

**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

15 **Introduction**

16 (First and second paragraphs as they are)

17 However, properties that enable a species to interact with a broad range of partners (*i.e.*, general-  
18 ized, high degree species), may switch partners depending on community context. The adaptive  
19 foraging theory predicts that there is a trade-off between foraging efficiency and resource avail-  
20 ability; thus, if competing species are present, it is expected that there will be a decrease in niche  
21 overlap among species present in a given area. In this sense, when other, competing species are  
22 present, generalist species can explore different resources, switching their interaction partners.  
23 This alternative assembly mechanism can be described as an opportunistic attachment process.  
24 In the opportunistic attachment process generalist species, instead of being part of a persistent  
25 species' core, are actually the species that explore, opportunistically, the most available resources,  
26 that is, the resources that are being used the less. Thus, when you consider the assembly process in  
27 a time series, the most persistent species are also the ones that, through time, exhibit the highest  
28 degree, but are also the most variable in their network position at each particular time. Species  
29 may have multiple interaction partners, but only interact when opportunity arises.

30 3) Focus on specific species in this paragraph, maybe link to niche theory? Mention [33, 39] to  
31 link species change in interactions (rewire) to their persistence and temporal variation; say that  
32 we want to restore habitats that are robust and persistent through time. However, the relationship  
33 between species persistence across years and their role in community assembly is still unclear. [H3  
34 and H4]

35 4) important to understand assembly because of habitat restoration and ecosystem services, biodi-  
36 versity crisis (input the former first paragraph). [H4] (Paragraph that starts with "Understanding  
37 network assembly...") [H1 and H2]

38 5) Paragraph on changing points; mention the control and the non-assembly hedgerows here [H1

39 and H2]

40 6) Maybe rephrase the last paragraph to more question driven statements?

41 We tested four theoretically motivated hypothesis exploring the process of community assembly  
42 using a eight-year dataset of plant-pollinator network development following hedgerow installment  
43 in the highly simplified and intensively managed agricultural landscape of California’s Central Val-  
44 ley. First, we determine whether network assembly was punctuated by significant reorganizations  
45 of interactions, and if assembling networks presented more change than the control, non-assembly  
46 hedgerows. We next tested whether the species that are most variable in their network position  
47 — and thus important contributors to network reorganizations — are less persistent and connected  
48 species, as would be expected by preferential attachment. To further explore the mechanisms  
49 underlying the temporal dynamics of the networks, also we examine patterns in the species and in-  
50 teraction temporal turnover. Finally, we investigate whether networks assemble toward predictable  
51 interaction patterns, and the ramifications for the robustness of the networks.

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

61 Preferential attachment, the most widely explored mechanism of network assembly, predicts that  
62 species entering a network are more likely to interact with species that are already well-connected  
63 [the “rich-get-richer” principle, 5]. In pollination systems — a particularly ubiquitous mutual-

64 ism [49, 36] — some studies have found support for this assembly mechanism. Investigating the  
65 day-to-day, temporal assembly of a plant-pollinator network within a season, [48] found that phe-  
66 nologically new plant and pollinator species tended to interact with already well-connected species,  
67 potentially because these species are either more abundant or temporally persistent. Using a space-  
68 for-time substitution to study primary succession, [2] also found evidence that assembly along a  
69 glacier foreland occurred through preferential attachment. Specifically, network nestedness (i.e.,  
70 a core group of generalists interacts with both specialist and generalist species) increased as the  
71 community aged [2]. An increase in nestedness could have occurred via the preferential attachment  
72 process, whereby specialist species attach to the well-connected, generalist core.

73 Significant reorganizations of interactions — change points — can also punctuate assembly [51]. A  
74 change point is caused by a merge, split, fragmentation or formation of modules within a network.  
75 Such interaction reorganizations are observed in social networks responding to abrupt shifts in  
76 the behavior of interactors [51]. In ecological communities, such shifts may occur if, as new  
77 species colonize, resident species change their interaction partners to optimize their foraging effort  
78 [54, 12, 63, 2, 62]. For preferential attachment to be at play, change points would need to be  
79 driven primarily by peripheral, temporally variable species while a stable, well-connected core  
80 of species remained stable in their interactions. No studies, however, have examined if network  
81 changing points occur during ecological network assembly and/or how these changes relate to  
82 species behavior.

83 Understanding network assembly is particularly relevant to ecological restoration, which is es-  
84 sentially “applied succession” [e.g., 50]. In pollination systems, time has been shown to affect the  
85 structure of networks in restored areas [25, 19], suggesting that interactions change as a community  
86 develops. Facilitating network restoration is especially imperative in areas where species interac-  
87 tions provide essential ecosystem services, such as crop pollination in agricultural landscapes. To  
88 promote pollinator services in agriculture, some farmers plant strips of native plants along farm

edges (hedgerows). By providing habitat, hedgerows augment the richness, abundance and trait diversity of pollinators in agricultural landscapes [44, 37, 53], and promote the persistence and colonization of floral resource specialists [42]. As the community assembles, it is important to understand how these new species are incorporated into the network as well as the consequences of adding species for interaction patterns and robustness.

