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Major network reorganizations punctuate the assembly of plant-pollinator communities

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Abstract

Species are being lost at an alarming rate and it is imperative to understand how communities assemble if we are to prevent their collapse or restore lost interactions. 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 assembly process to be punctuated by major network reorganizations. The most persistent and generalized species are also the most variable in their network positions, contrary to what assembly through preferential attachment predicts. 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.

¹⁵ community assembly, change points, robustness, nestedness, modularity, bipartite, preferential attachment

17 Introduction

18 Species in ecological communities are linked through ecological interactions. Global
19 change, however, has created a severe biodiversity crisis, and as species are lost, so are
20 their interactions [6, 22]. A community’s ability to resist collapse will depend on the com-
21 munity’s robustness to species and interaction loss [9, 40, 57, 61]. Furthermore, it has been
22 shown that biodiversity has a pivotal role in maintaining ecosystems services [15]. Thus,
23 to safeguard ecological function, it has become increasingly imperative to aid the recov-
24 ery of lost interactions and component biodiversity and by facilitating the assembly of
25 robust interaction networks via ecological restoration [41]. However, we know very little
26 about how ecological networks assemble in general, rendering restoration of interacting
27 communities quite difficult.

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

42 In contrast to the network build-up described by preferential attachment, significant re-
43 organizations of interactions can also punctuate assembly [51]. Such significant reorgani-
44 zations of interactions, or network changing points, are observed in social networks that
45 respond to abrupt shifts in the behavior of interactors [51]. A change point is caused by
46 a merge, split, fragmentation or formation of modules within a network. In ecological
47 communities, such shifts may occur if, as new species colonize, resident species change
48 their interaction partners to optimize their foraging effort. In plant-pollinator commu-
49 nities, theory predicts that pollinators optimize their use of floral resources to reduce
50 interspecific competition and improve resource-use efficiency [2, 12, 54, 62, 63]. No stud-
51 ies, however, have examined if network changing points occur during ecological network
52 assembly and/or how these changes relate to species behavior.

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

65 We explore the process of network development using a nine-year dataset of plant-pollinator
66 community assembly following hedgerow restoration in the highly simplified and inten-

67 sively managed agricultural landscape of California's Central Valley. We first determine
68 whether the mechanism underlying network assembly represents a buildup of interac-
69 tions as would be predicted by preferential attachment or significant reorganizations of
70 interactions (i.e., network changing points). Even with changing points in interaction
71 organization, networks could still assemble via preferential attachment if the network re-
72 organizations were primarily driven by peripheral, temporally variable species while a
73 stable, well-connected core of species persist. Therefore, we tested whether the species
74 that are most variable in their network position — and thus important contributors to
75 network reorganizations – are less persistent and connected species. To further explore
76 the mechanisms underlying the temporal dynamics of the networks, also we examine
77 patterns in the species and interaction temporal turnover. Finally, we investigate whether
78 networks assemble toward predictable interaction patterns, and the ramifications for the
79 robustness of the networks.

80 Materials & Methods

81 Study sites and collection methods

82 Study sites were located in the Central Valley of California in Yolo, Colusa and Solano
83 Counties. This area is composed of intensively managed agriculture — primarily mono-
84 cultures of conventional row crops, vineyards and orchards. Hedgerows border large
85 (ca. 30-hectare) crop fields and measured between 3 – 6 m wide and approximately
86 350 m long. Hedgerows consist of native, perennial, shrub and tree plantings [Fig. S1,
87 37, 41, 42].

88 We selected five farm edges to be restored as hedgerows. We monitored those locations

89 before the hedgerow was planted, and tracked the assembly of the community for up
90 to seven years as the hedgerow matured (from 2006 – 2014). For controls, we concur-
91 rently monitored non-assembling communities within mature hedgerows (greater than
92 10 years since planting, $N = 29$) and unrestored, weedy field margins ($N = 19$). The
93 mean distance between monitoring sites was 15 km, and the minimum distance between
94 sites sampled in the same year was 1 km. The entire area surveyed spanned almost 300
95 km^2 . The crop fields adjacent to all sites were similarly managed as intensive, high-input
96 monoculture.

97 Sites were sampled between two and five times per year (Tables S1-S3, mean 3.4 samples
98 per year). In each round of sampling, the order in which sites were sampled was random-
99 ized. Surveys were conducted under sunny conditions when the temperature was above
100 21°C and wind speed was below 2.5 meters/second.

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

112 Quantitative networks were generated for each site through time. Because the nuber of
113 sampling rounds varied between years (Tables S1-S3), we used the mean of the inter-

₁₁₄ actions between a pair of plants and pollinators within a year to represent interaction
₁₁₅ frequency.

₁₁₆ Change point analysis

₁₁₇ Identifying change points

₁₁₈ We employed a change point detection method [51] to identify fundamental reorgani-
₁₁₉ zations in large-scale interaction patterns. Change point detection methods have yet to
₁₂₀ be generalized to quantitative networks, so for this analysis we focused on qualitative
₁₂₁ (binary) networks. Following [51], we first defined a probability distribution over the
₁₂₂ networks using the generalized hierarchical random graph model (GHRG). The GHRG
₁₂₃ model captures both assortative and disassortative structure patterns at all scales in the
₁₂₄ network [51]. A network G is composed of vertices V and edges E . The GHRG model
₁₂₅ decomposes the N vertices into a series of nested groups, the relationships among which
₁₂₆ are represented by the dendrogram T . The tips of T are the vertices of G , and the prob-
₁₂₇ ability that two vertices u and v connect is given by the parameter p_r . The probability
₁₂₈ distribution of the network G is thus defined as:

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

₁₂₉ Where E_r is the observed number of edges between vertices with the common ancestor r ,
₁₃₀ and N_r is the total possible edges, and the rest of the notation is described above.

