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Major interaction reorganizations punctuate the assembly of pollination networks

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Abstract

The structure of interaction networks is related to the ability of communities to maintain function in the face of species extinction. Understanding network structure and how it relates to network assembly, therefore, is a priority for conservation biology. Using a nine-year-dataset comprising nearly 20,000 pollinator visitation records, we explore the assembly of plant-pollinator communities at native plant restorations in the Central Valley of California. Across years, species are highly dynamic in their network position, causing community assembly to be punctuated by major interaction reorganizations. Generalist species were the most persistent and also the most variable in their network positions, contrary to what is expected through preferential attachment theory. The sensitivity of networks to cascading perturbations, increased with assembly, at least partially due to accumulating species richness. We elucidate some of the mechanisms underlying plant-pollinator network assembly and restoration — challenging the widely-held hypothesis that mutualistic networks assemble through preferential attachment.

¹⁵ community assembly, change points, specialization, nestedness, modularity, bipartite, preferential
¹⁶ attachment

17 **Introduction**

18 Global change has created a severe biodiversity crisis, and as species are lost, so are their interac-
19 tions [20, 6]. Because mutualistic interactions are essential for maintaining the diversity of their
20 component guilds, these systems are particularly at risk from coextinction cascades. The nature
21 of these cascades will depend on the interaction patterns within a community [38, 55, 9, 59]. To
22 safeguard ecological function, it has become increasingly imperative to aid the recovery of lost
23 interactions and component biodiversity through ecological restoration, and a key restoration aim
24 is to facilitate assembly of robust interaction networks [39]. We know little, however, about how
25 to re-assemble interacting communities through restoration, or the process of ecological network
26 assembly more generally.

27 Preferential attachment, the most widely explored mechanism of network assembly, [5], predicts
28 that species entering a network are more likely to interact with species that are already well-
29 connected [the “rich-get-richer” principle, 5]. In pollination systems — a particularly ubiquitous
30 mutualism [47, 34] — some studies have found support for this assembly mechanism. Investigating
31 the day-to-day, temporal assembly of a plant-pollinator network within a season, [46] found that
32 phenologically new plant and pollinator species tended to interact with already well-connected
33 species, potentially because these species are either more abundant or more temporally persis-
34 tent. In addition, using a space-for-time substitution to study primary succession along a glacier
35 foreland, [2] also found some evidence that assembly occurred through preferential attachment.
36 Specifically, network nestedness (i.e, a core group of generalists interacts with both specialist and
37 generalist species) increased as the community aged [2]. An increase in nestedness could result
38 from the preferential attachment process where specialist species attach to the well-connected,
39 generalist core.

40 In contrast to the network build-up described by preferential attachment, significant reorganiza-

41 tions of interactions can punctuate assembly [49]. Such significant reorganizations of interactions,
42 or network changing points, are observed in social networks that respond to abrupt shifts in the
43 behavior of interactors [49]. In ecological communities, such shifts may occur if, as new species
44 colonize, resident species change their interaction partners to optimize their foraging effort. In
45 plant-pollinator communities, theory predicts that pollinators optimize their use of floral resources
46 to reduce interspecific competition and improve resource-use efficiency [52, 61, 60, 2, 12]. No
47 studies, however, have examined whether network changing points occur during ecological net-
48 work assembly, and how these changes relate to the species behavior.

49 Understanding network assembly is particularly relevant to ecological restoration, which is essen-
50 tially “applied succession” [e.g., 48]. In pollination systems, the time since an area was restored has
51 been shown to affect the structure of networks [23, 17], suggesting interactions are changing as the
52 community develops. Understanding the mechanisms of network assembly will help to guide com-
53 munity restoration. Facilitating network restoration is especially imperative in areas where species
54 interactions provide essential ecosystem services, such as crop pollination. To ensure the continued
55 provision of ecosystem services and curb biodiversity loss, it is critical to restore pollinators and
56 their interactions in agricultural landscapes. To promote pollinator services in agriculture, farmers
57 may chose to plant strips of native plants along farm edges (hedgerows) to help provide habitat
58 for pollinators without removing arable land from production. Hedgerows augment the richness,
59 abundance and trait diversity of pollinators in agricultural landscapes [42, 35, 51], and promote the
60 persistence and colonization of floral resource specialists [40]. It is important to understand how
61 these new species are being incorporated into the network as the community assembles, and the
62 consequences for interaction patterns and robustness.

