

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.

¹³ community assembly, change points, robustness, nestedness, modularity, restoration, mutualism,
¹⁴ preferential attachment

¹⁵ **Introduction**

- ¹⁶ 1) Stability x persistence x community assembly - maybe the easiest part to put a theory. [H4]
- ¹⁷ 2) Link assembly to restoration and ecosystem services, biodiversity crisis (input the former first
- ¹⁸ paragraph). [H4]
- ¹⁹ 3) Focus on specific species in this paragraph, maybe link to niche theory? Mention [33, 39] to
- ²⁰ link species change in interactions (rewire) to their persistence and temporal variation; say that
- ²¹ we want to restore habitats that are robust and persistent through time. However, the relationship
- ²² between species persistence across years and their role in community assembly is still unclear. [H3
- ²³ and H4]
- ²⁴ 4) Paragraph that starts with "Understanding network assembly..." [H1 and H2]
- ²⁵ 5) Paragraph on changing points; mention the control and the non-assembly hedgerows here [H1
- ²⁶ and H2]
- ²⁷ 6) Maybe rephrase the last paragraph to more question driven statements? We tested four theoreti-
- ²⁸ cally motivated hypothesis exploring the process of community assembly using a eight-year dataset
- ²⁹ of plant-pollinator network development following hedgerow installment in the highly simplified
- ³⁰ and intensively managed agricultural landscape of California's Central Valley. First, we determine
- ³¹ whether network assembly was punctuated by significant reorganizations of interactions, and if
- ³² assembling networks presented more change than the control, non-assembly hedgerows. We next
- ³³ tested whether the species that are most variable in their network position — and thus important
- ³⁴ contributors to network reorganizations — are less persistent and connected species, as would be
- ³⁵ expected by preferential attachment. To further explore the mechanisms underlying the tempo-
- ³⁶ ral dynamics of the networks, also we examine patterns in the species and interaction temporal
- ³⁷ turnover. Finally, we investigate whether networks assemble toward predictable interaction pat-
- ³⁸ terns, and the ramifications for the robustness of the networks.

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

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

60 Significant reorganizations of interactions — change points — can also punctuate assembly [51]. A
61 change point is caused by a merge, split, fragmentation or formation of modules within a network.
62 Such interaction reorganizations are observed in social networks responding to abrupt shifts in
63 the behavior of interactors [51]. In ecological communities, such shifts may occur if, as new

64 species colonize, resident species change their interaction partners to optimize their foraging effort
65 [54, 12, 63, 2, 62]. For preferential attachment to be at play, change points would need to be
66 driven primarily by peripheral, temporally variable species while a stable, well-connected core
67 of species remained stable in their interactions. No studies, however, have examined if network
68 changing points occur during ecological network assembly and/or how these changes relate to
69 species behavior.

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

81 We explore the process of network development using a eight-year dataset of plant-pollinator com-
82 munity assembly following hedgerow installment in the highly simplified and intensively managed
83 agricultural landscape of California’s Central Valley. We first determine whether network assembly
84 was punctuated by significant reorganizations of interactions. We next tested whether the species
85 that are most variable in their network position — and thus important contributors to network re-
86 organizations — are less persistent and connected species, as would be expected by preferential
87 attachment. To further explore the mechanisms underlying the temporal dynamics of the networks,
88 also we examine patterns in the species and interaction temporal turnover. Finally, we investigate

89 whether networks assemble toward predictable interaction patterns, and the ramifications for the
90 robustness of the networks.