We explore the process of network development using a eight-year dataset of plant-pollinator community assembly following hedgerow installment in the highly simplified and intensively managed agricultural landscape of California's Central Valley. We first determine whether network assembly was punctuated by significant reorganizations of interactions. We next tested whether the species that are most variable in their network position — and thus important contributors to network reorganizations — are less persistent and connected species, as would be expected by preferential attachment. To further explore the mechanisms underlying the temporal dynamics of the networks, also we examine patterns in the species and interaction temporal turnover. Finally, we investigate whether networks assemble toward predictable interaction patterns, and the ramifications for the robustness of the networks.

## Materials & Methods

### Study sites and collection methods

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

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

119 Sites were sampled between two and five times per year (Tables S1-S3, mean 3.4 samples per  
120 year). In each round of sampling, the order in which sites were sampled was randomized. Surveys  
121 were conducted under sunny conditions when the temperature was above  $21^\circ\text{C}$  and wind speed  
122 was below 2.5 meters/second.

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

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

<sup>136</sup> **Change point analysis**

<sup>137</sup> **Identifying change points**

<sup>138</sup> We employed a change point detection method [51] to identify fundamental reorganizations in  
<sup>139</sup> large-scale interaction patterns. Change point detection methods have yet to be generalized to  
<sup>140</sup> quantitative networks, so for this analysis we focused on qualitative (binary) networks. Following  
<sup>141</sup> [51], we first defined a probability distribution over the networks using the generalized hierarchi-  
<sup>142</sup> cal random graph model (GHRG). The GHRG model captures both assortative and disassortative  
<sup>143</sup> structure patterns at all scales in the network [51]. A network  $G$  is composed of vertices  $V$  and  
<sup>144</sup> edges  $E$ . The GHRG model decomposes the  $N$  vertices into a series of nested groups, the rela-  
<sup>145</sup> tionships among which are represented by the dendrogram  $T$ . The tips of  $T$  are the vertices of  $G$ ,  
<sup>146</sup> and the probability that two vertices  $u$  and  $v$  connect is given by the parameter  $p_r$ . The probability  
<sup>147</sup> distribution of the network  $G$  is thus defined as:

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

<sup>148</sup> Where  $E_r$  is the observed number of edges between vertices with the common ancestor  $r$ , and  $N_r$   
<sup>149</sup> is the total possible edges, and the rest of the notation is described above.

<sup>150</sup> Using Bayesian posterior inference and techniques from phylogenetic tree reconstruction, we fit  
<sup>151</sup> the GHRG model to the networks [51]. We used a Markov chain Monte Carlo (MCMC) procedure  
<sup>152</sup> to first sample the posterior distribution of bipartitions, from which a consensus tree was derived  
<sup>153</sup> [51]. We used  $\beta$  distributions with the hyperparameters  $\alpha = \beta = 1$  to define priors for  $p_r$ .

<sup>154</sup> Once the GHRG model was fit to the networks, we determined whether a change point occurred  
<sup>155</sup> between two time slices. To detect a change point, we used Bayes factors to compare the fit of two  
<sup>156</sup> models — one where a change point occurred between two networks, and one where no change  
<sup>157</sup> occurred. We chose a sliding window of length,  $w$ , of four years to detect change points. Larger

158 windows allow for more gradual changes, and four was the maximum possible with our eight years  
159 of data. Lastly, to calculate a *p*-value for the Bayes factors, we used parametric bootstrapping to  
160 numerically estimate the null distribution [51]. We employed code published online by L. Peel for  
161 the change point analysis. Analyses were conducted in Python 3.4.

162 We next tested whether the change points occurring in maturing hedgerows were a component of  
163 the assembly process or a product of environmental shifts that lead to network reorganizations in  
164 all types of communities. We modeled the number of change points as successes and the total  
165 number of sample years at each site as trials, and used a generalized linear model with Binomial  
166 error to test whether the probability of a change point occurrence varied by site type. We used  
167 standard techniques to determine whether the assumptions of the models were met for this and all  
168 subsequent models. For the non-assembling controls, only sites with five or greater survey years  
169 were included in this analysis ( $N = 11$ ). All statistical analyses were conducted in R 3.2.3 [55].

## 170 **Characteristics of species that contribute to change points**

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

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

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

180 To represent network position variability, we computed the coefficient of variation of weighted  
181 closeness centrality [26] at each site through time. Closeness centrality represents the importance

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

## Species and interaction turnover

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

To estimate the temporal species and interaction turnover, we used an approach similar to calculating spatial  $\beta$ -diversity. Instead of calculating the variation in community composition across sites within a year, we estimated turnover across years at a site. We first calculated the pairwise

206 dissimilarity of plants, pollinators and interactions between years within each site using the Chao  
207 dissimilarity estimator that incorporates abundances, while also accounting for unobserved records  
208 [16]. Dissimilarity estimates can be affected by the total number of species and individuals sam-  
209 pled at a site [e.g., 53]. For example, the probability that two sites do not share any species is  
210 higher when there are few individuals at those sites. Following [53], we used null models that con-  
211 strained species richness to estimate the deviation of the observed dissimilarity from that which  
212 would be expected under a random community assembly process. With the corrected dissimilarity  
213 values, we then calculated the multivariate dispersion of community composition across years [4].  
214 In order to test whether assembling hedgerows had more species and interactions turnover than  
215 non-assembling communities, the species and interaction temporal turnover estimates were mod-  
216 eled as responses in a linear mixed model with site type as an explanatory variable and site as a  
217 random effect [10, 38].

