly models of mutualistic network assembly [62, 46, 31]. In addition, the few developed models often borrow their mechanisms from competitive interactions, leading to inaccurate biological assumptions [32]. We need further development of mechanistic models of mutualistic systems to generate testable predictions, along with empirical exploration of network assembly. Plant-pollinator communities and mutualisms are vital for biodiversity maintenance and essential ecosystem service provision. We must therefore understand the processes underlying their assembly to facilitate restoration and conservation.

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415 **References**

- 416 1.
- 417 Ahn, Y.Y., Bagrow, J.P. & Lehmann, S. (2010). Link communities reveal multiscale complex-  
418 ity in networks. *Nature*, 466, 761–764.
- 419 2.
- 420 Albrecht, M., Riesen, M. & Schmid, B. (2010). Plant–pollinator network assembly along the  
421 chronosequence of a glacier foreland. *Oikos*, 119, 1610–1624.
- 422 3.
- 423 Almeida-neto, M., Guimarães, P., Guimarães, P., Loyola, R. & Ulrich, W. (2008). A consistent  
424 metric for nestedness analysis in ecological systems: reconciling concept and measurement.  
425 *Oikos*, 117, 1227–1239.
- 426 4.
- 427 Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders,  
428 N.J., Cornell, H.V., Comita, L.S., Davies, K.F. *et al.* (2011). Navigating the multiple meanings  
429 of  $\beta$  diversity: a roadmap for the practicing ecologist. *Ecol. Lett.*, 14, 19–28.
- 430 5.
- 431 Barabási, A.L. & Albert, R. (1999). Emergence of scaling in random networks. *Science*, 286,  
432 509–512.
- 433 6.
- 434 Barnosky, A.D., Matzke, N., Tomaia, S., Wogan, G.O., Swartz, B., Quental, T.B., Marshall,  
435 C., McGuire, J.L., Lindsey, E.L., Maguire, K.C. *et al.* (2011). Has the earth’s sixth mass  
436 extinction already arrived? *Nature*, 471, 51–57.
- 437 7.

- 438 Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). The nested assembly of  
439 plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. USA*, 100, 9383–9387.
- 440 8.
- 441 Bascompte, J., Jordano, P. & Olesen, J.M. (2006). Asymmetric coevolutionary networks fa-  
442 cilitate biodiversity maintenance. *Science*, 312, 431–433.
- 443 9.
- 444 Bascompte, J. & Stouffer, D.B. (2009). The assembly and disassembly of ecological networks.  
445 *Phil. Trans. R. Soc. B*, 364, 1781.
- 446 10.
- 447 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). *lme4: Linear mixed-effects models*  
448 *using Eigen and S4*. R package version 1.1-7.
- 449 11.
- 450 Blüthgen, N., Menzel, F. & Blüthgen, N. (2006). Measuring specialization in species interac-  
451 tion networks. *BMC Ecol.*, 6, 9.
- 452 12.
- 453 Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B. & Blüthgen, N. (2007). Specialization,  
454 constraints, and conflicting interests in mutualistic networks. *Curr. Biol.*, 17, 341–346.
- 455 13.
- 456 Burgos, E., Ceva, H., Perazzo, R.P., Devoto, M., Medan, D., Zimmermann, M. & Delbue,  
457 A.M. (2007). Why nestedness in mutualistic networks? *J. Theor. Biol.*, 249, 307–313.
- 458 14.
- 459 Burkle, L.A. & Alarcón, R. (2011). The future of plant-pollinator diversity: Understanding  
460 interaction networks across time, space, and global change. *Am. J. Bot.*, 98, 528.