₁₃₁ Using Bayesian posterior inference and techniques from phylogenetic tree reconstruction,
₁₃₂ we fit the GHRG model to the networks [51]. This is accomplished by using a Markov
₁₃₃ chain Monte Carlo (MCMC) procedure to first sample the posterior distribution of bi-

134 partitions, from which a consensus tree is derived [51]. We use β distributions with the
135 hyperparameters $\alpha = \beta = 1$ to define priors for p_r .

136 Once the GHRG model has been fit to the networks, we determine whether a change
137 point occurred between two time slices. To detect a change point, we use Bayes factors
138 to compare the fit of two models — one where a change point occurred between two
139 networks, and one where no change occurred. We chose a sliding window of length, w ,
140 of four years to detect change points. Larger windows allow for more gradual changes,
141 and four was the maximum possible with our eight years of data. Lastly, to calculate a
142 p -value for the Bayes factors, we use parametric bootstrapping to numerically estimate
143 the null distribution [51]. We employed code published online by L. Peel for the change
144 point analysis. Analyses were conducted in Python 3.4.

145 We next tested whether the change points occurring in maturing hedgerows were a com-
146 ponent of the assembly process or a product of environmental shifts that lead to network
147 reorganizations in all types of communities. We modeled the number of change points as
148 successes and the total number of sample years at each site as trials, and used a general-
149 ized linear model with Binomial error to test whether the probability of a change point
150 occurrence varied by site type. We used standard techniques to determine whether the
151 assumptions of the models were met for this and all subsequent models. For the non-
152 assembling controls, only sites with five or greater survey years were included in this
153 analysis ($N = 11$). All statistical analyses were conducted in R 3.2.3 [55].

154 Characteristics of species that contribute to change points

155 To further elucidate the nature of the change points, we examine the characteristics of
156 the species that contributed to interaction reorganization. Some species remained in rel-
157 atively similar network positions through time, whereas others were more variable in

their position and thus contributed more strongly to network reorganization. We tested whether the more persistent species with the highest degree (number of different interaction partners) were the most stable in their network positions, as would be expected if the networks were assembling via preferential attachment.

We calculated species persistence as the proportion of surveys in which a plant or pollinator is observed. Species observed consistently within and between years were thus maximally persistent. Weighted species degree is calculated from interaction observations from an extensive dataset from Yolo County (approx. 18000 interaction records) that included both the data included in this study and additional data from sites where we collected flower visitors using the same methods [42, 53]. To represent network position variability, we computed the coefficient of variation of weighted closeness centrality [26] at each site through time. Closeness centrality represents the importance of a space 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 increases through time.

180 **Species and interaction turnover**

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

192 To estimate the temporal species and interaction turnover, we used an approach similar
193 to calculating spatial β -diversity. Instead of calculating the variation in community com-
194 position across sites within a year, we estimated turnover across years at a site. We first
195 calculated the pairwise dissimilarity of plants, pollinators and interactions between years
196 within each site using the Chao dissimilarity estimator that incorporates abundances,
197 while also accounting for unobserved records [16]. Dissimilarity estimates can be affected
198 by the total number of species and individuals sampled at a site [e.g., 53]. For example,
199 the probability that two sites do not share any species is higher when there are few in-
200 dividuals at those sites. Following [53], we used null models that constrained species
201 richness to estimate the deviation of the observed dissimilarity from that which would be
202 expected under a random community assembly process. With the corrected dissimilarity
203 values, we then calculated the multivariate dispersion of community composition across
204 years [4]. In order to test whether assembling hedgerows had more species and interac-

205 tions turnover than non-assembling communities, the species and interaction temporal
206 turnover estimates were modeled as responses in a linear mixed model with site type as
207 an explanatory variable and site as a random effect [10, 38].

208 Though species may turnover across years, some groups of species may essentially re-
209 place each other if they fill similar roles in the network, occupying the same network
210 position and interacting with similar species. At non-assembling communities, species
211 turnover may overestimate the temporal changes in the networks if the interactions oc-
212 curring in one year are similar to those in the next year when they are weighted by the
213 similarity of their constituent species (Fig. 1). We developed a method to examine the tem-
214 poral turnover of interactions with weightings based on their similarity. We followed the
215 algorithm of [1] to cluster all the interactions (edges) hierarchically across sites and years
216 based on their similarity, and build a dendrogram. The interaction similarity is based how
217 many plants and pollinators (vertices) two edges share [1, 34]. The more species edges
218 shared in common, the shorter the branch length between them on the dendrogram. We
219 next calculated the temporal turnover of interactions weighted by their similarity, as ap-
220 proximated by “phylogenetic” distance [30, 35]. We then used linear mixed models to
221 test whether the weighted turnover of interactions varied between assembling and non-
222 assembling networks, including site as a random effect [10, 38].

223 **Temporal changes in interaction patterns**

224 **Network structure**

225 Any changing points in network structure may contribute to the reorganization of the as-
226 sembling networks into predictable interaction patterns. Pollination networks exhibit two

227 main structural patterns — modularity [e.g., 47] and nestedness [e.g., 7, 8]. In modular
228 networks, interactions are insular, occurring within separate groups or “modules” more
229 often than between modules. Modules in the network may fragment as the network as-
230 sembles, enhancing modularity. Conversely, nested networks are like a pyramid of inter-
231 actions, where there are some species that interact with many species, other species that
232 interact with a subset of those species, and so on. If species entering the network tend
233 to interact with the generalist base of the network pyramid as would be expected with
234 preferential attachment, nestedness would increase through time. The connectance — the
235 proportion of observed out of possible interactions — would decrease as new, specialist
236 species, preferentially attach to the core. Finally, the overall level of network specializa-
237 tion may change as the community assembles. Network-level specialization will increase
238 if specialist species colonize the network or species begin to limit their interaction niche
239 breadth as the network assembles [11].