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

232 **Temporal changes in interaction patterns**

233 **Network structure**

234 Any changing points in network structure may contribute to the reorganization of the assembling  
235 networks into predictable interaction patterns. Pollination networks exhibit two main structural  
236 patterns — modularity [e.g., 47] and nestedness [e.g., 8, 7]. In modular networks, interactions are  
237 insular, occurring within separate groups or “modules” more often than between modules. Mod-  
238 ules in the network may fragment as the network assembles, enhancing modularity. Conversely,  
239 nested networks are like a pyramid of interactions, where there are some species that interact with  
240 many species, other species that interact with a subset of those species, and so on. If species en-  
241 tering the network tend to interact with the generalist base of the network pyramid as would be  
242 expected with preferential attachment, nestedness would increase through time. The connectance  
243 — the proportion of observed out of possible interactions — would also decrease as new, special-  
244 ist species, preferentially attach to the core. Finally, network-level specialization will increase if  
245 specialist species colonize the network or species begin to limit their interaction niche breadth as  
246 the network assembles [11].

247 To evaluate network nestedness, we used the estimator weighted NODF [3]. NODF evaluates  
248 whether species with fewer partners interact with subsets of partners with which more connected  
249 species interact [3]. To estimate modularity, we used a hierarchical clustering algorithm [45, 18].  
250 We evaluated network specialization with the metric H2, which estimates the deviation of the  
251 observed interaction frequency between plants and pollinators from a null expectation where all  
252 partners interact in proportion to their abundances [11]. It ranges from zero for generalized net-  
253 works to one for specialized networks. We calculated standardized z-scores so that nestedness,  
254 modularity and specialization metrics could be compared across communities. The z-scores were  
255 calculated by generating an ensemble of 999 randomly assembled communities, subtracting the

256 mean of the statistic calculated across these communities from the observed value, and then divid-  
257 ing by the standard deviation. To assemble random communities, we reshuffled the interactions  
258 between species but fixed the total number of interactions, species and interaction frequency dis-  
259 tributions [27].

260 To test whether network modularity, nestedness, connectance or specialization changed linearly  
261 with assembly, we used linear mixed models with the descriptive network metrics as the response  
262 variable, year of assembly as the explanatory variable, and random effects of site and year. The  
263 number of species in a network affects the patterns of interaction possible, so we also examined  
264 the change in plant and pollinator species richness through time. We employed generalized linear  
265 mixed models with Poisson error to model richness [10]. We scaled explanatory variables.

## 266 Network robustness

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

276 We also explored how the robustness to cascading perturbations changed as the community as-  
277 sembled, using algebraic connectivity — the second smallest eigenvalue of the Laplacian matrix  
278 [23] — as a proxy for network robustness. Algebraic connectivity relates to how difficult it is to  
279 turn a network into completely disconnected groups of species [17, 28]. The larger the algebraic

connectivity, the more sensitive a network is to cascading perturbations. Perturbations, such as the decrease in abundance of a plant or pollinator, can have negative consequences for the species in the network. For example, a decrease in abundance of a pollinator will diminish the pollination services it provides to plants. The affected plants would set less seeds, and decrease in abundance the subsequent year. Consequently, other pollinators that depended on those plant species would also be affected, and the effects of this perturbation would continue to propagate throughout the network. Alternatively, perturbations could also have a positive effect if, for example, the increase in the abundance of a plant species lead to an increase in resource availability for pollinators. The examples of negative perturbations (e.g., resource collapse, disease spreading, parasites), however, outnumber possible positive perturbations. It is important to note that both robustness and algebraic connectivity assume that the network is static — they do not account for the ability of species to alter their interaction depending on circumstances and the resource availability.

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

## Results

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

299 **Change point analysis**

300 **Identifying change points**

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

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

311 In contradiction to the predictions of assembly by preferential attachment, both pollinator per-  
312 sistence and degree were positively related to network position variability (Fig. 4, estimate of  
313 the slope of closeness centrality variability and persistence  $\pm$  standard error of the estimate,  
314  $0.496 \pm 0.182$ ,  $p\text{-value}=0.016$ ; slope of closeness centrality variability and degree,  $0.004 \pm 0.002$ ,  
315  $p\text{-value}=0.056$ ). The slope of these relationships remained significant when the species with the  
316 top 10 persistence and degree scores were dropped. In addition, plant persistence and degree were  
317 not significantly related to network position variability (Fig. 4). The variability of species net-  
318 work position was not the result of closeness linearly increasing through time, and, in fact, plant  
319 and pollinator closeness decreased slightly through time (Fig. S2, estimate of the slope of close-  
320 ness through time  $\pm$  SE, pollinators:  $-0.082 \pm 0.021$ ,  $p\text{-value}=0.003$ ; plants  $-0.089 \pm 0.044$ ,  
321  $p\text{-value}=0.04$ ).