- 461 15.
- 462 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani,  
463 A., Mace, G.M., Tilman, D., Wardle, D.A. *et al.* (2012). Biodiversity loss and its impact on  
464 humanity. *Nature*, 486, 59–67.
- 465 16.
- 466 Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.J. (2005). A new statistical approach for  
467 assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.*, 8,  
468 148–159.
- 469 17.
- 470 Costa, L.d.F., Rodrigues, F.A., Travieso, G. & Villas Boas, P.R. (2007). Characterization of  
471 complex networks: A survey of measurements. *Adv. Phys.*, 56, 167–242.
- 472 18.
- 473 Csardi, G. & Nepusz, T. (2006). The igraph software package for complex network research.  
474 *InterJournal*, p. 1695.
- 475 19.
- 476 Devoto, M., Bailey, S., Craze, P. & Memmott, J. (2012). Understanding and planning ecolog-  
477 ical restoration of plant–pollinator networks. *Ecol. Lett.*, 15, 319–328.
- 478 20.
- 479 Díaz-Castelazo, C., Guimarães Jr, P.R., Jordano, P., Thompson, J.N., Marquis, R.J. & Rico-  
480 Gray, V. (2010). Changes of a mutualistic network over time: reanalysis over a 10-year period.  
481 *Ecology*, 91, 793–801.
- 482 21.
- 483 Dormann, C., Gruber, B. & Fründ, J. (2008). Introducing the bipartite package: analysing  
484 ecological networks. *R News*, 8, 8.

- 485 22.
- 486 Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P. & Sodhi, N.S. (2009). The sixth mass  
487 coextinction: are most endangered species parasites and mutualists? *Proc. R. Soc. Lond. B*,  
488 276, 3037–3045.
- 489 23.
- 490 Fiedler, M. (1973). Algebraic connectivity of graphs. *Czech. Math. J.*, 23, 298–305.
- 491 24.
- 492 Fort, H., Vázquez, D.P. & Lan, B.L. (2016). Abundance and generalisation in mutualistic  
493 networks: solving the chicken-and-egg dilemma. *Ecol. Lett.*, 19, 4–11.
- 494 25.
- 495 Forup, M., Henson, K., Craze, P. & Memmott, J. (2008). The restoration of ecological in-  
496 teractions: plant-pollinator networks on ancient and restored heathlands. *J. Appl. Ecol.*, 45,  
497 742–752.
- 498 26.
- 499 Freeman, L.C. (1978). Centrality in social networks conceptual clarification. *Soc. Networks*,  
500 1, 215–239.
- 501 27.
- 502 Galeano, J., Pastor, J.M. & Iriondo, J.M. (2009). Weighted-interaction nestedness estimator  
503 (wine): a new estimator to calculate over frequency matrices. *Environ. Model. Softw.*, 24,  
504 1342–1346.
- 505 28.
- 506 Gibert, J.P., Pires, M.M., Thompson, J.N. & Guimarães Jr, P.R. (2013). The spatial structure  
507 of antagonistic species affects coevolution in predictable ways. *Am. Nat.*, 182, 578–591.

- 508 29.
- 509 Gómez, J.M. & Zamora, R. (2006). Ecological factors that promote the evolution of gener-  
510 alization in pollination systems. *Plant-pollinator interactions*, NM Waser, J. Ollerton (eds.).  
511 *The University of Chicago Press, Chicago*, pp. 145–166.
- 512 30.
- 513 Graham, C.H. & Fine, P.V. (2008). Phylogenetic beta diversity: linking ecological and evolu-  
514 tionary processes across space in time. *Ecol. Lett.*, 11, 1265–1277.
- 515 31.
- 516 Guimarães, P.R., Jordano, P. & Thompson, J.N. (2011). Evolution and coevolution in mutual-  
517 istic networks. *Ecol. Lett.*, 14, 877–885.
- 518 32.
- 519 Holland, J.N., Okuyama, T. & DeAngelis, D.L. (2006). Comment on “asymmetric coevolu-  
520 tionary networks facilitate biodiversity maintenance”. *Science*, 313, 1887b–1887b.
- 521 33.
- 522 Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B. & Caflisch, A. (2010). The ro-  
523 bustness of pollination networks to the loss of species and interactions: a quantitative approach  
524 incorporating pollinator behaviour. *Ecol. Lett.*, 13, 442–452.
- 525 34.
- 526 Kalinka, A.T. & Tomancak, P. (2011). linkcomm: an r package for the generation, visualiza-  
527 tion, and analysis of link communities in networks of arbitrary size and type. *Bioinformatics*,  
528 27.
- 529 35.
- 530 Kembel, S., Cowan, P., Helmus, M., Cornwell, W., Morlon, H., Ackerly, D., Blomberg, S. &