91 Materials & Methods

92 Study sites and collection methods

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

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

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

110 During each sampling round, flower-visitors to plants in assembling hedgerows and non-assembling

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

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

123 Change point analysis

124 Identifying change points

125 We employed a change point detection method [51] to identify fundamental reorganizations in
126 large-scale interaction patterns. Change point detection methods have yet to be generalized to
127 quantitative networks, so for this analysis we focused on qualitative (binary) networks. Following
128 [51], we first defined a probability distribution over the networks using the generalized hierarchi-
129 cal random graph model (GHRG). The GHRG model captures both assortative and disassortative
130 structure patterns at all scales in the network [51]. A network G is composed of vertices V and
131 edges E . The GHRG model decomposes the N vertices into a series of nested groups, the rela-
132 tionships among which are represented by the dendrogram T . The tips of T are the vertices of G ,
133 and the probability that two vertices u and v connect is given by the parameter p_r . The probability

134 distribution of the network G is thus defined as:

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

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

137 Using Bayesian posterior inference and techniques from phylogenetic tree reconstruction, we fit
138 the GHRG model to the networks [51]. We used a Markov chain Monte Carlo (MCMC) procedure
139 to first sample the posterior distribution of bipartitions, from which a consensus tree was derived
140 [51]. We used β distributions with the hyperparameters $\alpha = \beta = 1$ to define priors for p_r .

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

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

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

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

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

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

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

169 of a species by calculating the path lengths to other vertices (species) in the network [26]. The
170 shorter the mean path length to other species, the higher the closeness centrality. We used linear
171 mixed models to test whether the species closeness variability (log) is related to the persistence
172 or degree of that species [10, 38]. We included random effects for species and site. Because

173 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

174 were not significantly correlated, but we used the same models as we did for the pollinators for
175 consistency. Because an approximately logarithmic increase in closeness centrality — as would
176 be expected with assembly by preferential attachment — we also tested whether log closeness
177 centrality increased through time.

179 **Species and interaction turnover**

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

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

random effect [10, 38].

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

Temporal changes in interaction patterns

Network structure

Any changing points in network structure may contribute to the reorganization of the assembling networks into predictable interaction patterns. Pollination networks exhibit two main structural patterns — modularity [e.g., 47] and nestedness [e.g., 8, 7]. In modular networks, interactions are insular, occurring within separate groups or “modules” more often than between modules. Modules in the network may fragment as the network assembles, enhancing modularity. Conversely, nested networks are like a pyramid of interactions, where there are some species that interact with

many species, other species that interact with a subset of those species, and so on. If species entering the network tend to interact with the generalist base of the network pyramid as would be expected with preferential attachment, nestedness would increase through time. The connectance — the proportion of observed out of possible interactions — would also decrease as new, specialist species, preferentially attach to the core. Finally, network-level specialization will increase if specialist species colonize the network or species begin to limit their interaction niche breadth as the network assembles [11].

To evaluate network nestedness, we used the estimator weighted NODF [3]. NODF evaluates whether species with fewer partners interact with subsets of partners with which more connected species interact [3]. To estimate modularity, we used a hierarchical clustering algorithm [45, 18]. We evaluated network specialization with the metric H2, which estimates the deviation of the observed interaction frequency between plants and pollinators from a null expectation where all partners interact in proportion to their abundances [11]. It ranges from zero for generalized networks to one for specialized networks. We calculated standardized z-scores so that nestedness, modularity and specialization metrics could be compared across communities. The z-scores were calculated by generating an ensemble of 999 randomly assembled communities, subtracting the mean of the statistic calculated across these communities from the observed value, and then dividing by the standard deviation. To assemble random communities, we reshuffled the interactions between species but fixed the total number of interactions, species and interaction frequency distributions [27].

To test whether network modularity, nestedness, connectance or specialization changed linearly with assembly, we used linear mixed models with the descriptive network metrics as the response variable, year of assembly as the explanatory variable, and random effects of site and year. The number of species in a network affects the patterns of interaction possible, so we also examined the change in plant and pollinator species richness through time. We employed generalized linear