322 **Species and interaction turnover**

323 The rates of plant, pollinator and interaction temporal turnover were similar across assembling  
324 hedgerows, non-assembling hedgerows and field margins, though mature hedgerows had marginally  
325 less pollinator turnover than field margins (Fig. 5, estimate  $\pm$  SE of the difference in turnover be-  
326 tween field margins and mature hedgerows,  $-0.051 \pm 0.026$ ,  $p\text{-value}=0.049$ ). The turnover of  
327 plants and interactions was not significantly different between site types. When interactions were  
328 weighted by their similarity, both assembling and mature hedgerows had higher rates of turnover  
329 than field margins (Fig. 5, estimate  $\pm$  SE of the difference in turnover between field margins  
330 and assembling hedgerows,  $0.115 \pm 0.027$ ,  $p\text{-value}=0.0002$ ; field margins and mature hedgerows,  
331  $0.082 \pm 0.024$ ,  $p\text{-value}=0.002$ ). The weighted interaction turnover at assembling hedgerows, how-  
332 ever, was not significantly higher than in non-assembling, mature hedgerows.

333 **Temporal changes in interaction patterns**

334 **Network structure**

335 Nestedness, modularity and specialization did not change predictably assembly (Fig. 6). All of the  
336 networks were significantly nested ( $z$ -scores  $> 2$ ), but not modular ( $z$ -scores  $< 2$ , Fig. 6). Most  
337 communities were more generalized than expected when interactions were randomized (Fig. 6).

338 Connectance decreased as the community assembled (Fig. 6, estimate of the slope of connectance  
339 through time  $\pm$  standard error of the estimate,  $-0.023 \pm 0.008$ ,  $p\text{-value}=0.007$ ).

340 Both plant and pollinator species richness increased through time (Fig. 6, estimate of the slope of  
341 richness through time  $\pm$  SE, pollinators:  $0.136 \pm 0.064$ ,  $p\text{-value}=0.034$ ; plants:  $0.140 \pm 0.060$ ,  
342  $p\text{-value}=0.012$ ). Unsurprisingly, pollinator species are colonizing and persisting at the assembling  
343 hedgerows. Plant species richness in the networks is based on the flowers actually visited by

<sup>344</sup> pollinators and not the presence of a particular plant species at a site. Thus, though some new plant  
<sup>345</sup> species may establish themselves in the hedgerows, the increase in plant richness in the networks is  
<sup>346</sup> likely due to previously unvisited plants attracting visitors as they mature and offer better rewards.

## <sup>347</sup> **Network robustness**

<sup>348</sup> Assembly did not affect network robustness to species extinction when species were removed  
<sup>349</sup> incrementally by degree or abundance (Fig. S3). Similarly, the sensitivity of networks to cascading  
<sup>350</sup> perturbations, as measured by the algebraic connectivity of the network, did not change predictably  
<sup>351</sup> as the community assembled (Fig. S3).

## <sup>352</sup> **Discussion**

<sup>353</sup> We show that the temporal assembly of plant-pollinator networks following restoration is a highly  
<sup>354</sup> dynamic process in which interactions often undergo significant reorganizations, or changing points.  
<sup>355</sup> If these network reorganizations were a product of environmental forces alone, we would expect to  
<sup>356</sup> observe the same changing points at the same time periods, consistently across all sites. However,  
<sup>357</sup> network changing points in non-assembling communities are less frequent, and there are few con-  
<sup>358</sup> sistent trends in the years when change points occurred across all sites. Several sites had network  
<sup>359</sup> changing points between years 2009 and 2011 (Fig. 2). In California, 2011 marked the begin-  
<sup>360</sup> ning of a multi-year drought. The assembling hedgerows were not sampled in 2010, so we cannot  
<sup>361</sup> disentangle whether the point changes are due to skipping a year of monitoring or the drought.  
<sup>362</sup> Interestingly, most assembling hedgerows did not undergo a significant interaction reorganization  
<sup>363</sup> immediately after planting (i.e., the transition from weedy field margin to hedgerow). This result  
<sup>364</sup> is consistent with the finding that hedgerow restoration takes several years to have an impact on the  
<sup>365</sup> plant-pollinator communities in our study system, as well as with the observation that hedgerows

366 do not begin to produce many flowers until 3 – 5 years following planting [37].

367 In a preferential attachment process, we expect that the most persistent and high degree species (the  
368 species with the most unique interaction partners) would remain stable in the network core during  
369 assembly [5]. Surprisingly, however, we encountered the opposite pattern. For example, the four  
370 most ubiquitous species in our study landscape — *Halictus ligatus*, *Halictus tripartitus*, *Lasioglos-*  
371 *um (Dialictus incompletum)*, and *Toxomerus marginatus* — were the only species that changed  
372 which module they were a member in across years in all the assembling hedgerows. Because  
373 species degree and persistence were strongly correlated, it is difficult to disentangle the causal  
374 mechanism for why species with those characteristics are so variable in their network position.  
375 Species that can interact with a relatively high number of partners may be better able to exploit the  
376 limited floral resources in the intensively managed agriculture landscape, and thus also be the most  
377 persistent [in ant-plant mutualisms, 20]. More persistent species usually have longer phenologies,  
378 so they can visit many different flowers, resulting in a higher degree [65, 24]. Either way, our result  
379 suggests that adaptable species can change their network position to utilize the most advantageous  
380 floral resources available, which may depend on both the other pollinator species that are present  
381 and the state of the plant community [67, 29, 39]. Thus given the opportunity and ability to use  
382 different resources, species will often change their network positions [39].

