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Major network reorganizations punctuate the assembly of plant-pollinator communities

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Abstract

As the world continues to lose species at an alarming rate, anticipating a community's ability to resist collapse will depend on the strength of interaction networks. We know little, however, about how to re-assemble interacting communities through restoration, or the process of ecological network assembly more generally. Using an eight-year dataset comprising nearly 20,000 pollinator visitation records, we explore the assembly of plant-pollinator communities at native plant restorations sites in an agricultural landscape. We find that species occupy highly dynamic network positions through time, causing the community assembly process to be punctuated by major network reorganizations. In contrast, the non-assembling networks do not restructure as frequently. The most persistent and generalized species are also the most variable in their network positions, contrary to what is expected by assembly following preferential attachment — a widely supported assembly mechanism. Our results fundamentally alter our understanding of how communities assembly and how species interactions change through time while helping to inform efforts to re-assemble robust communities through restoration.

¹⁷ community assembly, change points, robustness, nestedness, modularity, bipartite, preferential attachment

19 **Introduction**

20 When a species goes extinct, more than a species is lost. That species interacted with
21 other species in its community, likely in ways that were important or even crucial to oth-
22 ers' survival. When a community — a unique combination of interacting species — loses
23 one species, the system becomes weaker. Global change has created a severe biodiversity
24 crisis, and as species are lost, so are their interactions [1, 2]. A community's ability to re-
25 sist collapse will depend on the strength of each interaction network [3–6]. To safeguard
26 ecological function, it has become increasingly imperative to aid the recovery of lost inter-
27 actions and component biodiversity and by facilitating the assembly of robust interaction
28 networks via ecological restoration [7]. However, we know very little about how ecologi-
29 cal networks assemble in general, rendering restoration of interacting communities quite
30 difficult.

31 Preferential attachment, the most widely explored mechanism of network assembly, pre-
32 dicts that species entering a network are more likely to interact with species that are
33 already well-connected [the “rich-get-richer” principle, 8]. In pollination systems — a
34 particularly ubiquitous mutualism [9, 10] — some studies have found support for this as-
35 sembly mechanism. Investigating the day-to-day, temporal assembly of a plant-pollinator
36 network within a season, [11] found that phenologically new plant and pollinator species
37 tended to interact with already well-connected species, potentially because these species
38 are either more abundant or temporally persistent. Using a space-for-time substitution to
39 study primary succession, [12] also found evidence that assembly along a glacier foreland
40 occurred through preferential attachment. Specifically, network nestedness (i.e., a core
41 group of generalists interacts with both specialist and generalist species) increased as the
42 community aged [12]. An increase in nestedness could have occurred via the preferential
43 attachment process, whereby specialist species attach to the well-connected, generalist

44 core.

45 Preferential attachment, the most widely explored mechanism of network assembly, [8],
46 predicts that species entering a network are more likely to interact with species that are
47 already well-connected [the “rich-get-richer” principle, 8]. In pollination systems — a
48 particularly ubiquitous mutualism [9, 10] — some studies have found support for this as-
49 sembly mechanism. Investigating the day-to-day, temporal assembly of a plant-pollinator
50 network within a season, [11] found that phenologically new plant and pollinator species
51 tended to interact with already well-connected species, potentially because these species
52 are either more abundant or more temporally persistent. In addition, using a space-for-
53 time substitution to study primary succession along a glacier foreland, [12] also found
54 some evidence that assembly occurred through preferential attachment. Specifically, net-
55 work nestedness (i.e, a core group of generalists interacts with both specialist and gen-
56 eralist species) increased as the community aged [12]. An increase in nestedness could
57 result from the preferential attachment process where specialist species attach to the well-
58 connected, generalist core.

59 In contrast to the network build-up described by preferential attachment, significant re-
60 organizations of interactions can also punctuate assembly [13]. Such significant reorgani-
61 zations of interactions, or network changing points, are observed in social networks that
62 respond to abrupt shifts in the behavior of interactors [13]. A change point is caused by a
63 merge, split, fragmentation or formation of modules within a network. In ecological com-
64 munities, such shifts may occur if, as new species colonize, resident species change their
65 interaction partners to optimize their foraging effort. In plant-pollinator communities,
66 theory predicts that pollinators optimize their use of floral resources to reduce interspe-
67 cific competition and improve resource-use efficiency [12, 14–17]. No studies, however,
68 have examined if network changing points occur during ecological network assembly

69 and/or how these changes relate to species behavior.

70 Understanding network assembly is particularly relevant to ecological restoration, which
71 is essentially “applied succession” [e.g., 18]. In pollination systems, time has been shown
72 to affect the structure of networks in restored areas [19, 20], suggesting that interactions
73 change as a community develops. Facilitating network restoration is especially imper-
74 ative in areas where species interactions provide essential ecosystem services, such as
75 crop pollination in agricultural landscapes. To promote pollinator services in agriculture,
76 some farmers plant strips of native plants along farm edges (hedgerows). By providing
77 habitat, hedgerows augment the richness, abundance and trait diversity of pollinators
78 in agricultural landscapes [21–23], and promote the persistence and colonization of flo-
79 ral resource specialists [24]. As the community assembles, it is important to understand
80 how these new species are incorporated into the network as well as the consequences of
81 adding species for interaction patterns and robustness.

82 We explore the process of network development using a nine-year dataset of plant-pollinator
83 community assembly following hedgerow restoration in the highly simplified and inten-
84 sively managed agricultural landscape of California’s Central Valley. We first determine
85 whether the mechanism underlying network assembly represents a buildup of interac-
86 tions as would be predicted by preferential attachment or significant reorganizations of
87 interactions (i.e., network changing points). Even with changing points in interaction
88 organization, networks could still assemble via preferential attachment if the network re-
89 organizations were primarily driven by peripheral, temporally variable species while a
90 stable, well-connected core of species persist. Therefore, we tested whether the species
91 that are most variable in their network position — and thus important contributors to
92 network reorganizations – are less persistent and connected species. To further explore
93 the mechanisms underlying the temporal dynamics of the networks, also we examine

94 patterns in the species and interaction temporal turnover. Finally, we investigate whether
95 networks assemble toward predictable interaction patterns, and the ramifications for the
96 robustness of the networks.

97 Materials & Methods

98 Study sites and collection methods

99 Study sites were located in the Central Valley of California in Yolo, Colusa and Solano
100 Counties. This area is composed of intensively managed agriculture — primarily mono-
101 cultures of conventional row crops, vineyards and orchards. Hedgerows border large
102 (ca. 30-hectare) crop fields and measured between 3 – 6 m wide and approximately
103 350 m long. Hedgerows consist of native, perennial, shrub and tree plantings [Fig. S1,
104 7, 22, 24].