- 531        Webb, C. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*,  
532        26, 1463–1464.
- 533        36.
- 534        Klein, A., Vaissière, B., Cane, J., Steffan-Dewenter, I., Cunningham, S., Kremen, C. &  
535        Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops.  
536        *Proc. R. Soc. B*, 274, 303–313.
- 537        37.
- 538        Kremen, C. & M'Gonigle, L.K. (2015). Small-scale restoration in intensive agricultural land-  
539        scapes supports more specialized and less mobile pollinator species. *J. Appl. Ecol.*, 52, 602–  
540        610.
- 541        38.
- 542        Kuznetsova, A., Bruun Brockhoff, P. & Haubo Bojesen Christensen, R. (2014). *lmerTest: Tests*  
543        *for random and fixed effects for linear mixed effect models (lmer objects of lme4 package)*. R  
544        package version 2.0-11.
- 545        39.
- 546        MacLeod, M., Genung, M.A., Ascher, J.S. & Winfree, R. (2016). Measuring partner choice  
547        in plant–pollinator networks: Using null models to separate rewiring and fidelity from chance.  
548        *Ecology*.
- 549        40.
- 550        Memmott, J., Waser, N.M. & Price, M.V. (2004). Tolerance of pollination networks to species  
551        extinctions. *Proc. R. Soc. Lond. B*, 271, 2605–2611.
- 552        41.
- 553        Menz, M., Phillips, R., Winfree, R., Kremen, C., Aizen, M., Johnson, S. & Dixon, K. (2010).

- 554        Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms.
- 555        *Trends Plant Sci.*, 16, 4–12.
- 556        42.
- 557        M’Gonigle, L., Ponisio, L., Cutler, K. & Kremen, C. (2015). Habitat restoration promotes
- 558        pollinator persistence and colonization in intensively-managed agriculture. *Ecol. Appl.*, 25,
- 559        1557–1565.
- 560        43.
- 561        M’Gonigle, L.K., Williams, N.M., Lonsdorf, E. & Kremen, C. (2016). A tool for selecting
- 562        plants when restoring habitat for pollinators. *Conserv. Lett.*
- 563        44.
- 564        Morandin, L. & Kremen, C. (2013). Hedgerow restoration promotes pollinator populations
- 565        and exports native bees to adjacent fields. *Ecol. Appl.*, 23, 829–839.
- 566        45.
- 567        Newman, M.E.J. & Girvan, M. (2004). Finding and evaluating community structure in net-
- 568        works. *Phys. Rev. E*, 69, 026113.
- 569        46.
- 570        Nuismer, S.L., Jordano, P. & Bascompte, J. (2013). Coevolution and the architecture of mu-
- 571        tualistic networks. *Evolution*, 67, 338–354.
- 572        47.
- 573        Olesen, J.M., Bascompte, J., Dupont, Y. & Jordano, P. (2007). The modularity of pollination
- 574        networks. *Proc. Natl. Acad. Sci. USA*, 104, 19891–19896.
- 575        48.
- 576        Olesen, J.M., Bascompte, J., Elberling, H. & Jordano, P. (2008). Temporal dynamics in a
- 577        pollination network. *Ecology*, 89, 1573.

578 49.

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

581 50.

582 Parker, V.T. (1997). The scale of successional models and restoration objectives. *Restor. Ecol.*,  
583 5, 301–306.

584 51.

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

587 52.

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

591 53.

592 Ponisio, L.C., M'Gonigle, L.K. & Kremen, C. (2016). On-farm habitat restoration counters  
593 biotic homogenization in intensively managed agriculture. *Global Change Biol.*, 22, 704–715.

594 54.

595 Pyke, G.H. (1984). Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Evol. Syst.*,  
596 pp. 523–575.

597 55.

598 R Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Founda-  
599 tion for Statistical Computing, Vienna, Austria.

600 56.