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

253 **Network robustness**

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

263 We also explored how the robustness to cascading perturbations changed as the community as-
264 sembled, using algebraic connectivity — the second smallest eigenvalue of the Laplacian matrix
265 [23] — as a proxy for network robustness. Algebraic connectivity relates to how difficult it is to
266 turn a network into completely disconnected groups of species [17, 28]. The larger the algebraic
267 connectivity, the more sensitive a network is to cascading perturbations. Perturbations, such as the
268 decrease in abundance of a plant or pollinator, can have negative consequences for the species in
269 the network. For example, a decrease in abundance of a pollinator will diminish the pollination
270 services it provides to plants. The affected plants would set less seeds, and decrease in abundance
271 the subsequent year. Consequently, other pollinators that depended on those plant species would
272 also be affected, and the effects of this perturbation would continue to propagate throughout the
273 network. Alternatively, perturbations could also have a positive effect if, for example, the increase
274 in the abundance of a plant species lead to an increase in resource availability for pollinators. The
275 examples of negative perturbations (e.g., resource collapse, disease spreading, parasites), however,

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

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

282 **Results**

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

286 **Change point analysis**

287 **Identifying change points**

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

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

298 In contradiction to the predictions of assembly by preferential attachment, both pollinator per-
299 sistence and degree were positively related to network position variability (Fig. 4, estimate of
300 the slope of closeness centrality variability and persistence \pm standard error of the estimate,
301 0.496 ± 0.182 , $p\text{-value}=0.016$; slope of closeness centrality variability and degree, 0.004 ± 0.002 ,
302 $p\text{-value}=0.056$). The slope of these relationships remained significant when the species with the
303 top 10 persistence and degree scores were dropped. In addition, plant persistence and degree were
304 not significantly related to network position variability (Fig. 4). The variability of species net-
305 work position was not the result of closeness linearly increasing through time, and, in fact, plant
306 and pollinator closeness decreased slightly through time (Fig. S2, estimate of the slope of close-
307 ness through time \pm SE, pollinators: -0.082 ± 0.021 , $p\text{-value}=0.003$; plants -0.089 ± 0.044 ,
308 $p\text{-value}=0.04$).

309 **Species and interaction turnover**

310 The rates of plant, pollinator and interaction temporal turnover were similar across assembling
311 hedgerows, non-assembling hedgerows and field margins, though mature hedgerows had marginally
312 less pollinator turnover than field margins (Fig. 5, estimate \pm SE of the difference in turnover be-
313 tween field margins and mature hedgerows, -0.051 ± 0.026 , $p\text{-value}=0.049$). The turnover of
314 plants and interactions was not significantly different between site types. When interactions were
315 weighted by their similarity, both assembling and mature hedgerows had higher rates of turnover
316 than field margins (Fig. 5, estimate \pm SE of the difference in turnover between field margins
317 and assembling hedgerows, 0.115 ± 0.027 , $p\text{-value}=0.0002$; field margins and mature hedgerows,
318 0.082 ± 0.024 , $p\text{-value}=0.002$). The weighted interaction turnover at assembling hedgerows, how-
319 ever, was not significantly higher than in non-assembling, mature hedgerows.

320 **Temporal changes in interaction patterns**

321 **Network structure**

322 Nestedness, modularity and specialization did not change predictably assembly (Fig. 6). All of the
323 networks were significantly nested (z -scores > 2), but not modular (z -scores < 2 , Fig. 6). Most
324 communities were more generalized than expected when interactions were randomized (Fig. 6).
325 Connectance decreased as the community assembled (Fig. 6, estimate of the slope of connectance
326 through time \pm standard error of the estimate, -0.023 ± 0.008 , p -value=0.007).
327 Both plant and pollinator species richness increased through time (Fig. 6, estimate of the slope of
328 richness through time \pm SE, pollinators: 0.136 ± 0.064 , p -value=0.034; plants: 0.140 ± 0.060 ,
329 p -value=0.012). Unsurprisingly, pollinator species are colonizing and persisting at the assembling
330 hedgerows. Plant species richness in the networks is based on the flowers actually visited by
331 pollinators and not the presence of a particular plant species at a site. Thus, though some new plant
332 species may establish themselves in the hedgerows, the increase in plant richness in the networks is
333 likely due to previously unvisited plants attracting visitors as they mature and offer better rewards.