105 We selected five farm edges to be restored as hedgerows. We monitored those locations
106 before the hedgerow was planted, and tracked the assembly of the community for up
107 to seven years as the hedgerow matured (from 2006 – 2014). For controls, we concur-
108 rently monitored non-assembling communities within mature hedgerows (greater than
109 10 years since planting, $N = 29$) and unrestored, weedy field margins ($N = 19$). The
110 mean distance between monitoring sites was 15 km, and the minimum distance between
111 sites sampled in the same year was 1 km. The entire area surveyed spanned almost 300
112 km^2 . The crop fields adjacent to all sites were similarly managed as intensive, high-input
113 monoculture.

114 Sites were sampled between two and five times per year (Tables S1-S3, mean 3.4 samples
115 per year). In each round of sampling, the order in which sites were sampled was random-

¹¹⁶ ized. Surveys were conducted under sunny conditions when the temperature was above
¹¹⁷ 21°C and wind speed was below 2.5 meters/second.

¹¹⁸ During each sampling round, flower-visitors to plants in assembling hedgerows and non-
¹¹⁹ assembling controls were netted for one hour of active search time (the timer was paused
¹²⁰ when handling specimens). The identify of the plant being visited was recorded for each
¹²¹ floral visitor. Honeybees (*Apis mellifera*) were not collected because their abundance is
¹²² determined largely by hive placement by bee-keepers. All other insect flower visitors
¹²³ that touched the reproductive parts of the flower were collected; however, here we focus
¹²⁴ only on wild bees and syrphids — the most abundant and effective pollinators in the
¹²⁵ system (representing 49 and 19 percent of records, respectively, C. Kremen, A. Klein and
¹²⁶ L. Morandin, unpublished data). Bee and syrphid specimens were identified to species
¹²⁷ (or morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*) by expert
¹²⁸ taxonomists.

¹²⁹ Quantitative networks were generated for each site through time. Because the nuber of
¹³⁰ sampling rounds varied between years (Tables S1-S3), we used the mean of the inter-
¹³¹ actions between a pair of plants and pollinators within a year to represent interaction
¹³² frequency.

¹³³ Change point analysis

¹³⁴ Identifying change points

¹³⁵ We employed a change point detection method [13] to identify fundamental reorgani-
¹³⁶ zations in large-scale interaction patterns. Change point detection methods have yet to
¹³⁷ be generalized to quantitative networks, so for this analysis we focused on qualitative
¹³⁸ (binary) networks. Following [13], we first defined a probability distribution over the

139 networks using the generalized hierarchical random graph model (GHRG). The GHRG
140 model captures both assortative and disassortative structure patterns at all scales in the
141 network [13]. A network G is composed of vertices V and edges E . The GHRG model
142 decomposes the N vertices into a series of nested groups, the relationships among which
143 are represented by the dendrogram T . The tips of T are the vertices of G , and the prob-
144 ability that two vertices u and v connect is given by the parameter p_r . The probability
145 distribution of the network G is thus defined as:

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

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

148 Using Bayesian posterior inference and techniques from phylogenetic tree reconstruction,
149 we fit the GHRG model to the networks [13]. This is accomplished by using a Markov
150 chain Monte Carlo (MCMC) procedure to first sample the posterior distribution of bi-
151 partitions, from which a consensus tree is derived [13]. We use β distributions with the
152 hyperparameters $\alpha = \beta = 1$ to define priors for p_r .

153 Once the GHRG model has been fit to the networks, we determine whether a change
154 point occurred between two time slices. To detect a change point, we use Bayes factors
155 to compare the fit of two models — one where a change point occurred between two
156 networks, and one where no change occurred. We chose a sliding window of length, w ,
157 of four years to detect change points. Larger windows allow for more gradual changes,
158 and four was the maximum possible with our eight years of data. Lastly, to calculate a
159 p -value for the Bayes factors, we use parametric bootstrapping to numerically estimate
160 the null distribution [13]. We employed code published online by L. Peel for the change

161 point analysis. Analyses were conducted in Python 3.4.

162 We next tested whether the change points occurring in maturing hedgerows were a com-
163 ponent of the assembly process or a product of environmental shifts that lead to network
164 reorganizations in all types of communities. We modeled the number of change points as
165 successes and the total number of sample years at each site as trials, and used a general-
166 ized linear model with Binomial error to test whether the probability of a change point
167 occurrence varied by site type. We used standard techniques to determine whether the
168 assumptions of the models were met for this and all subsequent models. For the non-
169 assembling controls, only sites with five or greater survey years were included in this
170 analysis ($N = 11$). All statistical analyses were conducted in R 3.2.3 [25].

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

172 To further elucidate the nature of the change points, we examine the characteristics of
173 the species that contributed to interaction reorganization. Some species remained in rel-
174 atively similar network positions through time, whereas others were more variable in
175 their position and thus contributed more strongly to network reorganization. We tested
176 whether the more persistent species with the highest degree (number of different inter-
177 action partners) were the most stable in their network positions, as would be expected if
178 the networks were assembling via preferential attachment.

179 We calculated species persistence as the proportion of surveys in which a plant or pol-
180 linator is observed. Species observed consistently within and between years were thus
181 maximally persistent. Weighted species degree is calculated from interaction observa-
182 tions from an extensive dataset from Yolo County (approx. 18000 interaction records) that
183 included both the data included in this study and additional data from sites where we
184 collected flower visitors using the same methods [23, 24]. To represent network position

¹⁸⁵ variability, we computed the coefficient of variation of weighted closeness centrality [26]
¹⁸⁶ at each site through time. Closeness centrality represents the importance of a space by
¹⁸⁷ calculating the path lengths to other vertices (species) in the network [26]. The shorter
¹⁸⁸ the mean path length to other species, the higher the closeness centrality. We used linear
¹⁸⁹ mixed models to test whether the species closeness variability (log) is related to the persis-
¹⁹⁰ tence or degree of that species [27, 28]. We included random effects for species and site.
¹⁹¹ Because the degree and persistence of pollinators were strongly correlated, ($\rho = 0.071$,
¹⁹² p -value $< 2 * 10^{-16}$), we included each explanatory variable in separate models. Plant
¹⁹³ degree and persistence were not significantly correlated, but we used the same models as
¹⁹⁴ we did for the pollinators for consistency. Because an approximately logarithmic increase
¹⁹⁵ in closeness centrality — as would be expected with assembly by preferential attachment
¹⁹⁶ — we also tested whether log closeness centrality increases through time.