- 601       Ramos-Jiliberto, R., Valdovinos, F.S., Moisset de Espanés, P. & Flores, J.D. (2012). Topolog-  
602       ical plasticity increases robustness of mutualistic networks. *J. Anim. Ecol.*, 81, 896–904.
- 603       57.
- 604       Rezende, E.L., Lavabre, J.E., Guimarães, P.R., Jordano, P. & Bascompte, J. (2007). Non-  
605       random coextinctions in phylogenetically structured mutualistic networks. *Nature*, 448, 925–  
606       928.
- 607       58.
- 608       Santamaría, L. & Rodríguez-Gironés, M.A. (2007). Linkage rules for plant–pollinator net-  
609       works: Trait complementarity or exploitation barriers? *PLoS Biol.*, 5, e31.
- 610       59.
- 611       Stang, M., Klinkhamer, P., Waser, N.M., Stang, I. & van der, M.E. (2009). Size-specific  
612       interaction patterns and size matching in a plant-pollinator interaction web. *Ann. Bot.*, 103.
- 613       60.
- 614       Stang, M., Klinkhamer, P.G. & Van Der Meijden, E. (2006). Size constraints and flower  
615       abundance determine the number of interactions in a plant–flower visitor web. *Oikos*, 112,  
616       111–121.
- 617       61.
- 618       Thébault, E. & Fontaine, C. (2010). Stability of ecological communities and the architecture  
619       of mutualistic and trophic networks. *Science*, 329, 853–856.
- 620       62.
- 621       Valdovinos, F.S., Moisset de Espanés, P., Flores, J.D. & Ramos-Jiliberto, R. (2013). Adaptive  
622       foraging allows the maintenance of biodiversity of pollination networks. *Oikos*, 122, 907–917.
- 623       63.
- 624       Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P. & Dunne, J.A. (2010).

- 625       Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecol. Lett.*,  
626       13, 1546–1559.
- 627       64.
- 628       Vázquez, D.P. (2005). Degree distribution in plant-animal mutualistic networks: forbidden  
629       links or random interactions? *Oikos*, 108, 421–426.
- 630       65.
- 631       Vázquez, D.P., Blüthgen, N., Cagnolo, L. & Chacoff, N.P. (2009). Uniting pattern and process  
632       in plant-animal mutualistic networks: a review. *Ann. of Bot.*, 103, 1445–1457.
- 633       66.
- 634       Vázquez, D.P., Chacoff, N.P. & Cagnolo, L. (2009). Evaluating multiple determinants of the  
635       structure of plant-animal mutualistic networks. *Ecology*, 90, 2039–2046.
- 636       67.
- 637       Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. (1996). Generalization  
638       in pollination systems, and why it matters. *Ecology*, 77, 1043.

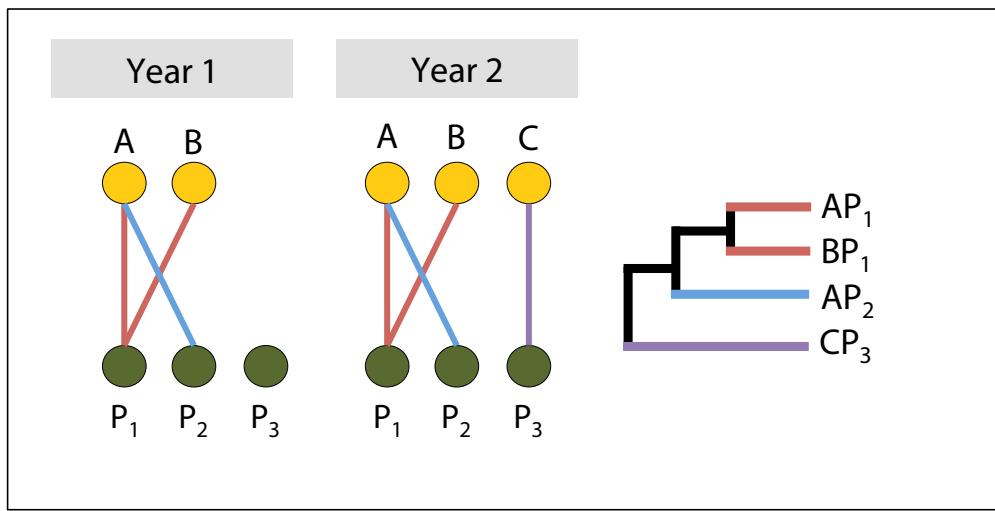


Figure 1: Diagram illustrating the analysis to examine the temporal turnover of interactions weighted based on their similarity. A, B and C are animal species, and Ps are plant species. The dendrogram depicts the interaction similarity across years based on the number of shared constituent species.