383 Interestingly, though assembling hedgerows had more network reorganizations than non-assembling  
384 communities, pollinator species and interaction turnover occurred at similar rates across site types.  
385 Assembling hedgerows have higher turnover than non-assembling field margins only when inter-  
386 actions were weighted by their similarity. This is likely because though species and interactions  
387 are turning over at the field margins, species and interactions that fill similar roles in the network  
388 are replacing each other. In contrast, at the assembling hedgerows, unique interactions are turn-  
389 ing over as the networks continually reorganize. Non-assembling mature hedgerow communities,  
390 however, had similar rates of weighted interaction turnover as assembling hedgerows but also the

391 lowest pollinator turnover. Pollinator communities at mature hedgerows may generally be more  
392 stable, but rare and/or specialized pollinators could generate this pattern if they entered a commu-  
393 nity, formed unique interactions with plants that did not previously share pollinators, but did not  
394 persist in the networks. These species would not contribute strongly to network reorganization or  
395 species turnover, but would enhance weighted interaction turnover. Mature hedgerows therefore  
396 both support more stable pollinator communities, while also providing resources for rare and/or  
397 specialized species [37, 42].

398 When we explored how network-level interaction patterns changed through time, we found few  
399 patterns. The connectance decreased, as would be expected if the network is being colonized by  
400 specialist species [42]. Network specialization, however, did not change predictably with assembly.  
401 Decreasing connectance without an accompanying increase in specialization would be possible  
402 if the increased colonization of specialized species was accompanied by an increase in the diet  
403 breath of resident species. This would be expected if resident species were able to minimize their  
404 foraging time by expanding their diet breath as plant diversity increases with hedgerow maturation  
405 [54, 67, 12, 2].

406 Interestingly, however, the changes in network patterns associated with assembly did not affect  
407 the hedgerow network robustness to species extinction or susceptibility to cascading perturbations.  
408 The hedgerows were designed to provide floral resources for the largest number of pollinators  
409 across the growing season [41]. The generalized nature of the floral community may explain why  
410 the networks tended to be more generalized than expected if interactions were randomly distributed  
411 across species (Fig. 6). In addition, the design of the hedgerow plantings may have facilitated the  
412 emergence of a single, highly connected module in all of the networks (see 3 for examples). This  
413 network configuration results in short path lengths (the distance between species in a network  
414 based on their shared partners), and thus, a perturbation in one species can more easily spread to  
415 other species. These networks are also vulnerable to the extinction of highly connected species

[13]. In order to promote more resilient communities, future restoration efforts should explore designing floral communities to promote more interaction partitioning using, for example, algorithms to optimize different network properties based on prior knowledge of pollinator floral preferences [43], and on desired network architectures that renders them more robust both to species loss and to cascading effects.

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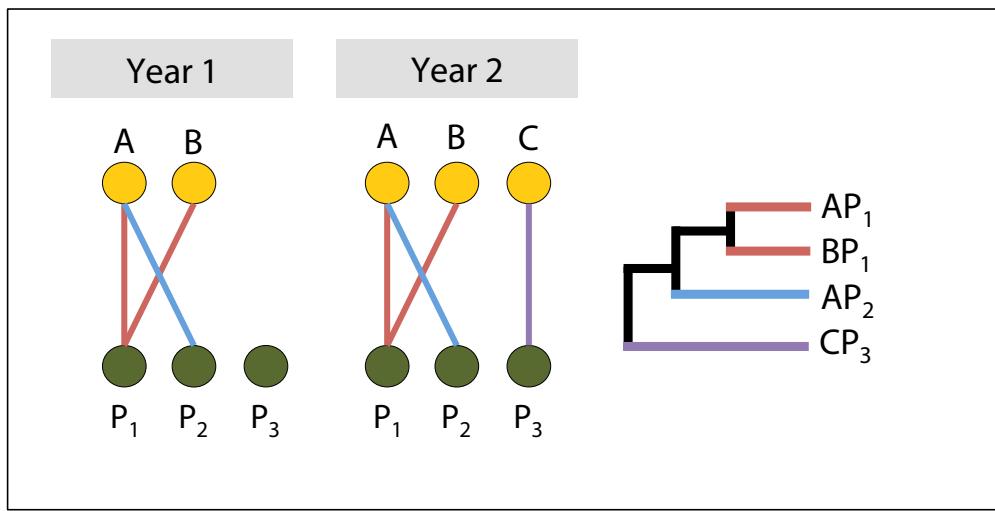


Figure 1: Diagram illustrating the analysis to examine the temporal turnover of interactions weighted based on their similarity. A, B and C are animal species, and Ps are plant species. The dendrogram depicts the interaction similarity across years based on the number of shared constituent species.