63 We explore the process of network development using a nine year dataset of plant-pollinator com-
64 munity assembly following hedgerow restoration in the highly simplified and intensively managed
65 agricultural landscape of California’s Central Valley. We first determine whether the mechanism

66 underlying network assembly is a build up of interactions as would be predicted by preferential
67 attachment, or instead is punctuated by significant reorganizations of interactions (i.e., network
68 changing points). Even with changing points in interaction organization, networks could still be
69 assembling via preferential attachment if the network reorganizations were primarily driven by pe-
70 ripheral, temporally variable species while a stable, well-connected core of species persist. We test
71 whether the species that are most variable in their network position — and thus important contrib-
72 utors to network reorganizations — are less persistent and connected species. To further explore
73 the mechanisms underlying the temporal dynamics of the networks, we examine patterns in the
74 species and interaction temporal turnover. Lastly, we investigate whether networks are assembling
75 toward predictable interaction patterns, and the ramifications for the robustness of the networks to
76 species extinction and cascading perturbations.

77 Materials & Methods

78 Study sites and collection methods

79 We surveyed plant-pollinator interaction networks of independent assembling hedgerows commu-
80 nities (N=5), and of two types of non-assembling communities to serve as controls: unrestored,
81 weedy field margins (N=19) and mature hedgerows (greater than 10 years since planting, N=29).
82 The sites were located in the Central Valley of California in Yolo, Colusa and Solano Counties.
83 This area is composed of intensively managed agriculture — primarily monocultures of conven-
84 tional row crops, vineyards and orchards. Hedgerows are ca. 3–6 m wide and approximately 350
85 m long, bordering large (ca. 30-hectare) crop fields. Hedgerows consist of native, perennial, shrub
86 and tree plantings including *Rosa californica*, *Cercis occidentalis*, *Ceanothus spp.*, *Heteromeles*
87 *arbutifolia*, *Sambucus mexicana*, *Eriogonum spp.*, *Baccharis spp.*, *Salvia spp.* and others [Fig. S1
88 39, 35, 40]. The mean distance between monitoring sites was 15 km, and the minimum distance

89 between sites sampled in the same year was 1 km. The entire area surveyed spanned almost 300
90 km². The crop fields adjacent to all sites were similarly managed as intensive, high-input mono-
91 culture.

92 Monitoring of assembling hedgerows began in 2006 and continued through 2014. Surveys of
93 these sites began the year before the area was restored. For logistical reasons, no sampling of
94 assembling hedgerows was conducted in 2010. Sites were sampled between two and five times per
95 year (Tables S1-S3, mean 3.4 samples per year). In each round of sampling, the order in which
96 sites were sampled was randomized. Surveys were conducted under sunny conditions when the
97 temperature was above 21°C and wind speed was below 2.5 meters/second.

98 Flower-visitors to plants in hedgerows and unrestored controls were netted for one hour of active
99 search time (the timer was paused when handling specimens). Honeybees (*Apis mellifera*) were
100 not collected because their abundance is determined largely by hive placement by bee-keepers.

101 All other insect flower visitors that touched the reproductive parts of the flower were collected;
102 however, here we focus only on wild bees and syrphids — the most abundant and effective pollinators
103 in the system (representing 49 and 19 percent of records, respectively, C. Kremen, A. Klein
104 and L. Morandin, unpublished data). Bee and syrphid specimens were identified to species (or
105 morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*) by expert tax-
106 onomists.

107 Quantitative networks were generated for each site through time. To account for the unequal
108 number of surveys between years (Tables S1-S3), we use the mean of the interactions between a
109 pair of plants and pollinators across surveys within a year to represent interaction frequency.