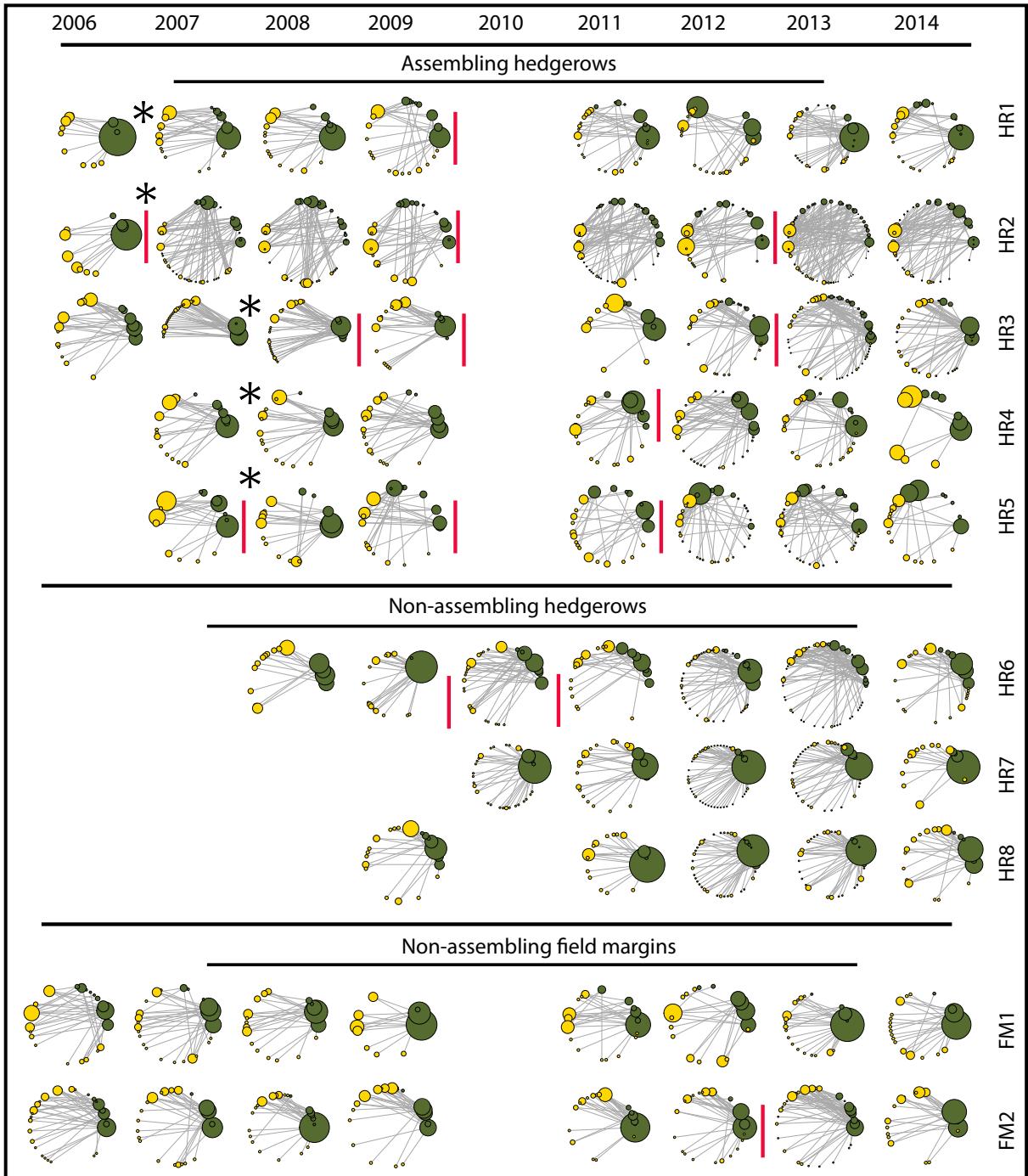


Figure 2: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, respectively,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