334 **Network robustness**

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

339 **Discussion**

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

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

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

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

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

389 if the increased colonization of specialized species was accompanied by an increase in the diet
390 breath of resident species. This would be expected if resident species were able to minimize their
391 foraging time by expanding their diet breath as plant diversity increases with hedgerow maturation
392 [54, 67, 12, 2].

393 Interestingly, however, the changes in network patterns associated with assembly did not affect
394 the hedgerow network robustness to species extinction or susceptibility to cascading perturbations.
395 The hedgerows were designed to provide floral resources for the largest number of pollinators
396 across the growing season [41]. The generalized nature of the floral community may explain why
397 the networks tended to be more generalized than expected if interactions were randomly distributed
398 across species (Fig. 6). In addition, the design of the hedgerow plantings may have facilitated the
399 emergence of a single, highly connected module in all of the networks (see 3 for examples). This
400 network configuration results in short path lengths (the distance between species in a network
401 based on their shared partners), and thus, a perturbation in one species can more easily spread to
402 other species. These networks are also vulnerable to the extinction of highly connected species
403 [13]. In order to promote more resilient communities, future restoration efforts should explore de-
404 signing floral communities to promote more interaction partitioning using, for example, algorithms
405 to optimize different network properties based on prior knowledge of pollinator floral preferences
406 [43], and on desired network architectures that renders them more robust both to species loss and
407 to cascading effects.

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

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

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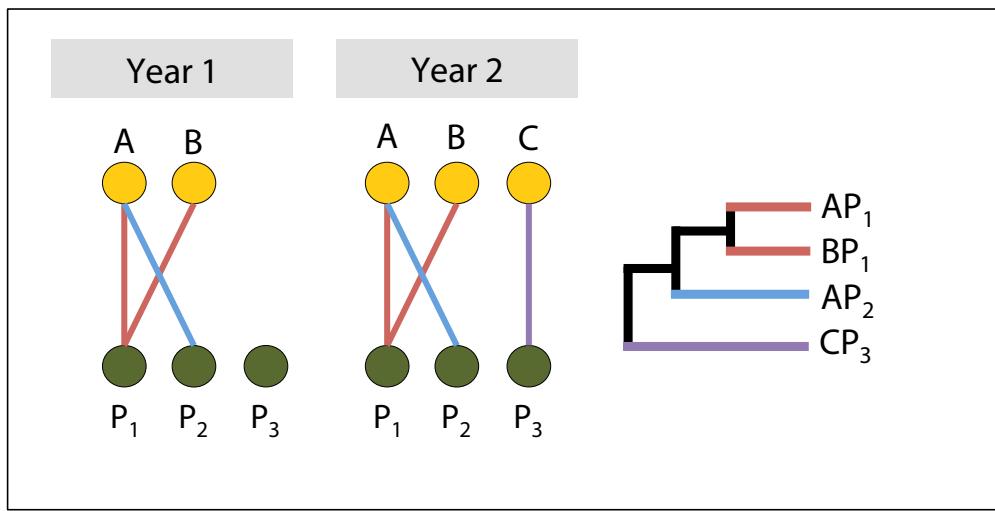


Figure 1: Diagram illustrating the analysis to examine the temporal turnover of interactions weighted based on their similarity. A, B and C are animal species, and Ps are plant species. The dendrogram depicts the interaction similarity across years based on the number of shared constituent species.