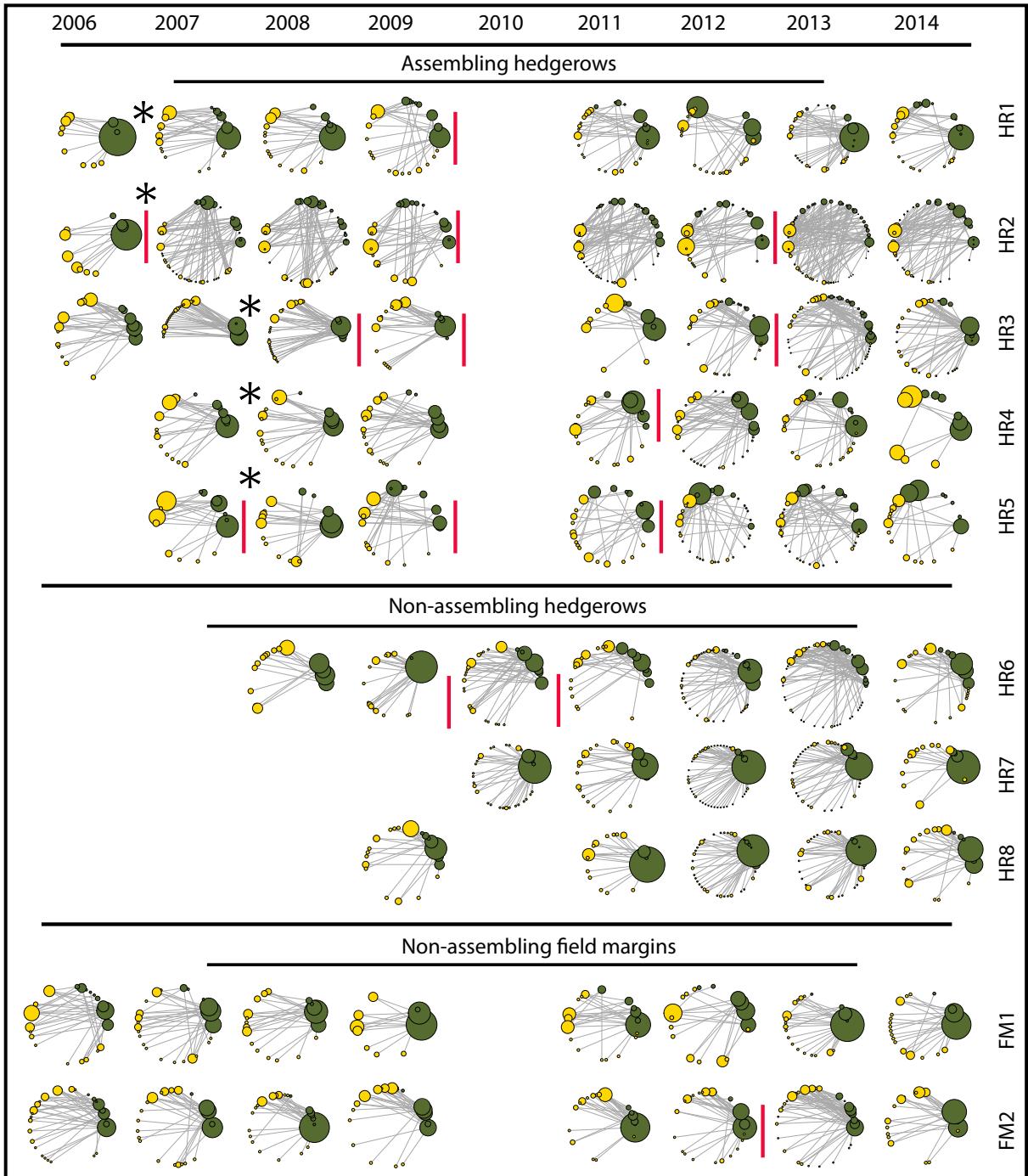


Figure 2: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, weighted 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.