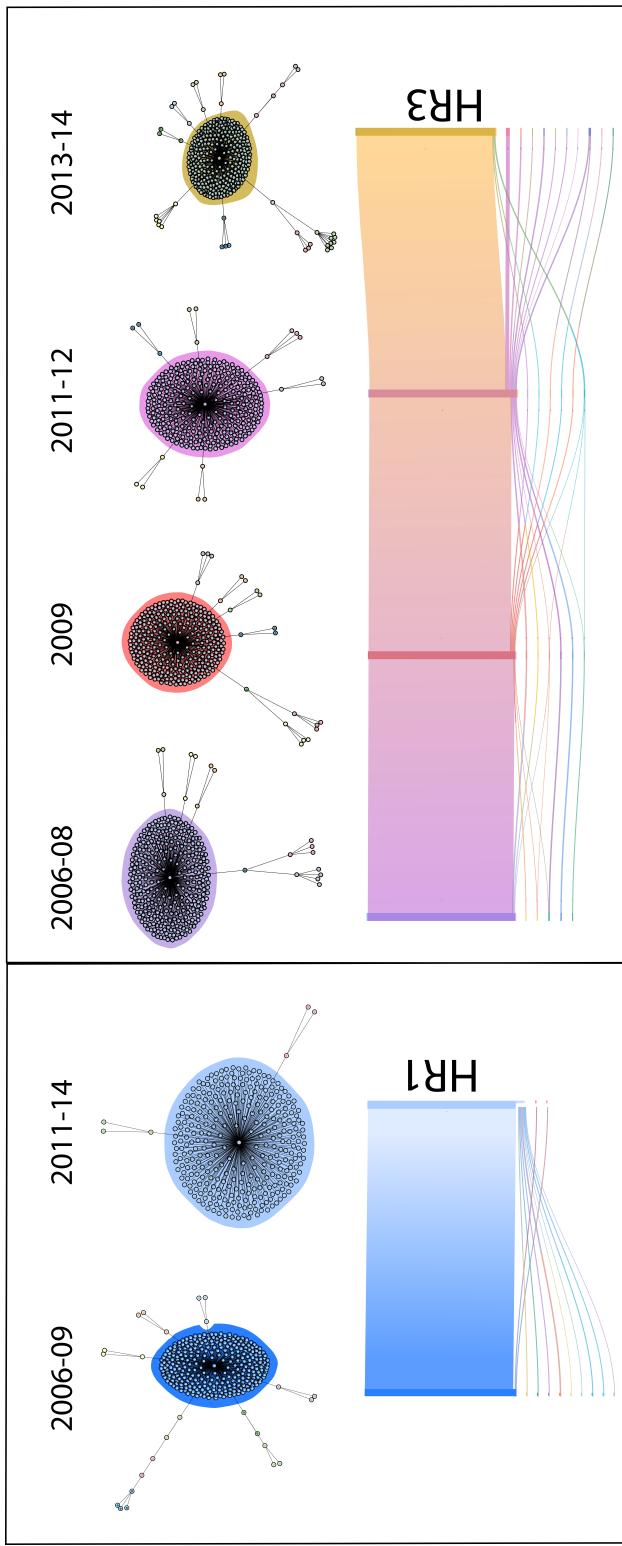


Figure 3: The species module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species to different modules between change points.