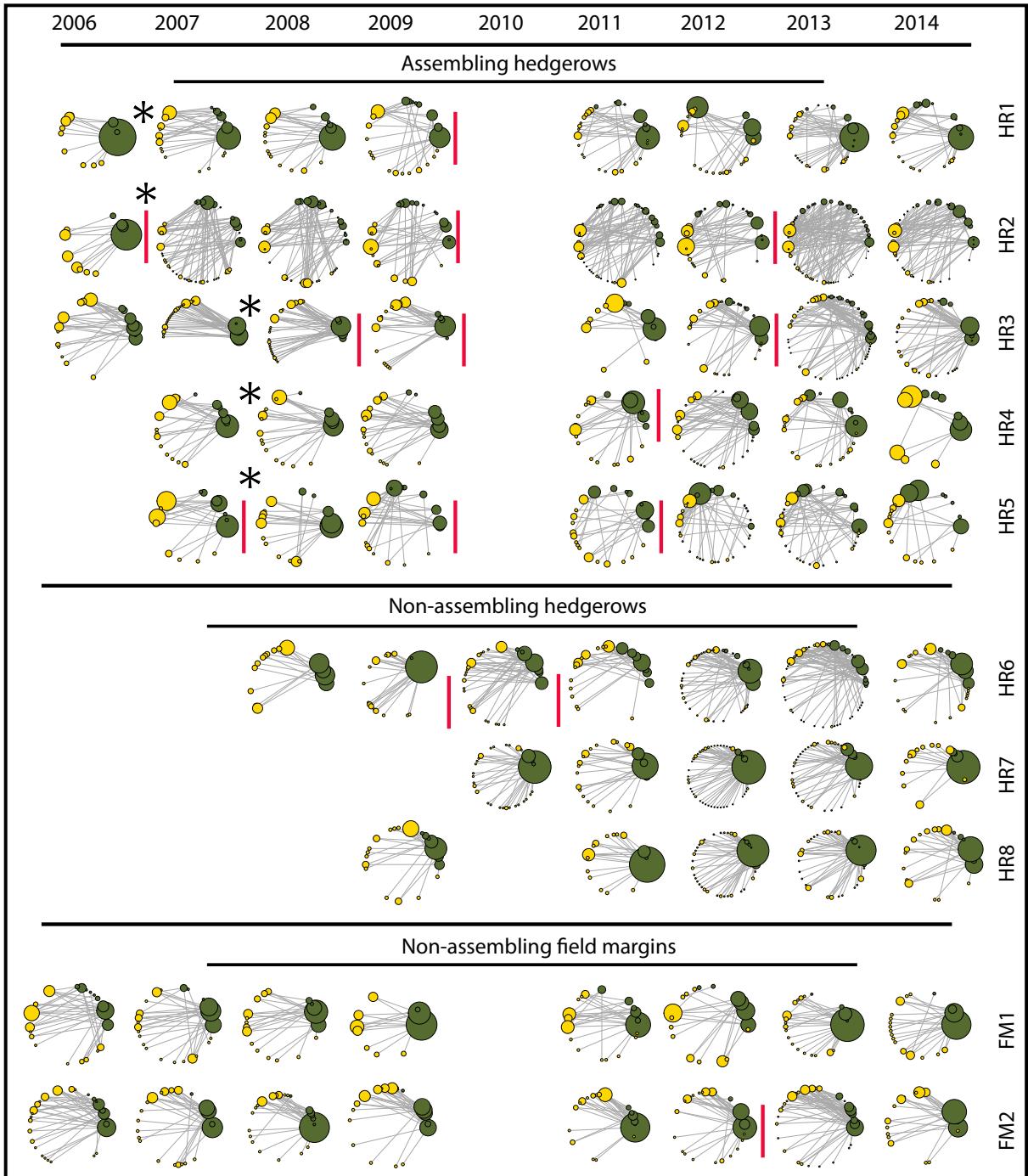


Figure 2: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, weighted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