¹⁹⁷ Species and interaction turnover

¹⁹⁸ Reorganizations of network structure can be the result of species turnover or species
¹⁹⁹ changing their interaction partners (i.e., re-wiring). To better understand the mechanisms
²⁰⁰ underlying the temporal dynamics of the assembling networks, we examined patterns
²⁰¹ of species and interaction turnover. For example, assembling networks may have higher
²⁰² rates of pollinator turnover than non-assembling communities because new pollinator
²⁰³ species are colonizing and establishing themselves [24]. Similarly, because species are
²⁰⁴ turning over and pollinators are trying to maximize their foraging efficiency based on the
²⁰⁵ species present, interactions may turnover more quickly than in established communities.
²⁰⁶ In addition, at assembling hedgerows, plants that are unvisited in early years may appear
²⁰⁷ to “colonize” the networks as they became more attractive resources and establish new
²⁰⁸ interactions with pollinators.

209 To estimate the temporal species and interaction turnover, we used an approach similar
210 to calculating spatial β -diversity. Instead of calculating the variation in community com-
211 position across sites within a year, we estimated turnover across years at a site. We first
212 calculated the pairwise dissimilarity of plants, pollinators and interactions between years
213 within each site using the Chao dissimilarity estimator that incorporates abundances,
214 while also accounting for unobserved records [29]. Dissimilarity estimates can be affected
215 by the total number of species and individuals sampled at a site [e.g., 23]. For example,
216 the probability that two sites do not share any species is higher when there are few in-
217 dividuals at those sites. Following [23], we used null models that constrained species
218 richness to estimate the deviation of the observed dissimilarity from that which would be
219 expected under a random community assembly process. With the corrected dissimilarity
220 values, we then calculated the multivariate dispersion of community composition across
221 years [30]. In order to test whether assembling hedgerows had more species and inter-
222 actions turnover than non-assembling communities, the species and interaction temporal
223 turnover estimates were modeled as responses in a linear mixed model with site type as
224 an explanatory variable and site as a random effect [27, 28].

225 Though species may turnover across years, some groups of species may essentially re-
226 place each other if they fill similar roles in the network, occupying the same network
227 position and interacting with similar species. At non-assembling communities, species
228 turnover may overestimate the temporal changes in the networks if the interactions oc-
229 curring in one year are similar to those in the next year when they are weighted by the
230 similarity of their constituent species (Fig. 1). We developed a method to examine the tem-
231 poral turnover of interactions with weightings based on their similarity. We followed the
232 algorithm of [31] to cluster all the interactions (edges) hierarchically across sites and years
233 based on their similarity, and build a dendrogram. The interaction similarity is based how
234 many plants and pollinators (vertices) two edges share [31, 32]. The more species edges

²³⁵ shared in common, the shorter the branch length between them on the dendrogram. We
²³⁶ next calculated the temporal turnover of interactions weighted by their similarity, as ap-
²³⁷ proximated by “phylogenetic” distance [33, 34]. We then used linear mixed models to
²³⁸ test whether the weighted turnover of interactions varied between assembling and non-
²³⁹ assembling networks, including site as a random effect [27, 28].

²⁴⁰ **Temporal changes in interaction patterns**

²⁴¹ **Network structure**

²⁴² Any changing points in network structure may contribute to the reorganization of the as-
²⁴³ sembling networks into predictable interaction patterns. Pollination networks exhibit two
²⁴⁴ main structural patterns — modularity [e.g., 35] and nestedness [e.g., 36, 37]. In modular
²⁴⁵ networks, interactions are insular, occurring within separate groups or “modules” more
²⁴⁶ often than between modules. Modules in the network may fragment as the network as-
²⁴⁷ sembles, enhancing modularity. Conversely, nested networks are like a pyramid of inter-
²⁴⁸ actions, where there are some species that interact with many species, other species that
²⁴⁹ interact with a subset of those species, and so on. If species entering the network tend
²⁵⁰ to interact with the generalist base of the network pyramid as would be expected with
²⁵¹ preferential attachment, nestedness would increase through time. The connectance — the
²⁵² proportion of observed out of possible interactions — would decrease as new, specialist
²⁵³ species, preferentially attach to the core. Finally, the overall level of network specializa-
²⁵⁴ tion may change as the community assembles. Network-level specialization will increase
²⁵⁵ if specialist species colonize the network or species begin to limit their interaction niche
²⁵⁶ breadth as the network assembles [38].

257 To evaluate network nestedness, we used the estimator weighted NODF [39]. NODF eval-
258 uates whether species with fewer partners interact with subsets of partners with which
259 more connected species interact [39]. To estimate modularity, we used a hierarchical clus-
260 tering algorithm [40, 41]. We evaluate network specialization with the metric H2, which
261 estimates the deviation of the observed interaction frequency between plants and pollina-
262 tors from a null expectation where all partners interact in proportion to their abundances
263 [38]. It ranges from zero for generalized networks to one for specialized networks. We cal-
264 culated standardized z-scores so that nestedness, modularity and specialization metrics
265 could be compared across communities. The z-scores were calculated by generating an
266 ensemble of 999 randomly assembled communities, subtracting the mean of the statistic
267 calculated across these communities from the observed value, and then dividing by the
268 standard deviation. To assemble random communities, we reshuffled the interactions be-
269 tween species but fixed the total number of interactions, species and interaction frequency
270 distributions [42].

271 To test whether network modularity, nestedness, connectance or specialization changed
272 linearly with assembly, we used linear mixed models with the descriptive network met-
273 rics as the response variable, year of assembly as the explanatory variable, and random
274 effects of site and year. The number of species in a network affects the patterns of inter-
275 action possible, so we also examined the change in plant and pollinator species richness
276 through time. We employ generalized linear mixed models with Poisson error to model
277 richness [27]. We scaled explanatory variables.

278 Network robustness

279 Lastly, we tested whether the changes in interaction patterns associated with network as-
280 sembly affect the robustness of the network to species loss and cascading perturbations.

281 Following [3], we simulated plant species extinction and the subsequent extinction cas-
282 cades of pollinator species. Because the reproduction of plant species is facilitated by
283 active restoration efforts, it is unlikely the extinction of pollinator species would affect
284 plant populations in the hedgerows. However, plants ceasing to bloom, for example in
285 response to drought, will likely affect the pollinators that depend on them. We elimi-
286 nated plants species based on their degree or abundance, and then calculated the number
287 of pollinators that secondarily went extinct. The area below the extinction curve is an
288 estimate of network robustness [3, 43].