240 To evaluate network nestedness, we used the estimator weighted NODF [3]. NODF eval-
241 uates whether species with fewer partners interact with subsets of partners with which
242 more connected species interact [3]. To estimate modularity, we used a hierarchical clus-
243 tering algorithm [18, 45]. We evaluate network specialization with the metric H2, which
244 estimates the deviation of the observed interaction frequency between plants and pollina-
245 tors from a null expectation where all partners interact in proportion to their abundances
246 [11]. It ranges from zero for generalized networks to one for specialized networks. We cal-
247 culated standardized z-scores so that nestedness, modularity and specialization metrics
248 could be compared across communities. The z-scores were calculated by generating an
249 ensemble of 999 randomly assembled communities, subtracting the mean of the statistic
250 calculated across these communities from the observed value, and then dividing by the
251 standard deviation. To assemble random communities, we reshuffled the interactions be-
252 tween species but fixed the total number of interactions, species and interaction frequency

253 distributions [27].

254 To test whether network modularity, nestedness, connectance or specialization changed
255 linearly with assembly, we used linear mixed models with the descriptive network met-
256 rics as the response variable, year of assembly as the explanatory variable, and random
257 effects of site and year. The number of species in a network affects the patterns of inter-
258 action possible, so we also examined the change in plant and pollinator species richness
259 through time. We employ generalized linear mixed models with Poisson error to model
260 richness [10]. We scaled explanatory variables.

261 Network robustness

262 Lastly, we tested whether the changes in interaction patterns associated with network as-
263 sembly affect the robustness of the network to species loss and cascading perturbations.
264 Following [40], we simulated plant species extinction and the subsequent extinction cas-
265 cades of pollinator species. Because the reproduction of plant species is facilitated by
266 active restoration efforts, it is unlikely the extinction of pollinator species would affect
267 plant populations in the hedgerows. However, plants ceasing to bloom, for example in
268 response to drought, will likely affect the pollinators that depend on them. We elimi-
269 nated plants species based on their degree or abundance, and then calculated the number
270 of pollinators that secondarily went extinct. The area below the extinction curve is an
271 estimate of network robustness [21, 40].

272 We also explored how the robustness to cascading perturbations changed as the com-
273 munity assembled, using algebraic connectivity — the second smallest eigenvalue of the
274 Laplacian matrix [23] — as a proxy for network robustness. Algebraic connectivity relates
275 to how difficult it is to 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.

²⁹⁷ **Change point analysis**

²⁹⁸ **Identifying change points**

²⁹⁹ The majority (76%) of the sites underwent at least one significant interaction reorgani-
³⁰⁰ zation (Fig. 2, 3). All five of the assembling hedgerows experienced network chang-
³⁰¹ ing points, whereas only 40% and 81% of non-assembling hedgerows and field margins,
³⁰² respectively, underwent significant interaction reorganizations. Assembling hedgerows
³⁰³ had significantly more changing points than the non-assembling networks (estimate of
³⁰⁴ the difference in the odds ratios between assembling and non-assembling networks, 3.316,
³⁰⁵ 95% CI [1.314, 8.572], *p*-value= 0.0117). Network assembly following restoration is thus
³⁰⁶ punctuated by more interaction reorganizations than would be expected by external fac-
³⁰⁷ tors such as environmental shifts that would have affected all networks (assembling or
³⁰⁸ non-assembling) similarly.

³⁰⁹ **Characteristics of species that contribute to change points**

³¹⁰ In contradiction to the predictions of assembly by preferential attachment, both pollina-
³¹¹ tor persistence and degree were positively related to network position variability (Fig. 4,
³¹² estimate of the slope of closeness centrality variability and persistence \pm standard er-
³¹³ ror of the estimate, 0.496 ± 0.182 , *p*-value=0.016; slope of closeness centrality variability
³¹⁴ and degree, 0.004 ± 0.002 , *p*-value=0.056). The slope of these relationships remained sig-
³¹⁵ nificant when the species with the top 10 persistence and degree scores were dropped.
³¹⁶ In addition, plant persistence and degree were not significantly related to network posi-
³¹⁷ tion variability (Fig. 4). The variability of species network position was not the result of
³¹⁸ closeness linearly increasing through time, and, in fact, plant and pollinator closeness de-
³¹⁹ creased slightly through time (Fig. S2, estimate of the slope of closeness through time \pm

³²⁰ SE, pollinators: -0.082 ± 0.021 , $p\text{-value}=0.003$; plants -0.089 ± 0.044 , $p\text{-value}=0.04$).

³²¹ Species and interaction turnover

³²² The rates of plant, pollinator and interaction temporal turnover were similar across as-
³²³ sembling hedgerows, non-assembling hedgerows and field margins, though mature hedgerows
³²⁴ had marginally less pollinator turnover than field margins (Fig. 5, estimate \pm SE of the
³²⁵ difference in turnover between field margins and mature hedgerows, -0.051 ± 0.026 , $p\text{-}$
³²⁶ value=0.049). The turnover of plants and interactions was not significantly different be-
³²⁷ tween site types. When interactions were weighted by their similarity, both assembling
³²⁸ and mature hedgerows had higher rates of turnover than field margins (Fig. 5, estimate
³²⁹ \pm SE of the difference in turnover between field margins and assembling hedgerows,
³³⁰ 0.115 ± 0.027 , $p\text{-value}=0.0002$; field margins and mature hedgerows, 0.082 ± 0.024 , $p\text{-}$
³³¹ value=0.002). The weighted interaction turnover at assembling hedgerows, however, was
³³² not significantly higher than in non-assembling, mature hedgerows.