110 **Change point analysis**

111 **Identifying change points**

112 We employed a change point detection method [49] to identify fundamental reorganizations in
113 large-scale interaction patterns. A change point is caused by a merge, split, fragmentation or
114 formation of modules (also called compartments). Change point detection methods have yet to
115 be generalized to quantitative networks, so for this analysis we focused on qualitative (binary)
116 networks. Following [49], we first defined a probability distribution over the networks using the
117 generalized hierarchical random graph model (GHRG). The GHRG model is able to capture both
118 assortative and disassortative structure patterns at all scales in the network [49]. A network G is
119 composed of vertices V and edges E . The GHRG model decomposes the N vertices into a series
120 of nested groups, the relationships among which are represented by the dendrogram T . The tips
121 of T are the vertices of G , and the probability that two vertices u and v connect is given by the
122 parameter p_r . The probability distribution of the network G is thus defined as:

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

123 Where E_r is the observed number of edges between vertices with the common ancestor r , and N_r
124 is the total possible edges.

125 Using Bayesian posterior inference and techniques from phylogenetic tree reconstruction, we fit
126 the GHRG model to the networks [49]. This is accomplished by using a Markov chain Monte
127 Carlo (MCMC) procedure to first sample the posterior distribution of bipartitions, from which a
128 consensus tree is derived [49]. We use β distributions with the hyperparameters $\alpha = \beta = 1$ to
129 define priors for p_r .

130 Once the GHRG model has been fit to the networks, we determine whether a change point occurred

131 between two time slices. To detect a change point, we use Bayes factors to compare the fit of
132 two models — one where a change point occurred between two networks, and one where no
133 change occurred. We chose a sliding window of length, w , of four, within which to find change
134 points. Larger windows allow for more gradual changes, and four was the maximum possible with
135 our eight years of data. Lastly, to calculate a p -value for the Bayes factors, we use parametric
136 bootstrapping to numerically estimate the null distribution [49]. We employed code published
137 online by L. Peel for the change point analysis. Analyses were conducted in Python 3.4.

138 We next test whether the change points occurring in maturing hedgerows were a component of
139 the assembly process or a product of environmental shifts that lead to network reorganizations
140 in all types of communities. We model the number of change points as successes and the total
141 number of years each site was sampled as trials, and use a generalized linear model with Binomial
142 error to test whether the probability of a change point occurring varied by site type [10]. We used
143 standard techniques to determine whether the assumptions of the models were met for this and all
144 subsequent models. For the non-assembling hedgerows and weedy field margins, only sites with
145 five or greater survey years were included in this analysis ($N=11$). All statistical analyses were
146 conducted in R 3.2.3 [53].

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

148 To further elucidate the nature of the change points, we examine the characteristics of the species
149 that contributed to interaction reorganization. Some species remain in relatively similar network
150 positions through time, whereas others are more variable in their position and thus contribute more
151 strongly to network reorganization. We test whether the more persistent species with the highest
152 degree (number of different interaction partners) are the most stable in their network positions, as
153 would be expected if the networks were assembling via preferential attachment.

154 We calculate species persistence as the proportion of surveys in which a plant or pollinator is

155 observed. Species observed consistently within and between years are thus maximally persistent.
156 Weighted species degree is calculated from interaction observations from an extensive dataset from
157 Yolo County (approx. 18000 interaction records) that included both the data included in this study
158 and additional data from sites where we collected flower visitors using the same methods [40, 51].
159 To represent network position variability, we computed the coefficient of variation of weighted
160 closeness centrality [24] at each site through time. Closeness centrality represents the importance
161 of a space by calculating the path lengths to other vertices (species) in the network [24]. The
162 shorter the mean path length to other species, the higher the closeness centrality. We use linear
163 mixed models to test whether the species closeness variability (log) is related to the persistence
164 or degree of that species [10, 36]. We included random effects for species and site. Because the
165 degree and persistence of pollinators were strongly correlated, ($\rho = 0.071$, p -value $< 2 * 10^{-16}$),
166 we include each explanatory variable in separate models. Plant degree and persistence were not
167 significantly correlated, but we use the same models as we did for the pollinators for consistency.
168 Because an approximately logarithmic increase in closeness centrality, as would be expected with
169 assembly by preferential attachment, would also lead to high variability in closeness scores, we
170 also test whether log closeness centrality increases through time.

171 Species and interaction turnover

172 Reorganizations of network structure can be the result of species turnover or species changing
173 their interaction partners (i.e., re-wiring). To better understand the mechanisms underlying the
174 temporal dynamics of the assembling networks, we examined patterns of species and interac-
175 tion turnover. For example, assembling networks may have higher rates of pollinator turnover
176 than non-assembling communities because new pollinator species are colonizing and establishing
177 themselves [40]. Similarly, because species are turning over and pollinators are trying to maximize
178 their foraging efficiency based on the species present, interactions may turnover more quickly than

179 in established communities. In addition, at assembling hedgerows, plants that are unvisited in
180 early years may appear to “colonize” the networks as they became more attractive resources and
181 establish new interactions with pollinators.