289 We also explored how the robustness to cascading perturbations changed as the com-
290 munity assembled, using algebraic connectivity — the second smallest eigenvalue of the
291 Laplacian matrix [44] — as a proxy for network robustness. Algebraic connectivity relates
292 to how difficult it is to turn a network into completely disconnected groups of species
293 [45, 46]. The larger the algebraic connectivity, the more sensitive a network is to cascading
294 perturbations. Perturbations, such as the decrease in abundance of a plant or pollinator,
295 can have negative consequences for the species in the network. For example, a decrease
296 in abundance of a pollinator will diminish the pollination services it provides to plants.
297 The affected plants would set less seeds, and decrease in abundance the subsequent year.
298 Consequently, other pollinators that depended on those plant species would also be af-
299 fected, and the effects of this perturbation would continue to propagate throughout the
300 network. Alternatively, perturbations could also have a positive effect if, for example, the
301 increase in the abundance of a plant species lead to an increase in resource availability
302 for pollinators. The examples of negative perturbations (e.g., resource collapse, disease
303 spreading, parasites), however, outnumber possible positive perturbations. It is impor-
304 tant to note that both robustness and algebraic connectivity assume that the network is
305 static. They do not account for the ability of species to alter their interaction depending
306 on circumstances and the resource availability.

307 In order to test whether hedgerows changed in robustness as the communities assembled,
308 the three measures of robustness were modeled as responses in a linear mixed model with
309 site type as an explanatory variable and site as a random effect [27, 28].

310 Results

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

314 Change point analysis

315 Identifying change points

316 The majority (76%) of the sites underwent at least one significant interaction reorgani-
317 zation (Fig. 2, 3). All five of the assembling hedgerows experienced network chang-
318 ing points, whereas only 40% and 81% of non-assembling hedgerows and field margins,
319 respectively, underwent significant interaction reorganizations. Assembling hedgerows
320 had significantly more changing points than the non-assembling networks (estimate of
321 the difference in the odds ratios between assembling and non-assembling networks, 3.316,
322 95% CI [1.314, 8.572], p -value= 0.0117). Network assembly following restoration is thus
323 punctuated by more interaction reorganizations than would be expected by external fac-
324 tors such as environmental shifts that would have affected all networks (assembling or
325 non-assembling) similarly.

³²⁶ **Characteristics of species that contribute to change points**

³²⁷ In contradiction to the predictions of assembly by preferential attachment, both pollina-
³²⁸ tor persistence and degree were positively related to network position variability (Fig. 4,
³²⁹ estimate of the slope of closeness centrality variability and persistence \pm standard er-
³³⁰ ror of the estimate, 0.496 ± 0.182 , $p\text{-value}=0.016$; slope of closeness centrality variability
³³¹ and degree, 0.004 ± 0.002 , $p\text{-value}=0.056$). The slope of these relationships remained sig-
³³² nificant when the species with the top 10 persistence and degree scores were dropped.
³³³ In addition, plant persistence and degree were not significantly related to network posi-
³³⁴ tion variability (Fig. 4). The variability of species network position was not the result of
³³⁵ closeness linearly increasing through time, and, in fact, plant and pollinator closeness de-
³³⁶ creased slightly through time (Fig. S2, estimate of the slope of closeness through time \pm
³³⁷ SE, pollinators: -0.082 ± 0.021 , $p\text{-value}=0.003$; plants -0.089 ± 0.044 , $p\text{-value}=0.04$).

³³⁸ **Species and interaction turnover**

³³⁹ The rates of plant, pollinator and interaction temporal turnover were similar across as-
³⁴⁰ sembling hedgerows, non-assembling hedgerows and field margins, though mature hedgerows
³⁴¹ had marginally less pollinator turnover than field margins (Fig. 5, estimate \pm SE of the
³⁴² difference in turnover between field margins and mature hedgerows, -0.051 ± 0.026 , $p\text{-}
³⁴³ value}=0.049). The turnover of plants and interactions was not significantly different be-
³⁴⁴ tween site types. When interactions were weighted by their similarity, both assembling
³⁴⁵ and mature hedgerows had higher rates of turnover than field margins (Fig. 5, estimate
³⁴⁶ \pm SE of the difference in turnover between field margins and assembling hedgerows,
³⁴⁷ 0.115 ± 0.027 , $p\text{-value}=0.0002$; field margins and mature hedgerows, 0.082 ± 0.024 , $p\text{-}
³⁴⁸ value}=0.002). The weighted interaction turnover at assembling hedgerows, however, was$$

³⁴⁹ not significantly higher than in non-assembling, mature hedgerows.

³⁵⁰ **Temporal changes in interaction patterns**

³⁵¹ **Network structure**

³⁵² Nestedness and modularity did not change in any predictable pattern with assembly
³⁵³ (Fig. 6). All of the networks were significantly nested (z -scores > 1.96), but not modu-
³⁵⁴ lar (z -scores < 2 , Fig. 6).

³⁵⁵ Connectance decreased as the community assembled (Fig. 6, estimate of the slope of con-
³⁵⁶ nectance through time \pm standard error of the estimate, -0.023 ± 0.008 , p -value=0.007).
³⁵⁷ Specialization also decreased, though the slope was not significantly different from zero.
³⁵⁸ Most communities were more generalized than expected when interactions were random-
³⁵⁹ ized (Fig. 6).

³⁶⁰ Both plant and pollinator species richness increased through time (Fig. 6, estimate of the
³⁶¹ slope of richness through time \pm SE, pollinators: 0.136 ± 0.064 , p -value=0.034; plants:
³⁶² 0.140 ± 0.060 , p -value=0.012). Unsurprisingly, pollinator species are colonizing and per-
³⁶³ sisting at the assembling hedgerows. Plant species richness in the networks is based
³⁶⁴ on the flowers actually visited by pollinators and not the presence of a particular plant
³⁶⁵ species at a site. Thus, though some new plant species may establish themselves in the
³⁶⁶ hedgerows, the increase in plant richness in the networks is likely due to previously un-
³⁶⁷ visited plants attracting visitors as they mature and offer better rewards.