³³³ Temporal changes in interaction patterns

³³⁴ Network structure

³³⁵ Nestedness and modularity did not change in any predictable pattern with assembly
³³⁶ (Fig. 6). All of the networks were significantly nested (z -scores > 1.96), but not modu-
³³⁷ lar (z -scores < 2 , Fig. 6).

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

³⁴⁰ Specialization also decreased, though the slope was not significantly different from zero.
³⁴¹ Most communities were more generalized than expected when interactions were random-
³⁴² ized (Fig. 6).

³⁴³ Both plant and pollinator species richness increased through time (Fig. 6, estimate of the
³⁴⁴ slope of richness through time \pm SE, pollinators: 0.136 ± 0.064 , *p*-value=0.034; plants:
³⁴⁵ 0.140 ± 0.060 , *p*-value=0.012). Unsurprisingly, pollinator species are colonizing and per-
³⁴⁶ sisting at the assembling hedgerows. Plant species richness in the networks is based
³⁴⁷ on the flowers actually visited by pollinators and not the presence of a particular plant
³⁴⁸ species at a site. Thus, though some new plant species may establish themselves in the
³⁴⁹ hedgerows, the increase in plant richness in the networks is likely due to previously un-
³⁵⁰ visited plants attracting visitors as they mature and offer better rewards.

³⁵¹ Network robustness

³⁵² Assembly did not affect network robustness to species extinction when species were re-
³⁵³ moved incrementally by degree or abundance In contrast, the sensitivity of networks to
³⁵⁴ cascading perturbations, as measured by the algebraic connectivity of the network, in-
³⁵⁵ creased as the network assembled (Fig. S3), estimate of the slope of sensitivity to cascad-
³⁵⁶ ing perturbations through time \pm SE, 0.6814 ± 0.272 , *p*-value=0.042).

³⁵⁷ Discussion

³⁵⁸ We show that the temporal assembly of plant-pollinator networks following restoration
³⁵⁹ is a highly dynamic process in which interactions often undergo significant reorganiza-
³⁶⁰ tions, or changing points. If these network reorganizations were a product of environ-

361 mental forces alone, we would expect to observe the same changing points at the same
362 time periods, consistently across all sites. However, network changing points in non-
363 assembling communities are less frequent, and there are few consistent trends in the
364 years when change points occurred across all sites. Several sites had network changing
365 points between years 2009 and 2011 (Fig. 2). In California, 2011 marked the beginning of
366 a multi-year drought. The assembling hedgerows were not sampled in 2010, so we can-
367 not disentangle whether the point changes are due to skipping a year of monitoring or
368 the drought. Interestingly, most assembling hedgerows did not undergo a significant in-
369 teraction reorganization immediately after planting (i.e., the transition from weedy field
370 margin to hedgerow). This result is consistent with the finding that hedgerow restoration
371 takes several years to have an impact on the plant-pollinator communities in our study
372 system, as well as with the observation that hedgerows do not begin to produce many
373 flowers until 3 – 5 years following planting [37].

374 In a preferential attachment process, we expect that the most persistent and high degree
375 species (the species with the most unique interaction partners) would remain stable in the
376 network core during assembly [5]. Surprisingly, however, we encountered the opposite
377 pattern. For example, the four most ubiquitous species in our study landscape — *Halictus*
378 *ligatus*, *Halictus tripartitus*, *Lasioglossum (Dialictus) incompletum*, and *Toxomerus marginata*
379 — were the only species that changed which module they were a member in across
380 years in all the assembling hedgerows. Because species degree and persistence were
381 strongly correlated, it is difficult to disentangle the causal mechanism for why species
382 with those characteristics are so variable in their network position. Species that can inter-
383 action with a relatively high number of interaction partners may be better able to exploit
384 the limited floral resources in the intensively managed agriculture landscape, and thus
385 also be the most persistent [in ant-plant mutualisms, 20]. More persistent species usually
386 have longer phenologies, so they can visit many different flowers, resulting in a higher

³⁸⁷ degree [24, 65]. Either way, our result suggests that adaptable species can change their
³⁸⁸ network position to utilize the most advantageous floral resources available, which may
³⁸⁹ depend on both the other pollinator species that are present and the state of the plant
³⁹⁰ community [29, 39, 67]. Thus given the opportunity and ability to use different resources,
³⁹¹ species will often change their network positions [39].

³⁹² Interestingly, though assembling hedgerows had more network reorganizations than non-
³⁹³ assembling communities, pollinator species and interaction turnover occurred at similar
³⁹⁴ rates across site types. Assembling hedgerows have higher turnover than non-assembling
³⁹⁵ field margins only when interactions were weighted by their similarity. This is likely be-
³⁹⁶ cause though species and interactions are turning over at the field margins, species and
³⁹⁷ interactions that fill similar roles in the network are replacing each other. In contrast, at
³⁹⁸ the assembling hedgerows, unique interactions are turning over as the networks contin-
³⁹⁹ ually reorganize. Non-assembling mature hedgerow communities, however, had similar
⁴⁰⁰ rates of weighted interaction turnover as assembling hedgerows but also the lowest pol-
⁴⁰¹ linator turnover. Pollinator communities at mature hedgerows may generally be more
⁴⁰² stable, but rare and/or specialized pollinators could generate this pattern if they entered
⁴⁰³ a community, formed unique interactions with plants that did not previously share polli-
⁴⁰⁴ nators, but did not persist in the networks. These species would not contribute strongly
⁴⁰⁵ to network reorganization or species turnover, but would enhance weighted interaction
⁴⁰⁶ turnover. Mature hedgerows therefore both support more stable pollinator communities,
⁴⁰⁷ while also providing resources for rare and/or specialized species [37, 42].