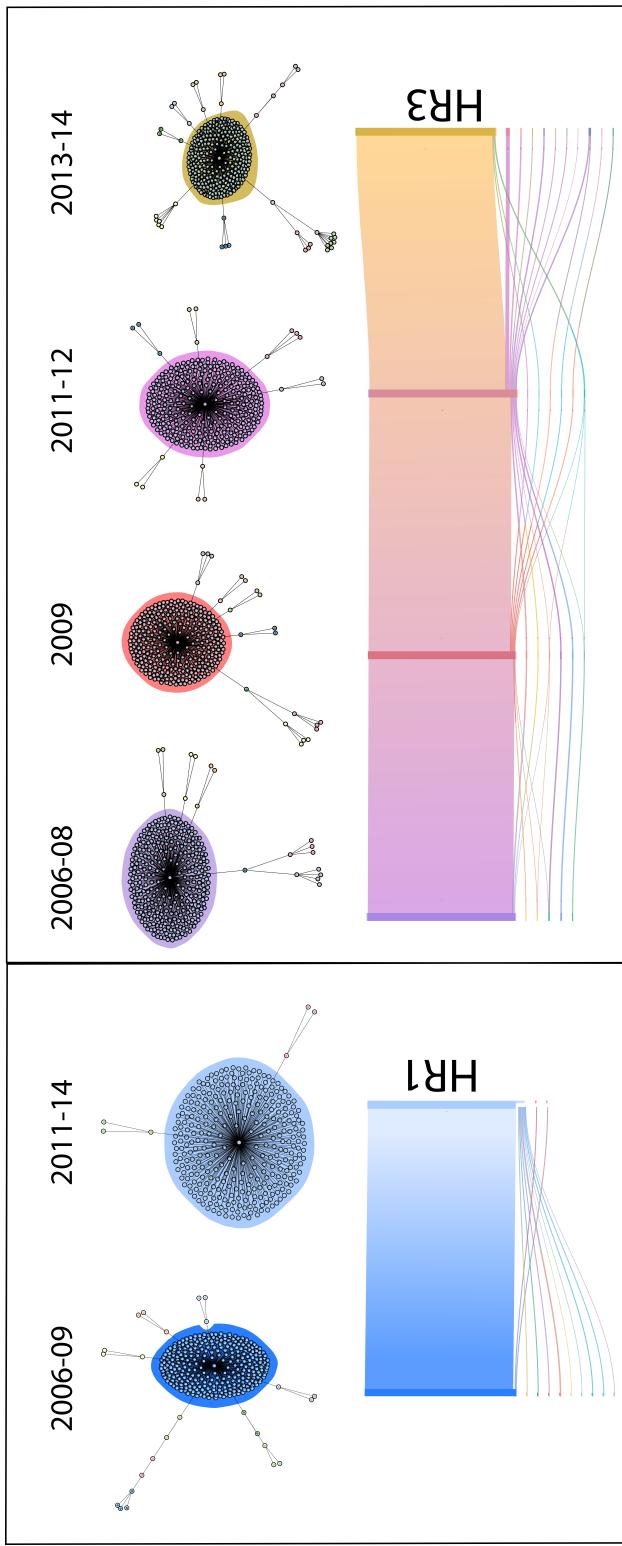


Figure 3: The species module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species to different modules between change points.

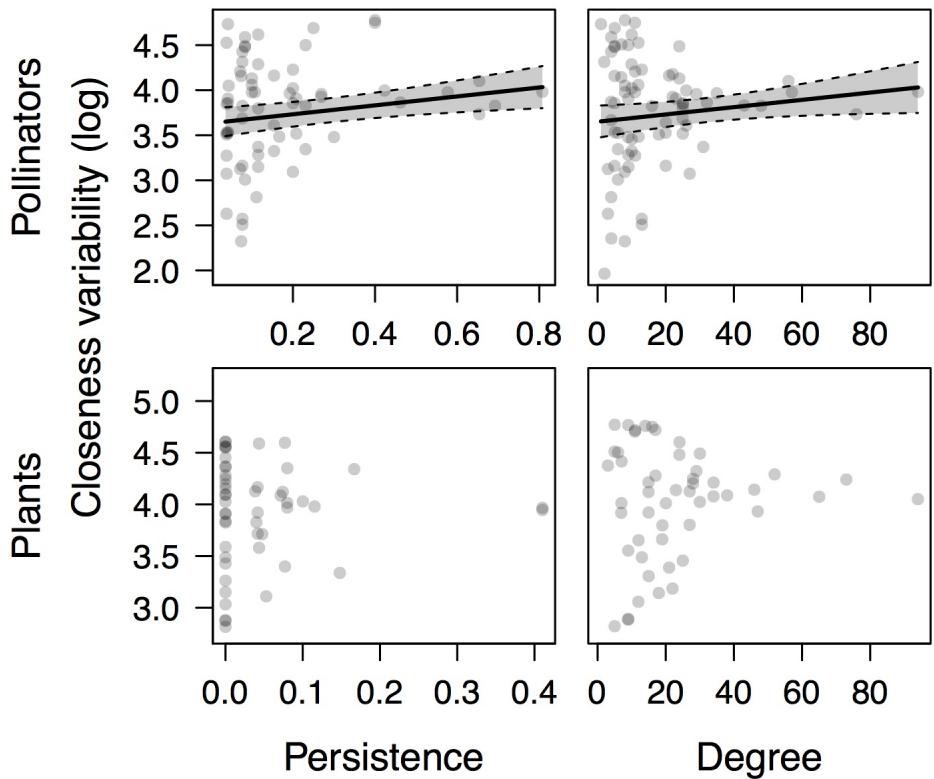


Figure 4: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across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