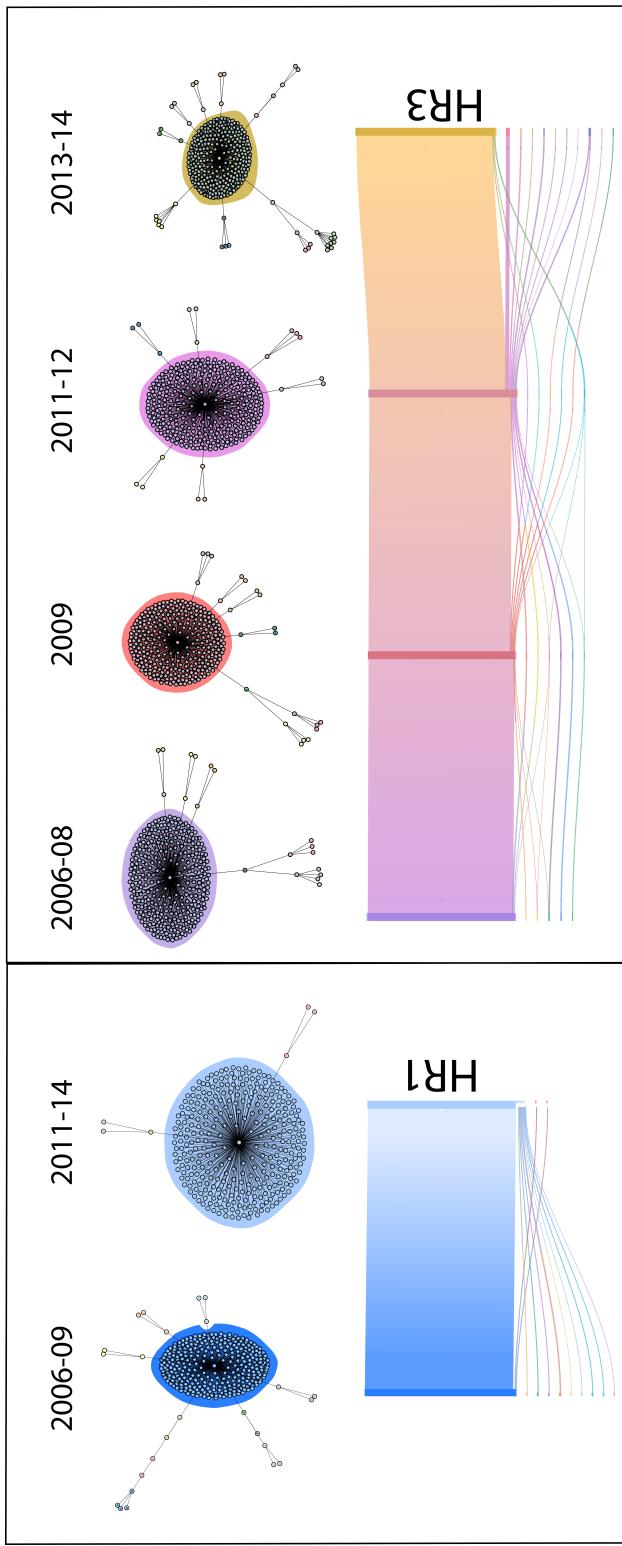


Figure 3: The species module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species to different modules between change points.