⁴⁰⁸ When we explored how network-level interaction patterns changed through time, we
⁴⁰⁹ found few patterns. The connectance decreased, as would be expected if the network
⁴¹⁰ is being colonized by specialist species [42]. Network specialization, however, did not
⁴¹¹ change predictably with assembly. Decreasing connectance without an accompanying

⁴¹² increase in specialization would be possible if the increased colonization of specialized
⁴¹³ species was accompanied by an increase in the diet breath of resident species. This would
⁴¹⁴ be expected if resident species were able to minimize their foraging time by expand-
⁴¹⁵ ing their diet breath as plant diversity increases with hedgerow maturation [2, 12, 54,
⁴¹⁶ 67].

⁴¹⁷ Interestingly, however, the changes in network patterns associated with assembly did
⁴¹⁸ not affect the hedgerow network robustness to species extinction or susceptibility to cas-
⁴¹⁹ cading perturbations. The hedgerows were designed to provide floral resources for the
⁴²⁰ largest number of pollinators across the growing season [41]. The generalized nature of
⁴²¹ the floral community may explain why the networks tended to be more generalized than
⁴²² expected if interactions were randomly distributed across species (Fig. 6). In addition, the
⁴²³ design of the hedgerow plantings may have facilitated the emergence of a single, highly
⁴²⁴ connected module in all of the networks (see 3 for examples). This network configuration
⁴²⁵ results in short path lengths (the distance between species in a network based on their
⁴²⁶ shared partners), and thus, a perturbation in one species can more easily spread to other
⁴²⁷ species. These networks are also vulnerable to the extinction of highly connected species
⁴²⁸ [13]. In order to promote more resilient communities, future restoration efforts should
⁴²⁹ explore designing floral communities to promote more interaction partitioning using, for
⁴³⁰ example, algorithms to optimize different network properties based on prior knowledge
⁴³¹ of pollinator floral preferences [43], and on desired network architectures that renders
⁴³² them more robust both to species loss and to cascading effects.

⁴³³ In general, plant-pollinator networks are highly dynamic, with high turnover of species
⁴³⁴ and interactions both within and between seasons [14]. Though our non-assembling com-
⁴³⁵ munities experienced fewer network reorganizations than the assembling hedgerows,
⁴³⁶ 82% of field margins and 40% of mature hedgerows underwent at least one changing

437 point in network structure. Pollinators are also highly opportunistic [2, 52, 64], though
438 trait complementarity such as tongue length and corolla depth impose some biophysical
439 limits to the interactions between plants and pollinators [58–60, 65, 66]. Such opportunism
440 may buffer plant-pollinator communities from global change [e.g., 33, 56], but our limited
441 understanding of the assembly of these communities impedes making such predictions
442 [14, 65]. Unlike in the broader food web literature, we have few assembly models of
443 mutualistic network assembly [31, 46, 62]. In addition, the few developed models often
444 borrow their mechanisms from competitive interactions, leading to inaccurate biological
445 assumptions [32]. We need further development of mechanistic models of mutualistic
446 systems to generate testable predictions, along with empirical exploration of network
447 assembly. Plant-pollinator communities and mutualisms are vital for biodiversity main-
448 tenance and essential ecosystem service provision. We must therefore understand the
449 processes underlying their assembly to facilitate restoration and conservation.

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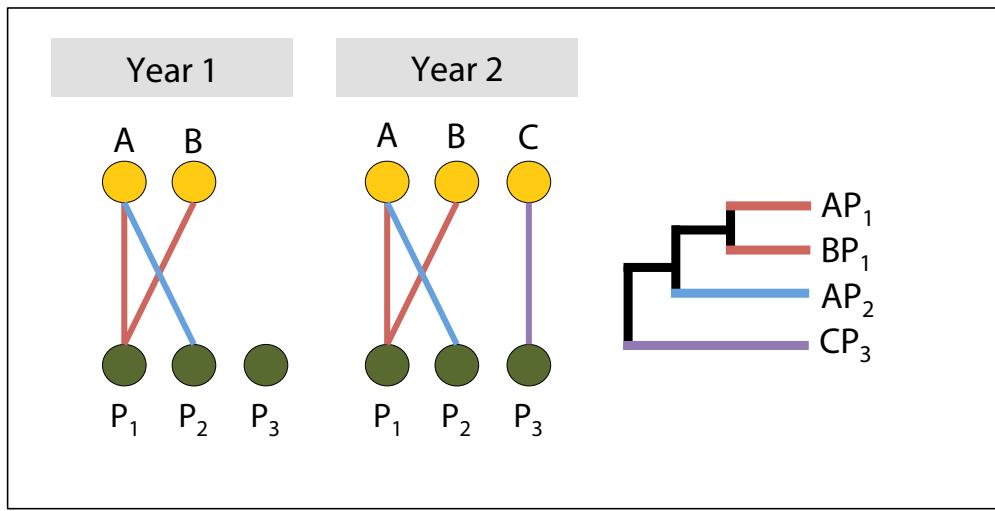


Figure 1: Diagram illustrating the analysis to examine the temporal turnover of interactions weighted based on their similarity. A, B and C are animal species, and Ps are plant species. The dendrogram depicts the interaction similarity across years based on the number of shared constituent species.