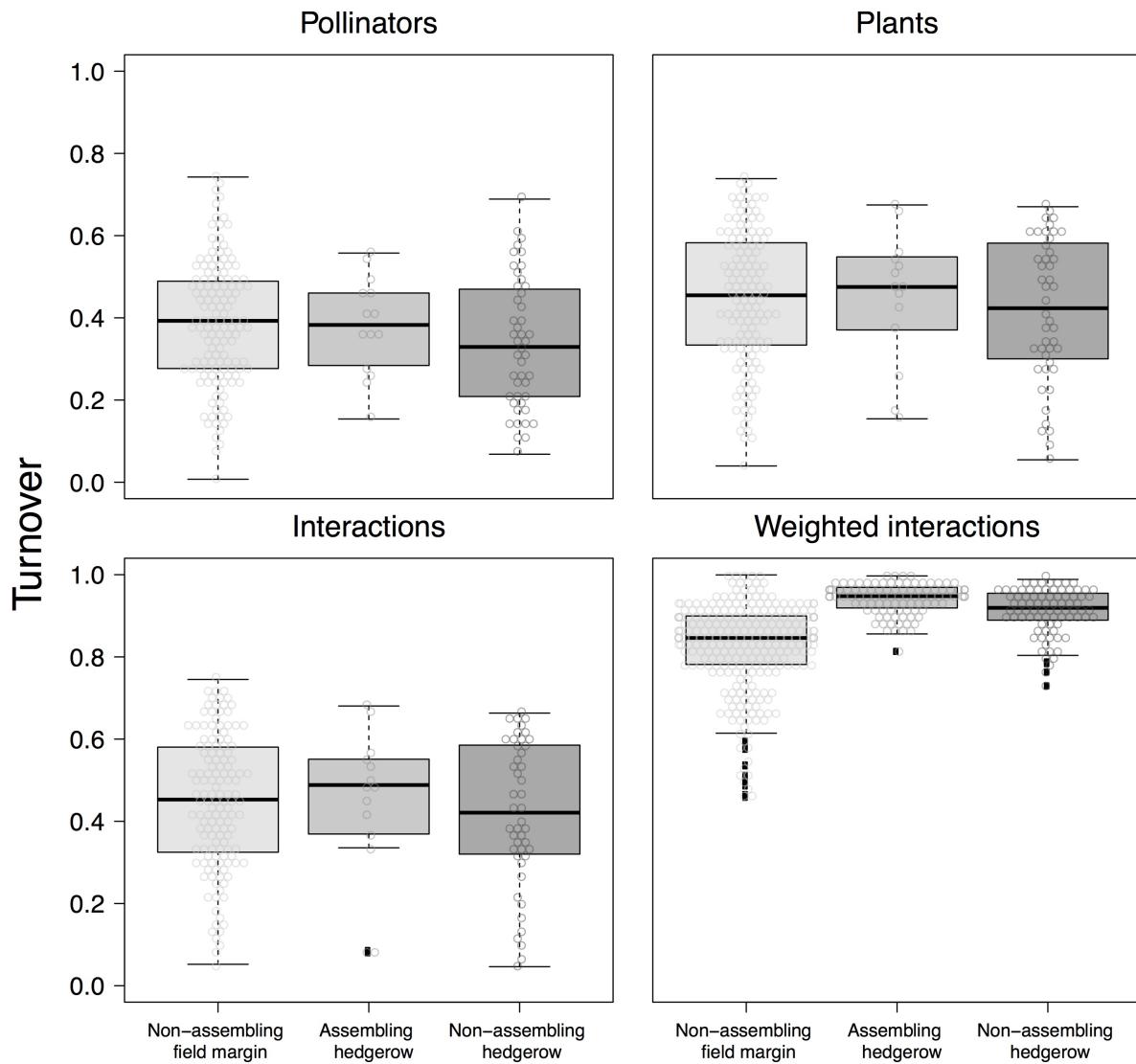


Figure 5: Species interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally 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).

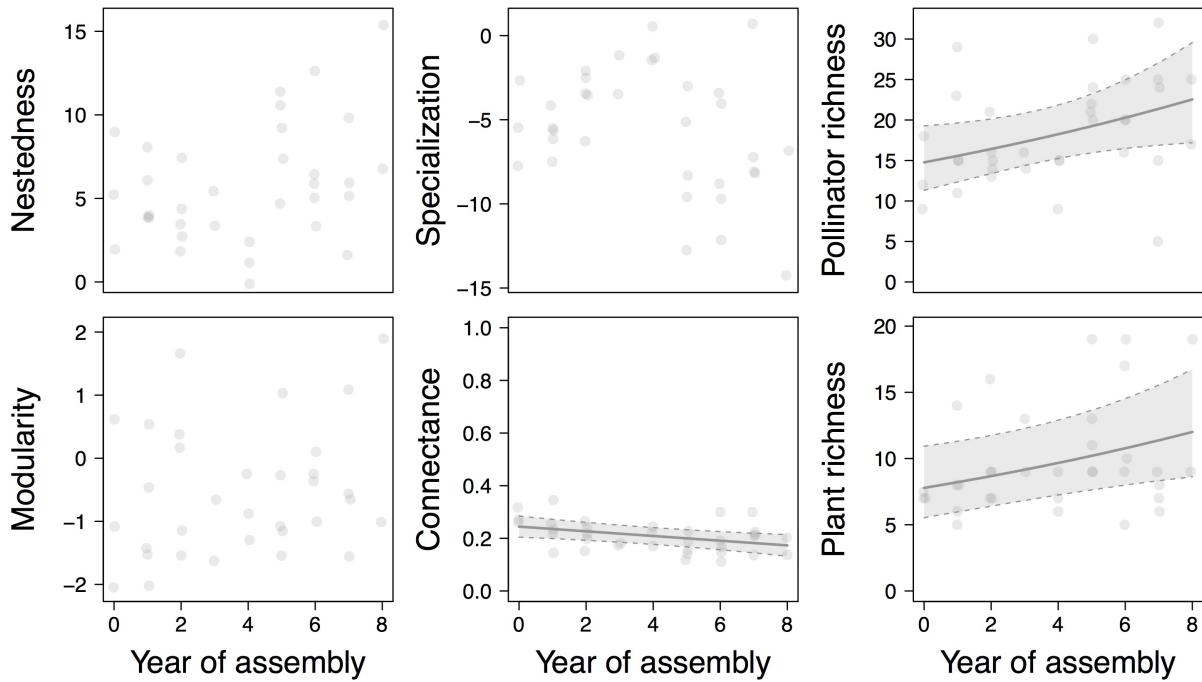


Figure 6: Plant richness and pollinator richness increased as the networks assembled. Nestedness, modularity and specialization did not change predictable across years, while connectance decreased. The nestedness, modularity and specialization scores represent z-scores. Scores greater than  $\sim 2$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