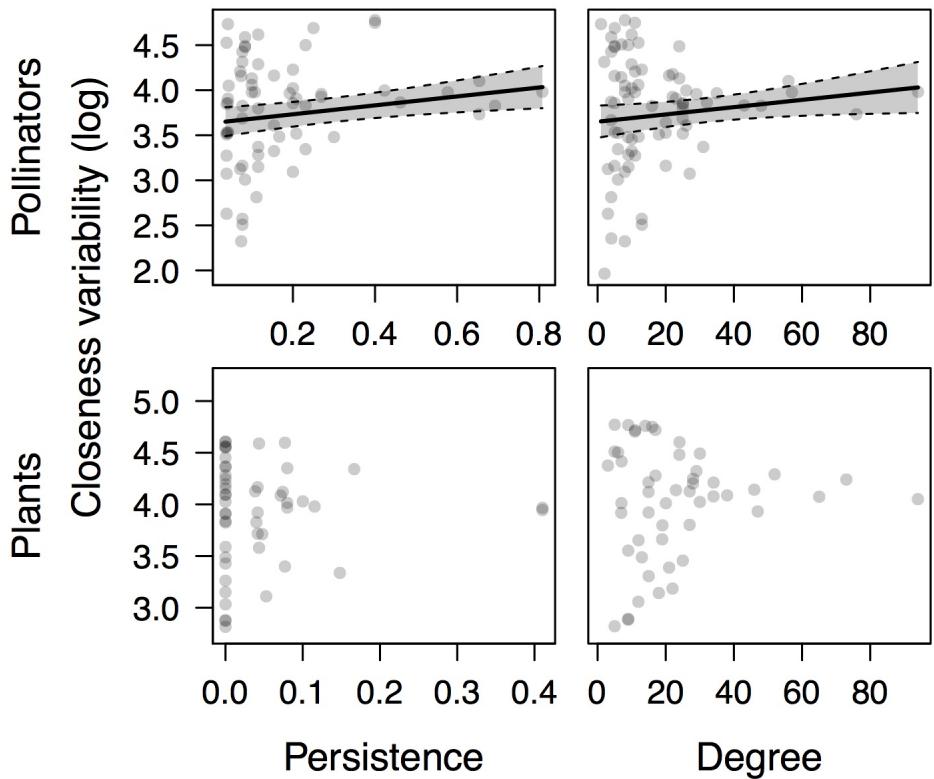


Figure 4: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across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