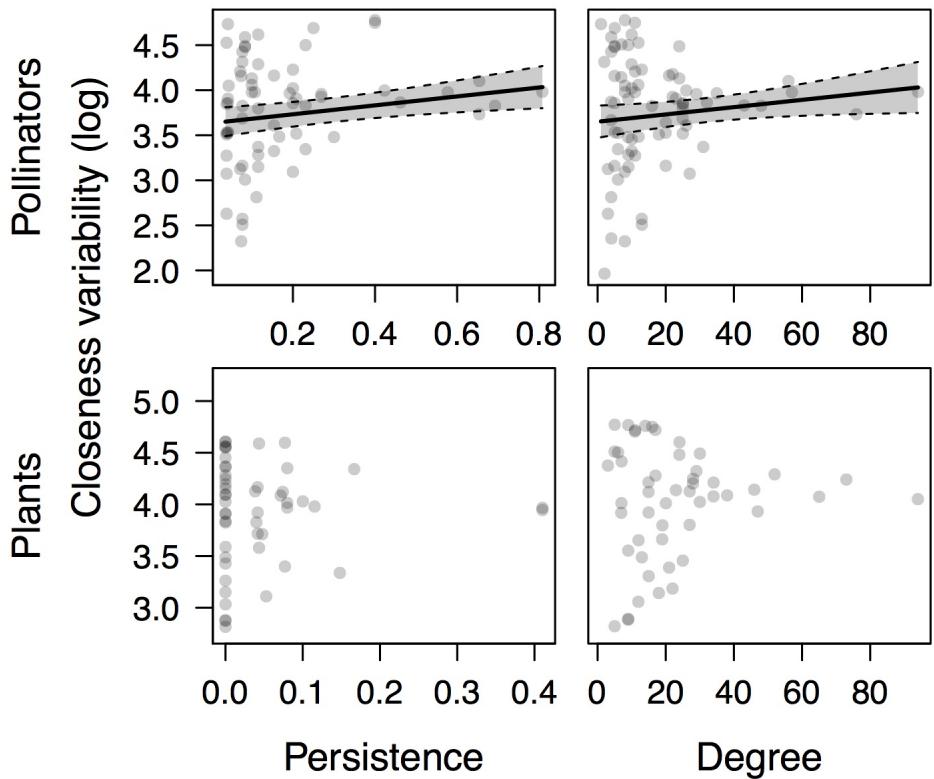


Figure 4: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across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