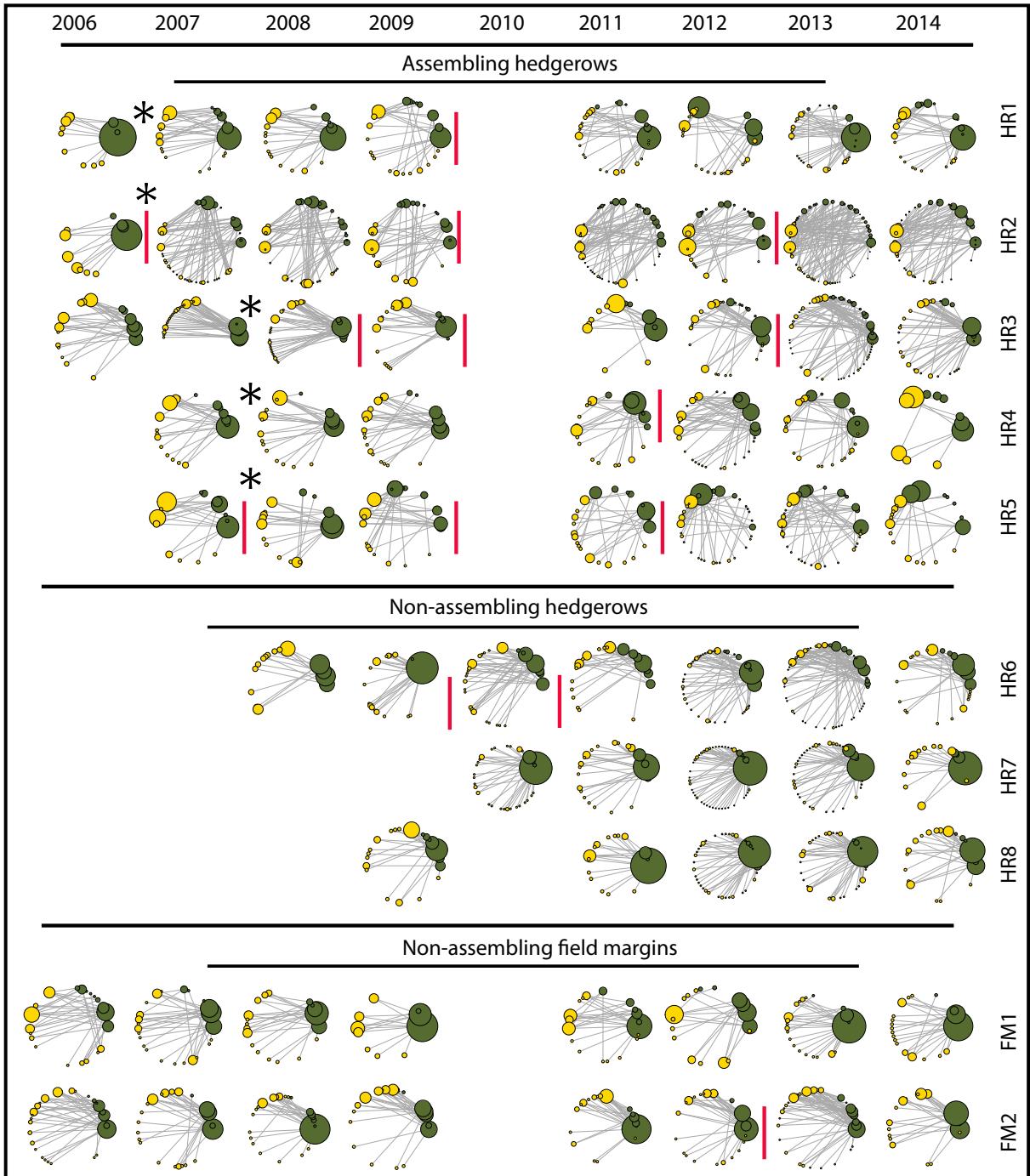


Figure 2: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, respectively,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