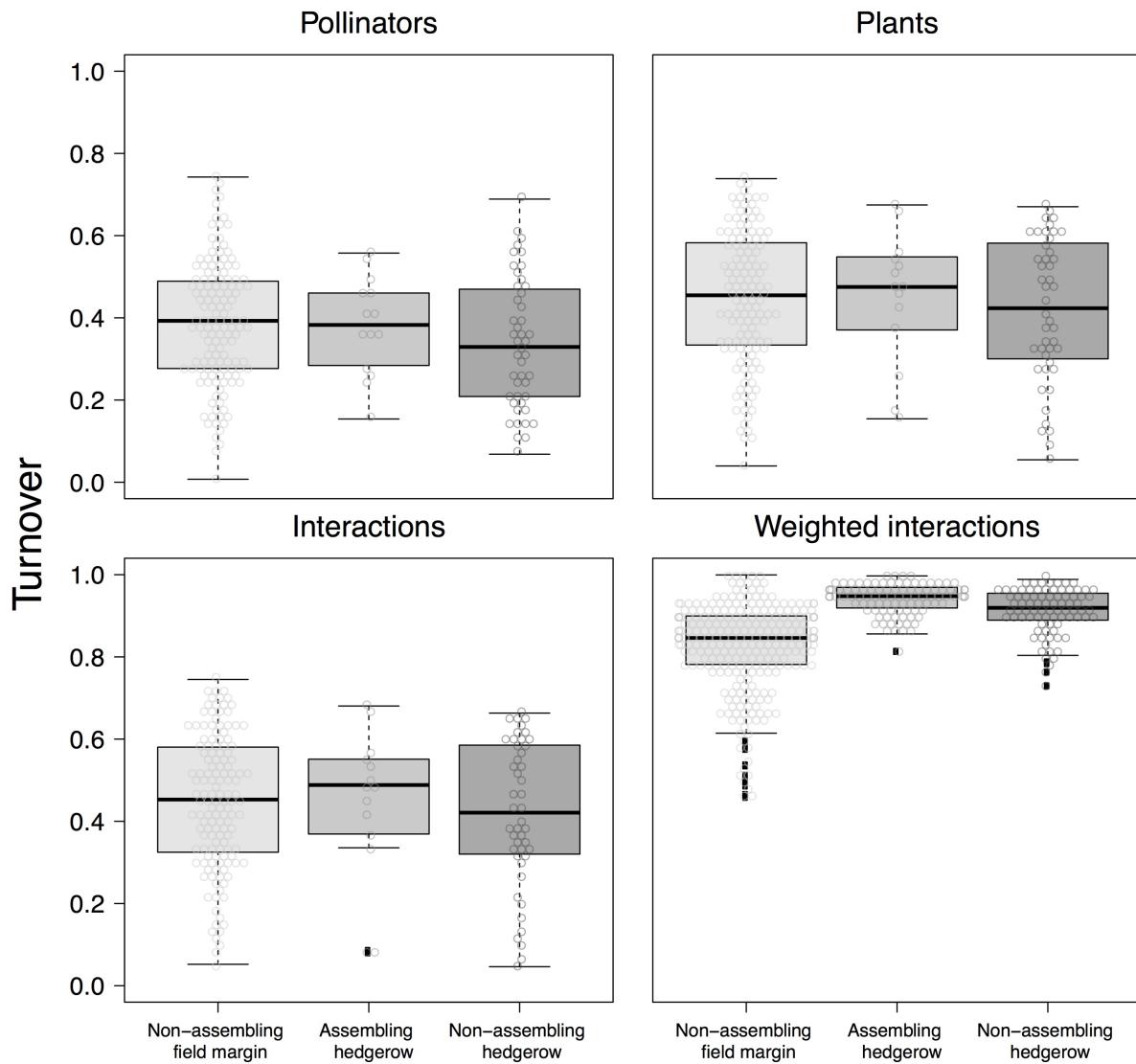


Figure 5: Species interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally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

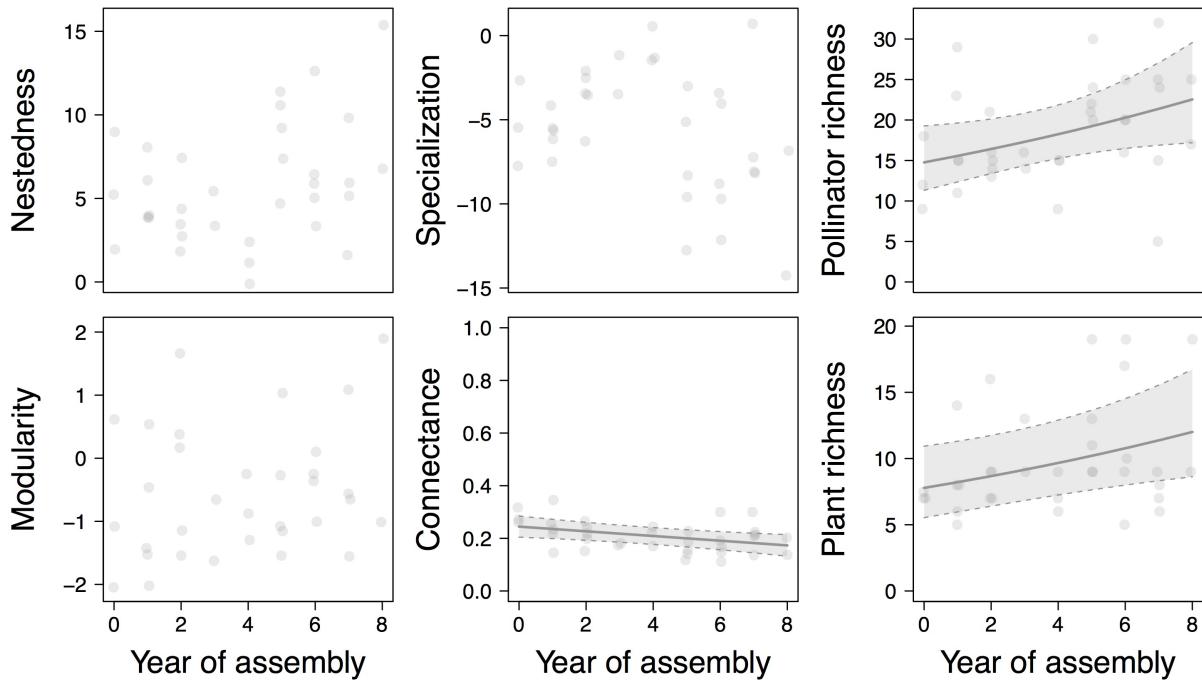


Figure 6: Plant richness and pollinator richness increased as the networks assembled. Nestedness, modularity and specialization did not change predictable across years, while connectance decreased. The nestedness, modularity and specialization scores represent z-scores. Scores greater than ~ 2 or less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