³⁶⁸ **Network robustness**

³⁶⁹ Assembly did not affect network robustness to species extinction when species were re-
³⁷⁰ moved incrementally by degree or abundance In contrast, the sensitivity of networks to
³⁷¹ cascading perturbations, as measured by the algebraic connectivity of the network, in-
³⁷² creased as the network assembled (Fig. S3), estimate of the slope of sensitivity to cascad-
³⁷³ ing perturbations through time \pm SE, 0.6814 ± 0.272 , $p\text{-value}=0.042$.

³⁷⁴ **Discussion**

³⁷⁵ We show that the temporal assembly of plant-pollinator networks following restoration
³⁷⁶ is a highly dynamic process in which interactions often undergo significant reorganiza-
³⁷⁷ tions, or changing points. If these network reorganizations were a product of environ-
³⁷⁸ mental forces alone, we would expect to observe the same changing points at the same
³⁷⁹ time periods, consistently across all sites. However, network changing points in non-
³⁸⁰ assembling communities are less frequent, and there are few consistent trends in the
³⁸¹ years when change points occurred across all sites. Several sites had network changing
³⁸² points between years 2009 and 2011 (Fig. 2). In California, 2011 marked the beginning of
³⁸³ a multi-year drought. The assembling hedgerows were not sampled in 2010, so we can-
³⁸⁴ not disentangle whether the point changes are due to skipping a year of monitoring or
³⁸⁵ the drought. Interestingly, most assembling hedgerows did not undergo a significant in-
³⁸⁶ teraction reorganization immediately after planting (i.e., the transition from weedy field
³⁸⁷ margin to hedgerow). This result is consistent with the finding that hedgerow restoration
³⁸⁸ takes several years to have an impact on the plant-pollinator communities in our study
³⁸⁹ system, as well as with the observation that hedgerows do not begin to produce many
³⁹⁰ flowers until 3 – 5 years following planting [22].

391 In a preferential attachment process, we expect that the most persistent and high degree
392 species (the species with the most unique interaction partners) would remain stable in the
393 network core during assembly [8]. Surprisingly, however, we encountered the opposite
394 pattern. For example, the four most ubiquitous species in our study landscape — *Halictus*
395 *ligatus*, *Halictus tripartitus*, *Lasioglossum (Dialictus) incompletum*, and *Toxomerus marginata*
396 — were the only species that changed which module they were a member in across
397 years in all the assembling hedgerows. Because species degree and persistence were
398 strongly correlated, it is difficult to disentangle the causal mechanism for why species
399 with those characteristics are so variable in their network position. Species that can inter-
400 action with a relatively high number of interaction partners may be better able to exploit
401 the limited floral resources in the intensively managed agriculture landscape, and thus
402 also be the most persistent [in ant-plant mutualisms, 47]. More persistent species usually
403 have longer phenologies, so they can visit many different flowers, resulting in a higher
404 degree [48, 49]. Either way, our result suggests that adaptable species can change their
405 network position to utilize the most advantageous floral resources available, which may
406 depend on both the other pollinator species that are present and the state of the plant
407 community [50–52]. Thus given the opportunity and ability to use different resources,
408 species will often change their network positions [50].

409 Interestingly, though assembling hedgerows had more network reorganizations than non-
410 assembling communities, pollinator species and interaction turnover occurred at similar
411 rates across site types. Assembling hedgerows have higher turnover than non-assembling
412 field margins only when interactions were weighted by their similarity. This is likely be-
413 cause though species and interactions are turning over at the field margins, species and
414 interactions that fill similar roles in the network are replacing each other. In contrast, at
415 the assembling hedgerows, unique interactions are turning over as the networks contin-
416 ually reorganize. Non-assembling mature hedgerow communities, however, had similar

417 rates of weighted interaction turnover as assembling hedgerows but also the lowest pol-
418 linator turnover. Pollinator communities at mature hedgerows may generally be more
419 stable, but rare and/or specialized pollinators could generate this pattern if they entered
420 a community, formed unique interactions with plants that did not previously share polli-
421 nators, but did not persist in the networks. These species would not contribute strongly
422 to network reorganization or species turnover, but would enhance weighted interaction
423 turnover. Mature hedgerows therefore both support more stable pollinator communities,
424 while also providing resources for rare and/or specialized species [22, 24].

425 When we explored how network-level interaction patterns changed through time, we
426 found few patterns. The connectance decreased, as would be expected if the network
427 is being colonized by specialist species [24]. Network specialization, however, did not
428 change predictably with assembly. Decreasing connectance without an accompanying
429 increase in specialization would be possible if the increased colonization of specialized
430 species was accompanied by an increase in the diet breath of resident species. This would
431 be expected if resident species were able to minimize their foraging time by expand-
432 ing their diet breath as plant diversity increases with hedgerow maturation [12, 14, 17,
433 52].

434 Interestingly, however, the changes in network patterns associated with assembly did
435 not affect the hedgerow network robustness to species extinction or susceptibility to cas-
436 cading perturbations. The hedgerows were designed to provide floral resources for the
437 largest number of pollinators across the growing season [7]. The generalized nature of
438 the floral community may explain why the networks tended to be more generalized than
439 expected if interactions were randomly distributed across species (Fig. 6). In addition, the
440 design of the hedgerow plantings may have facilitated the emergence of a single, highly
441 connected module in all of the networks (see 3 for examples). This network configuration

⁴⁴² results in short path lengths (the distance between species in a network based on their
⁴⁴³ shared partners), and thus, a perturbation in one species can more easily spread to other
⁴⁴⁴ species. These networks are also vulnerable to the extinction of highly connected species
⁴⁴⁵ [53]. In order to promote more resilient communities, future restoration efforts should
⁴⁴⁶ explore designing floral communities to promote more interaction partitioning using, for
⁴⁴⁷ example, algorithms to optimize different network properties based on prior knowledge
⁴⁴⁸ of pollinator floral preferences [54], and on desired network architectures that renders
⁴⁴⁹ them more robust both to species loss and to cascading effects.