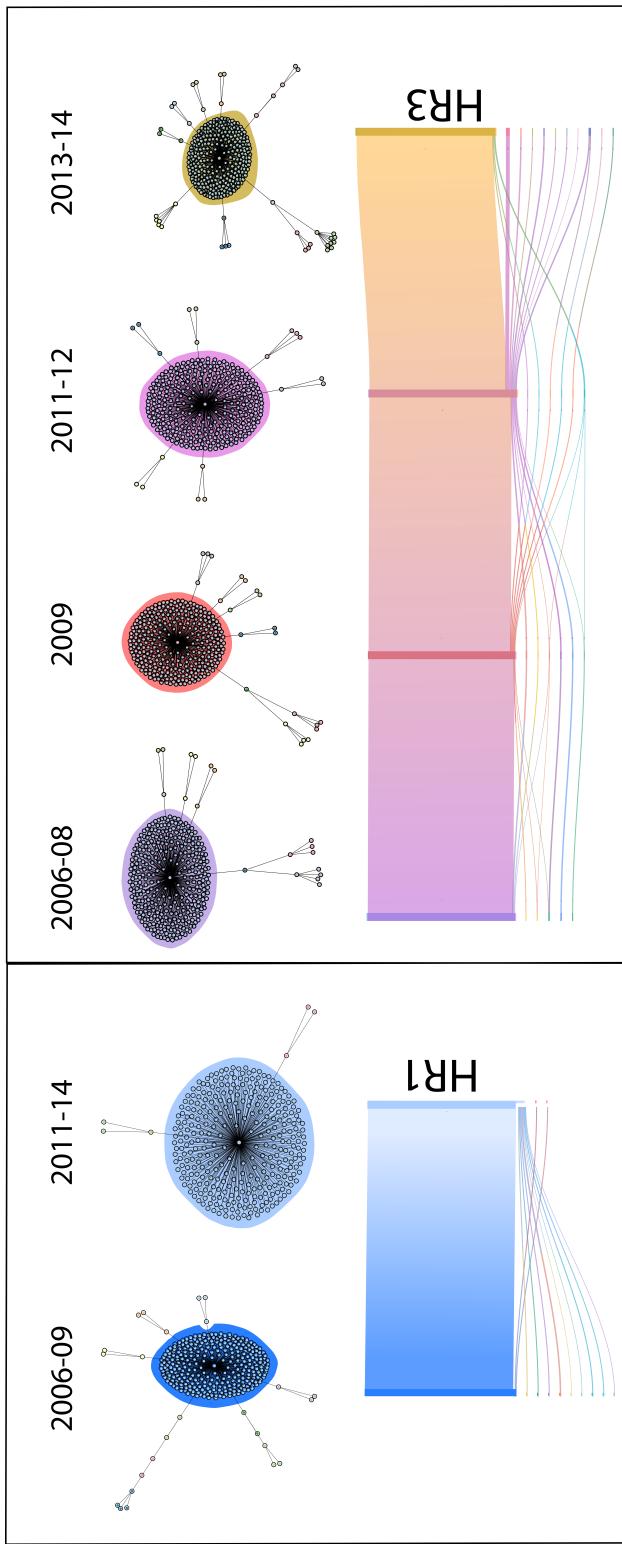


Figure 3: The species module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species between modules between changing points. Each line represents the change of s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

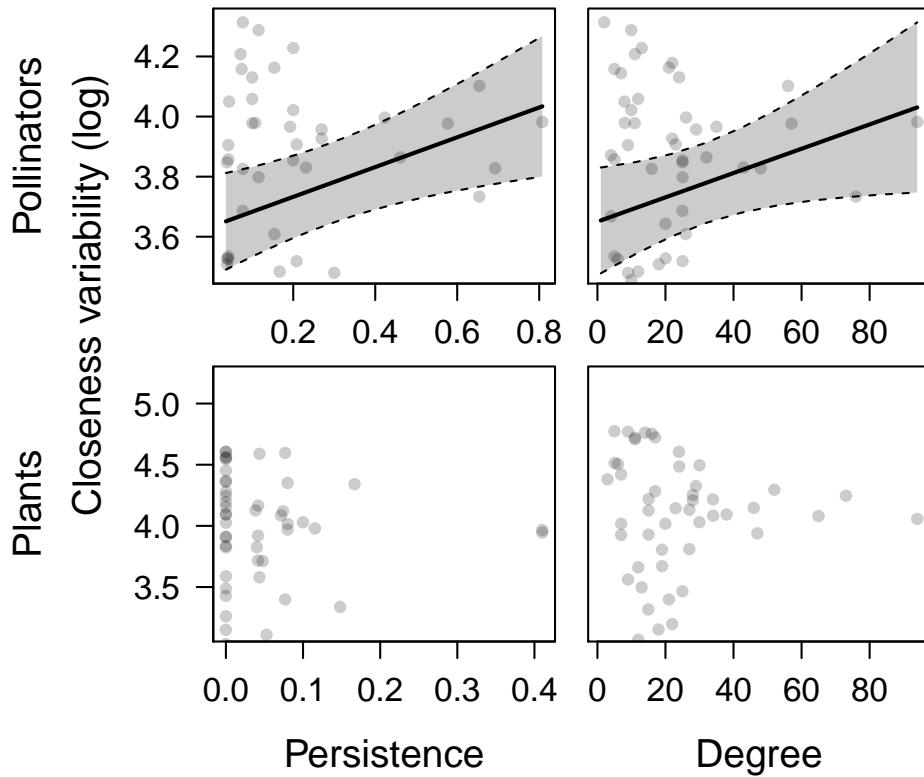


Figure 4: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across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