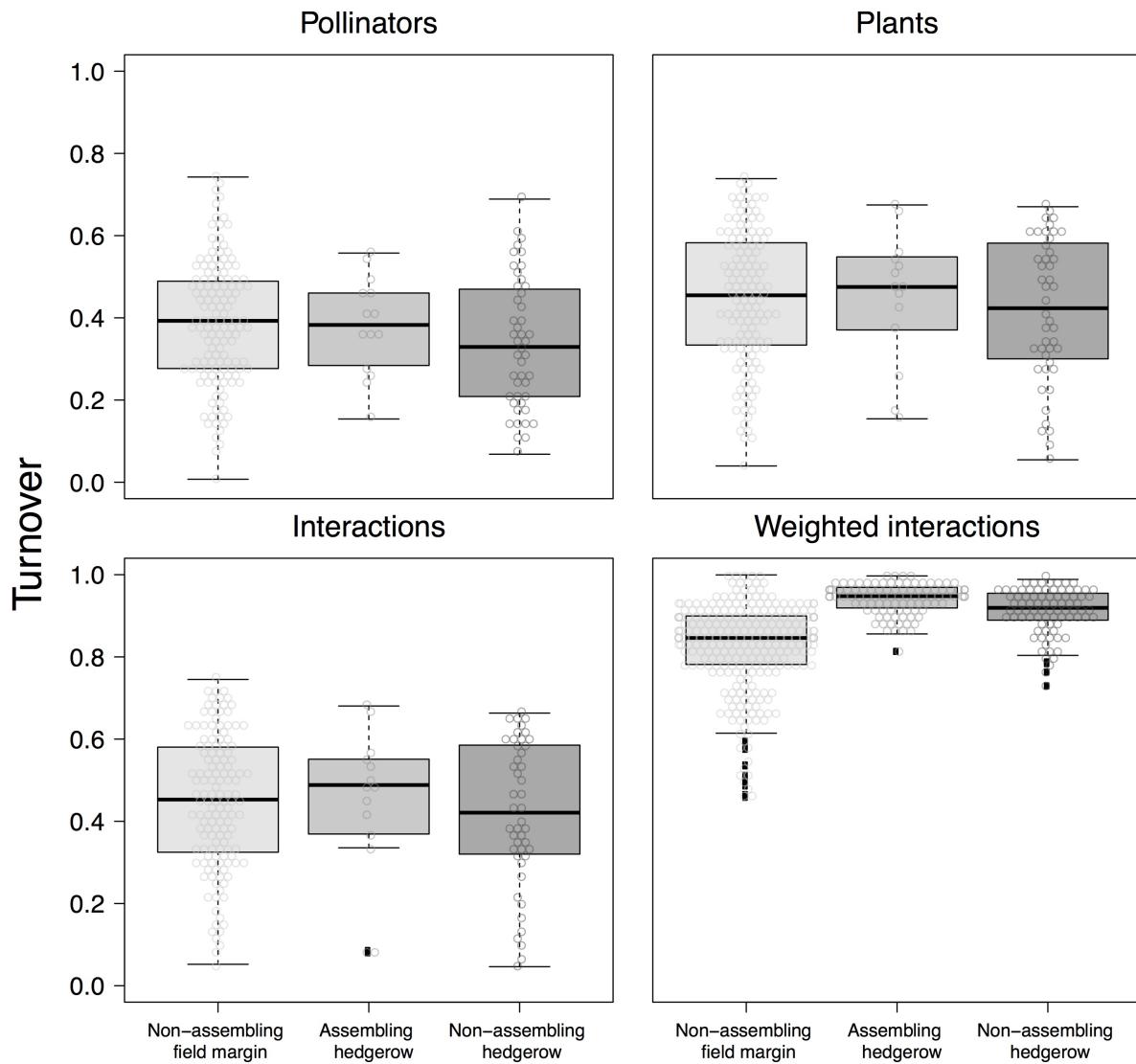


Figure 5: Species interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally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

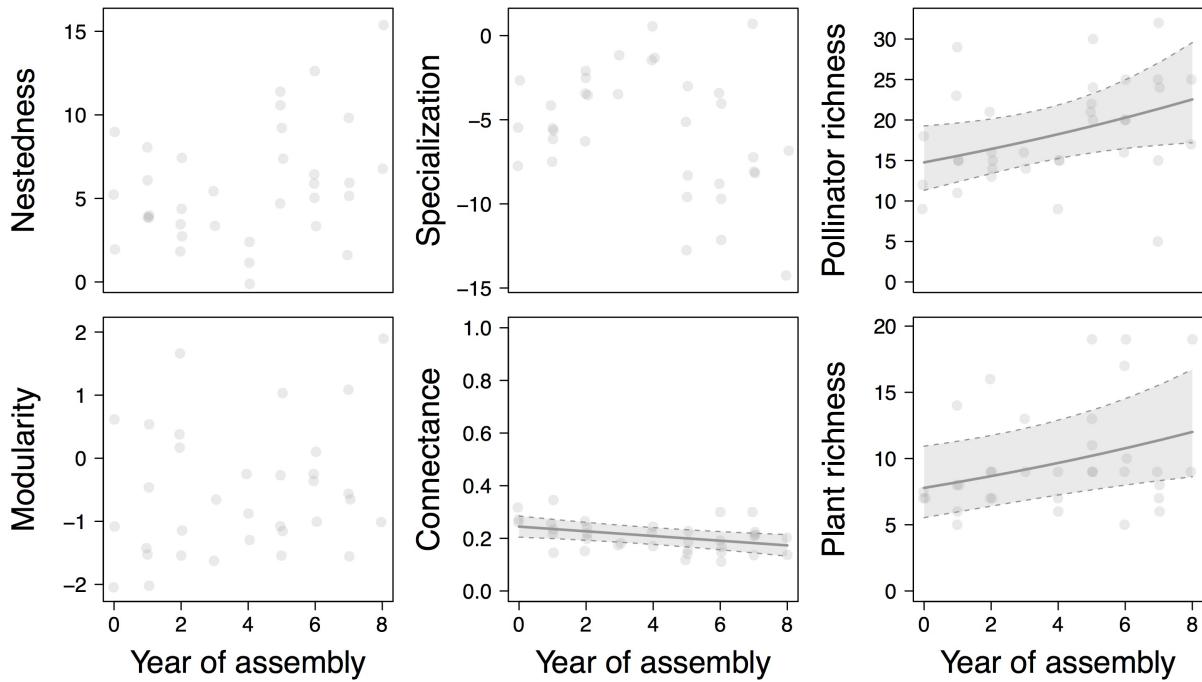


Figure 6: Plant richness and pollinator richness increased as the networks assembled. Nestedness, modularity and specialization did not change predictable across years, while connectance decreased. The nestedness, modularity and specialization scores represent z-scores. Scores greater than  $\sim 2$  or less than  $\sim -2$  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.