⁴⁵⁰ In general, plant-pollinator networks are highly dynamic, with high turnover of species
⁴⁵¹ and interactions both within and between seasons [55]. Though our non-assembling com-
⁴⁵² munities experienced fewer network reorganizations than the assembling hedgerows,
⁴⁵³ 82% of field margins and 40% of mature hedgerows underwent at least one changing
⁴⁵⁴ point in network structure. Pollinators are also highly opportunistic [12, 56, 57], though
⁴⁵⁵ trait complementarity such as tongue length and corolla depth impose some biophysical
⁴⁵⁶ limits to the interactions between plants and pollinators [48, 58–61]. Such opportunism
⁴⁵⁷ may buffer plant-pollinator communities from global change [e.g., 62, 63], but our limited
⁴⁵⁸ understanding of the assembly of these communities impedes making such predictions
⁴⁵⁹ [48, 55]. Unlike in the broader food web literature, we have few assembly models of
⁴⁶⁰ mutualistic network assembly [16, 64, 65]. In addition, the few developed models often
⁴⁶¹ borrow their mechanisms from competitive interactions, leading to inaccurate biological
⁴⁶² assumptions [66]. We need further development of mechanistic models of mutualistic
⁴⁶³ systems to generate testable predictions, along with empirical exploration of network
⁴⁶⁴ assembly. Plant-pollinator communities and mutualisms are vital for biodiversity main-
⁴⁶⁵ tenance and essential ecosystem service provision. We must therefore understand the
⁴⁶⁶ processes underlying their assembly to facilitate restoration and conservation.

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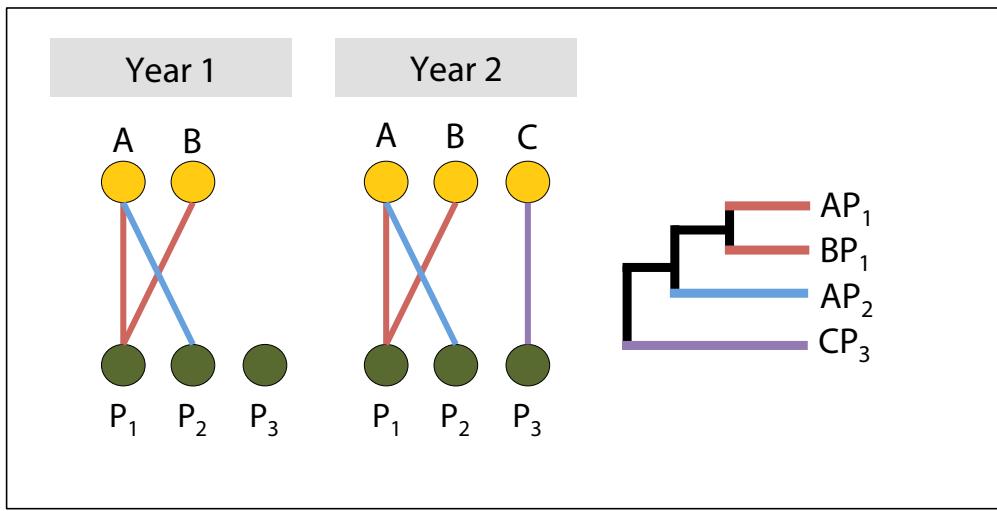


Figure 1: Diagram illustrating the analysis to examine the temporal turnover of interactions weighted based on their similarity. A, B and C are animal species, and Ps are plant species. The dendrogram depicts the interaction similarity across years based on the number of shared constituent species.

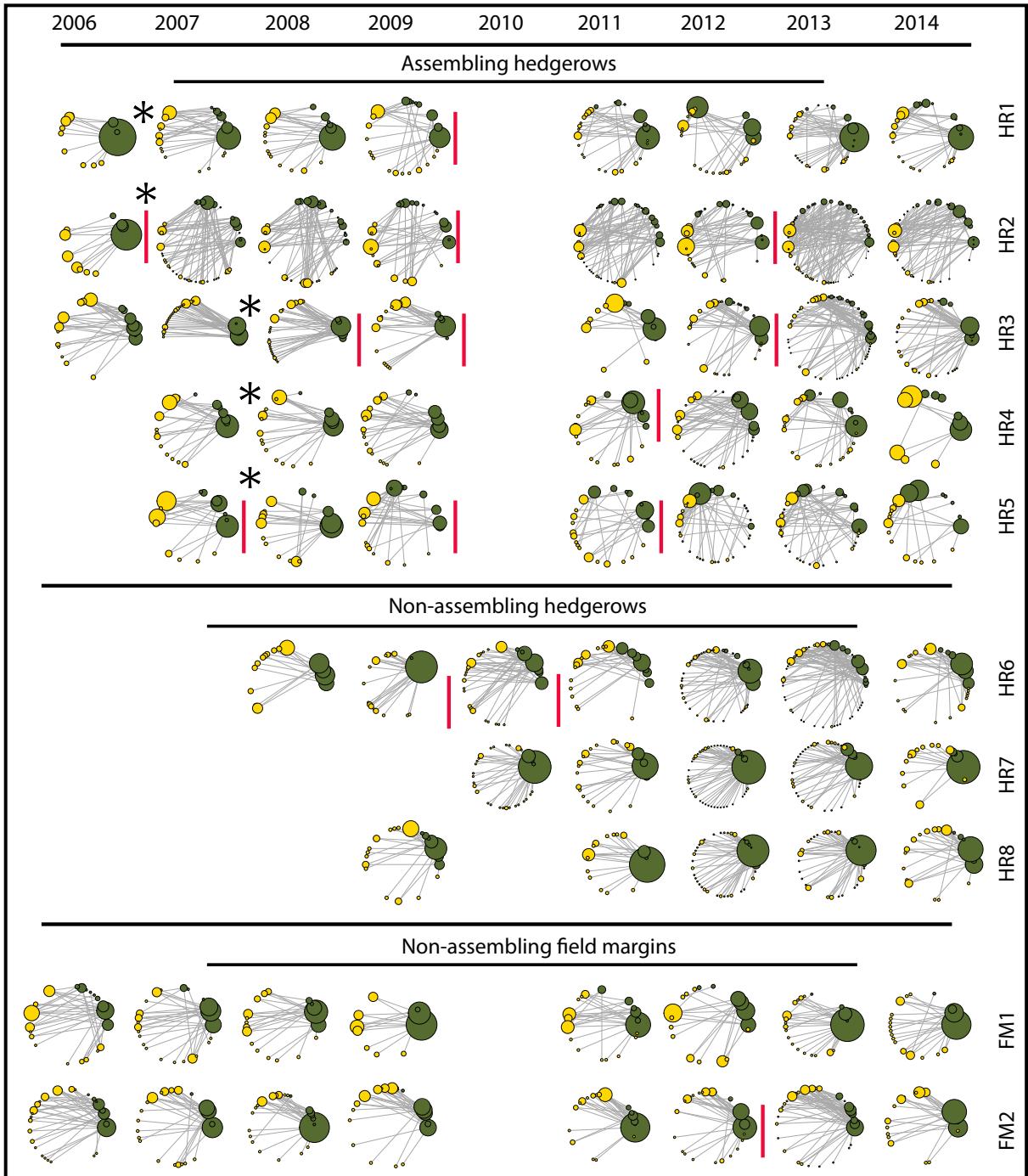


Figure 2: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, respectively,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