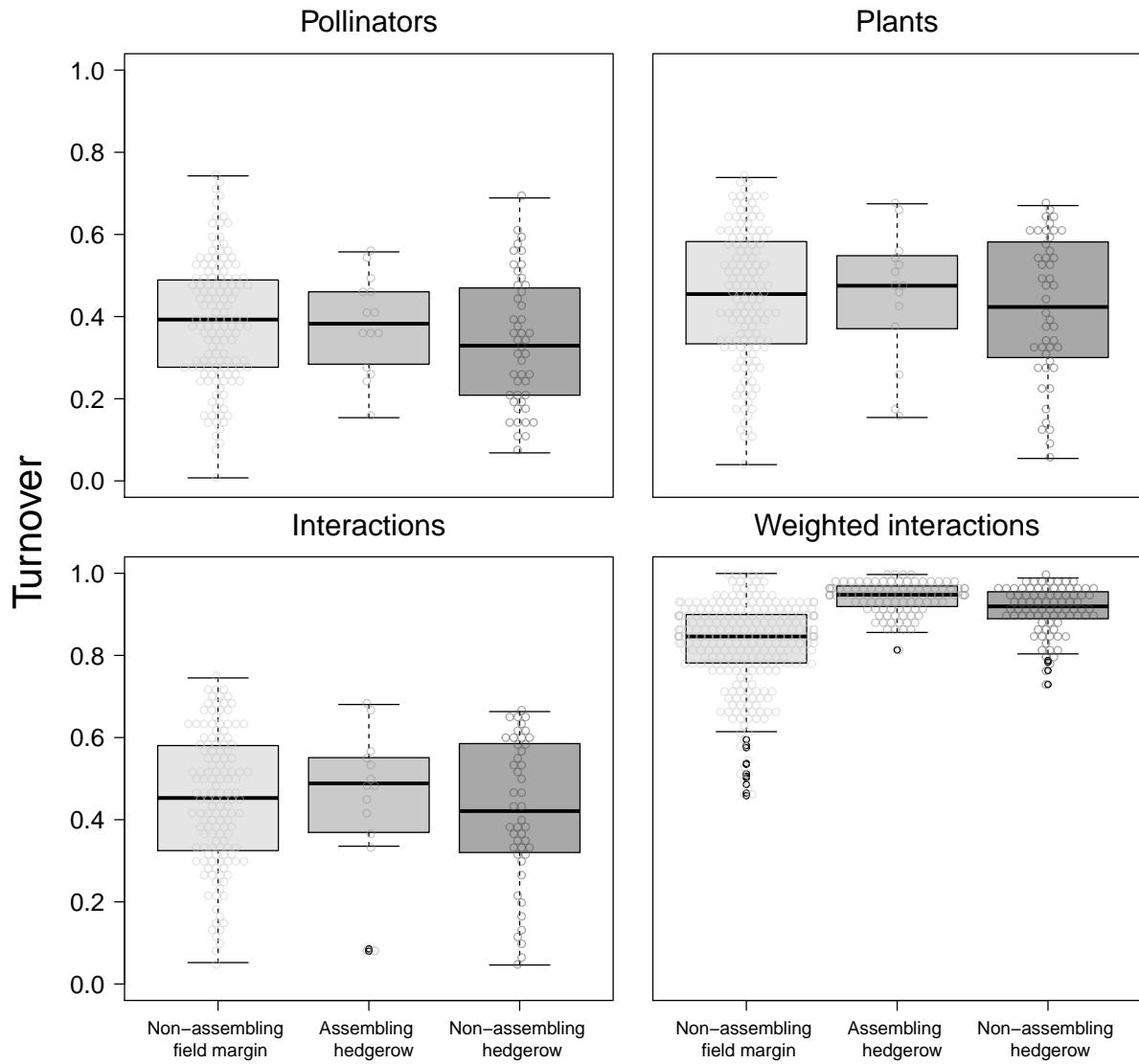


Figure 5: Species interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally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

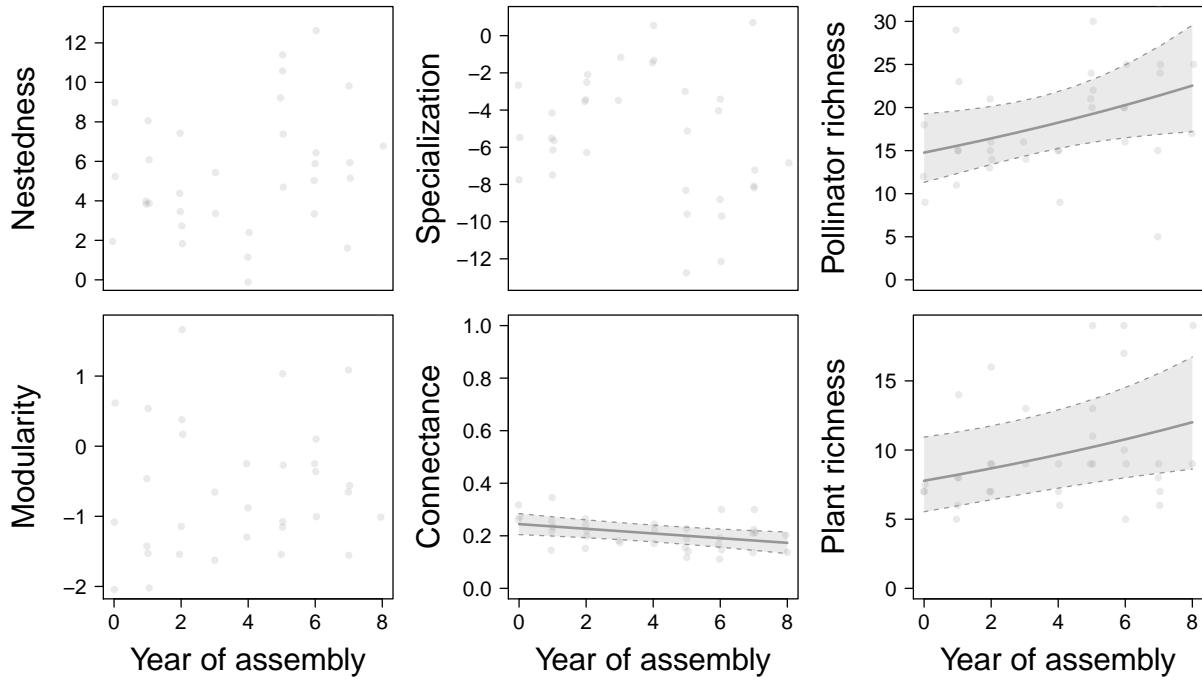


Figure 6: Nestedness, plant richness and pollinator richness increased as the networks assembled. Specialization and modularity remained consistent across years, while connectance decreased. The nestedness, modularity and specialization scores represent z -scores. Scores greater than ~ 2 or less than ~ -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.