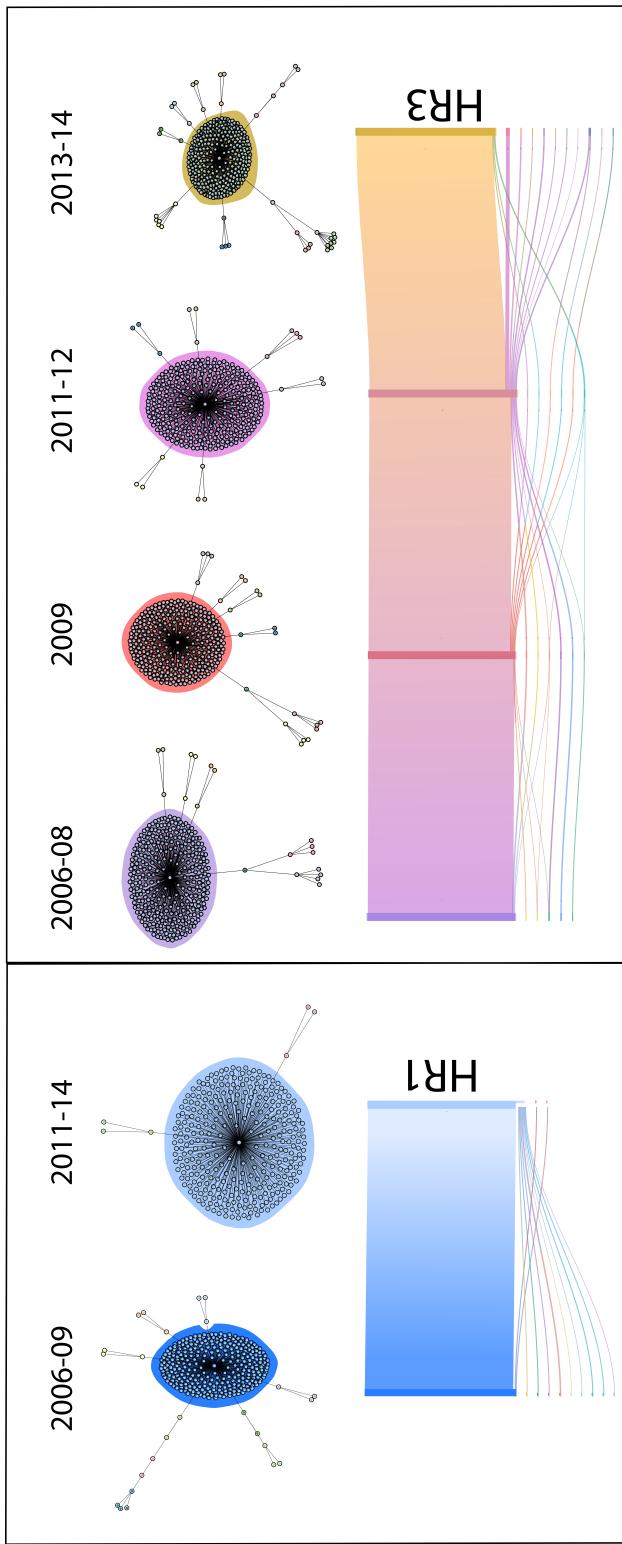


Figure 3: The species module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species between modules between changing points. Each line represents the change of s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

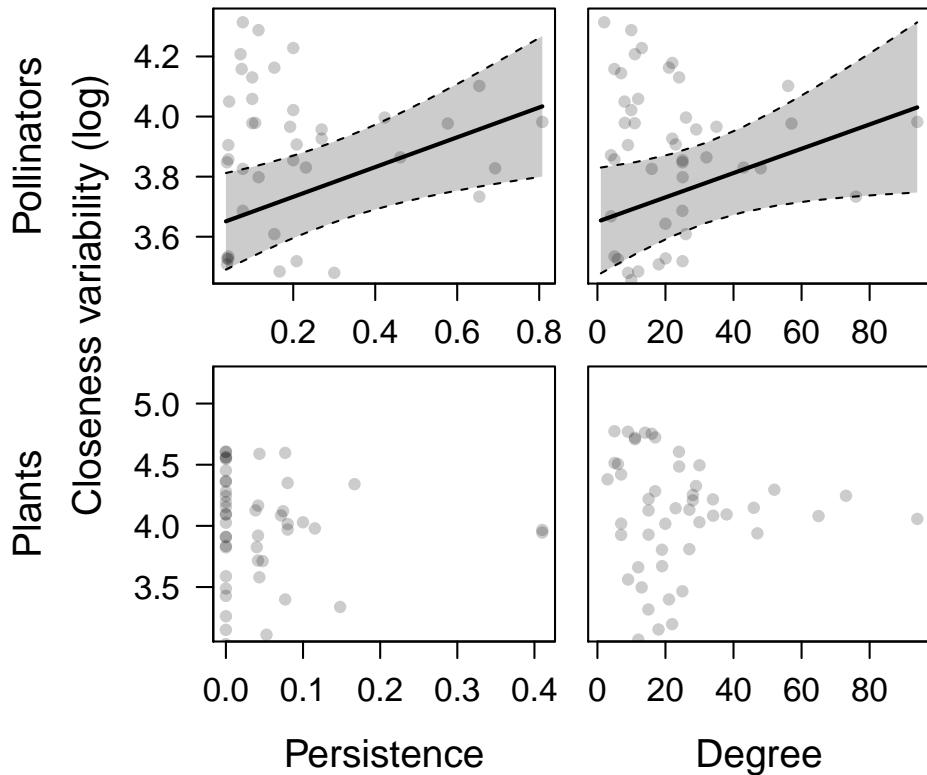


Figure 4: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across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

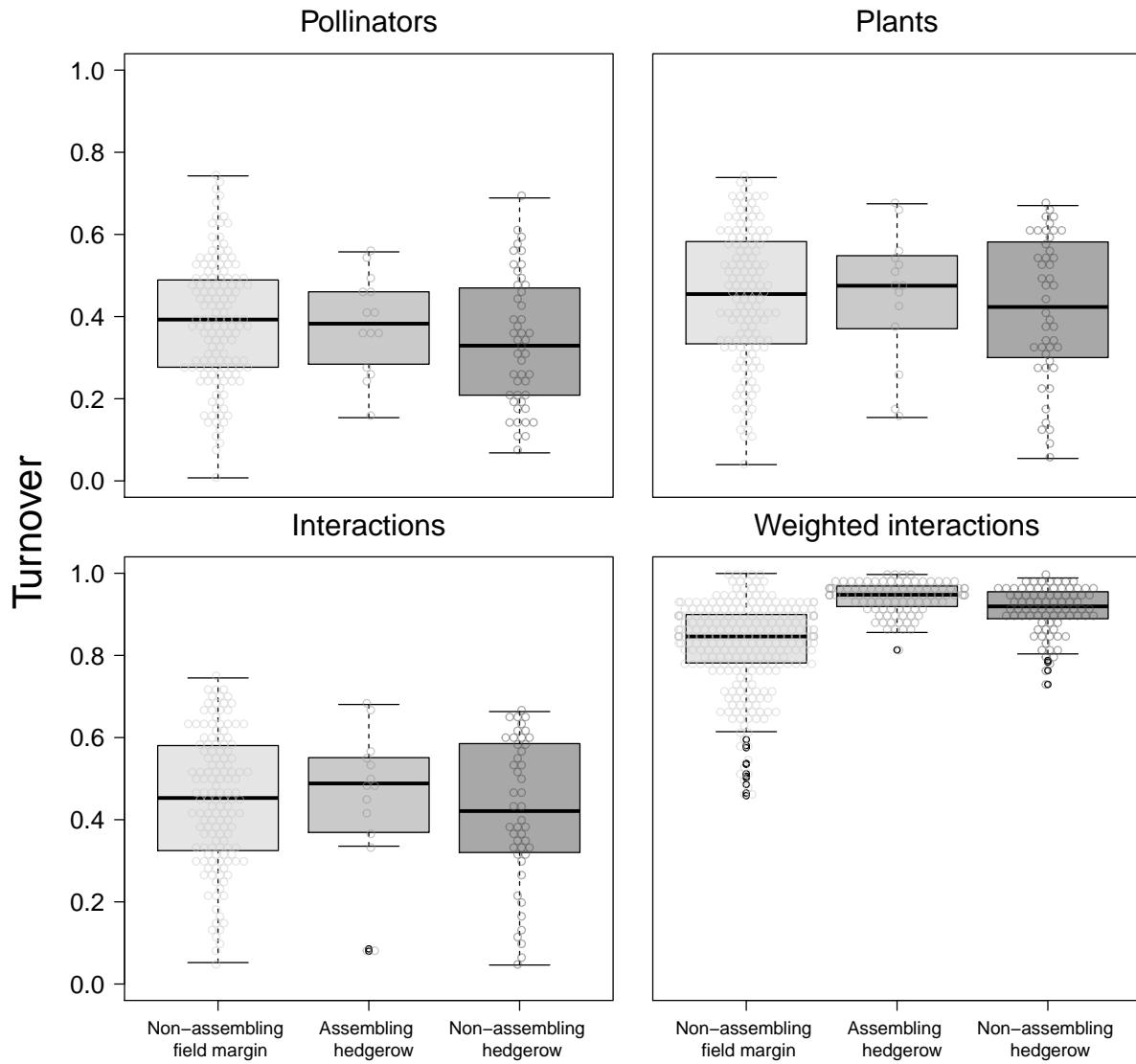


Figure 5: Species interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally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

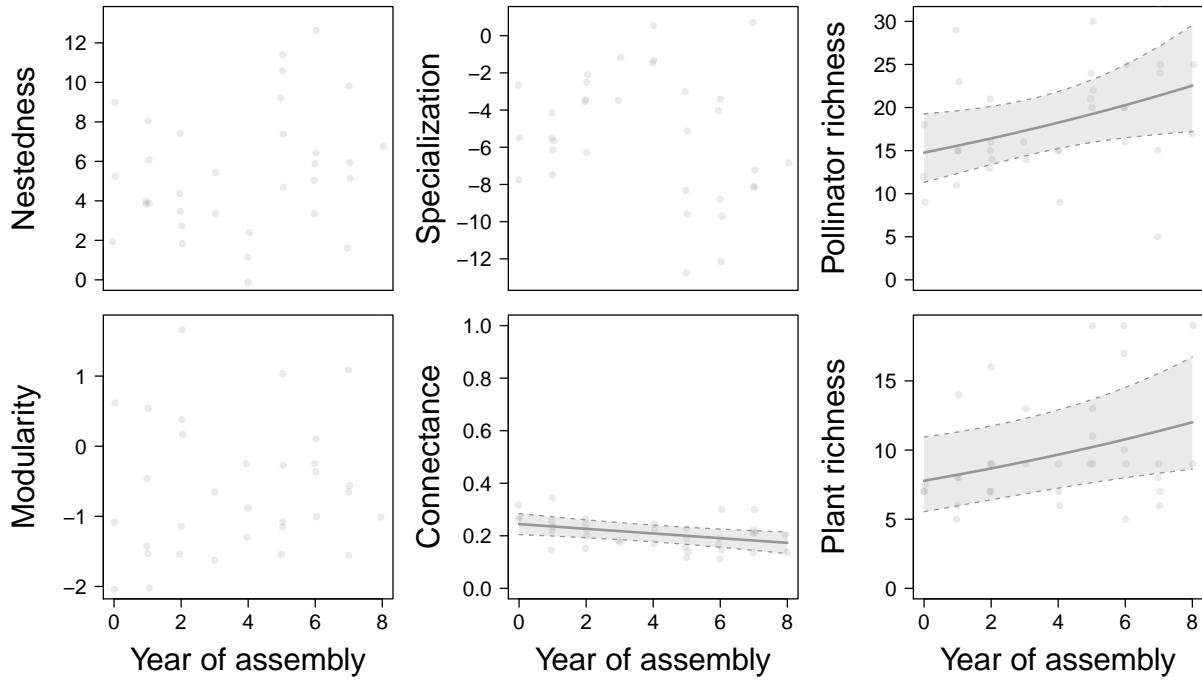


Figure 6: Nestedness, plant richness and pollinator richness increased as the networks assembled. Specialization and modularity remained consistent across years, while connectance decreased. The nestedness, modularity and specialization scores represent z -scores. Scores greater than ~ 2 or less than ~ -2 are significantly more or less structured than randomly assembled networks. Points are the metric value for each site at each year of assembly. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.