182 To estimate the temporal species and interaction turnover, we use an approach similar to calcu-
183 lating spatial β -diversity. Instead of calculating the variation in community composition across
184 sites within a year, we estimated turnover across years at a site. We first calculated the pairwise
185 dissimilarity of plants, pollinators and interactions between years within each site using the Chao
186 dissimilarity estimator that incorporates abundances, while also accounting for unobserved records
187 [14]. Dissimilarity estimates can be affected by the total number of species and individuals sam-
188 pled at a site [e.g., 51]. For example, the probability that two sites do not share any species is
189 higher when there are few individuals at those sites. Following [51], we use null models that con-
190 strained species richness to estimate the deviation of the observed dissimilarity from that which
191 would be expected under a random community assembly process. With the corrected dissimilarity
192 values, we then calculated the multivariate dispersion of community composition across years [4].
193 In order to test whether assembling hedgerows had more species and interactions turnover than
194 non-assembling communities, the species and interaction temporal turnover estimates were mod-
195 eled as responses in a linear mixed model with site type as an explanatory variable and site as a
196 random effect [10, 36].

197 Though species may turnover across years, some groups of species may essentially replace each
198 other if they fill similar roles in the network, occupying the same network position and interact-
199 ing with similar species. At non-assembling communities, species turnover may overestimate the
200 temporal changes in the networks if the interactions occurring in one year are similar to those in
201 the next year when they are weighted by the similarity of their constituent species (Fig. S2). We
202 develop a method to examine the temporal turnover of interactions with weightings based on their
203 similarity. We followed the algorithm of [1] to cluster all the interactions (edges) hierarchically

204 across sites and years based on their similarity, and build a dendrogram. The interaction similar-
205 ity is based how many plants and pollinators (vertices) two edges share [1, 32]. The more species
206 edges shared in common, the shorter the branch length between them on the dendrogram. We next
207 calculated the temporal turnover of interactions weighted by their similarity, as approximated by
208 “phylogenetic” distance [28, 33]. We then use linear mixed models to test whether the weighted
209 turnover of interactions varied between assembling and non-assembling networks, including site
210 as a random effect [10, 36].

211 **Temporal changes in interaction patterns**

212 **Network structure**

213 Any changing points in network structure may contribute to the reorganization of the assembling
214 networks into predictable interaction patterns. Pollination networks exhibit two main structural
215 patterns — modularity [e.g., 45] and nestedness [e.g., 8, 7]. In modular networks, interactions are
216 insular, occurring within separate groups or “modules” more often than between modules. Modules
217 in the network may fragment as the network assembles, enhancing modularity. Conversely, nested
218 networks are like a pyramid of interactions, where there are some species that interact with many
219 species, other species that interact with a subset of those species, and so on. If species entering
220 the network tend to interact with the generalist base of the network pyramid as would be expected
221 with preferential attachment, nestedness would increase through time. The connectance — the
222 proportion of observed out of possible interactions — would decrease as new, specialist species,
223 preferentially attach to the core. Lastly, the overall level of network specialization may change
224 as the community assembles. Network-level specialization will increase if specialist species colo-
225 nize the network or species begin to limit their interaction niche breadth as the network assembles
226 [11].

227 To evaluate network nestedness, we used the estimator weighted NODF [3]. NODF evaluates
228 whether species with fewer partners interact with subsets of partners with which more connected
229 species interact [3]. To estimate modularity, we use a hierarchical clustering algorithm [43, 16]. We
230 evaluate network specialization with the metric H2, which estimates the deviation of the observed
231 interaction frequency between plants and pollinators from a null expectation where all partners
232 interact in proportion to their abundances [11]. It ranges from zero for generalized networks to
233 one for specialized networks. We calculated standardized z-scores so that nestedness, modularity
234 and specialization metrics could be compared across communities. The z-scores were calculated
235 by generating an ensemble of 999 randomly assembled communities, subtracting the mean of the
236 statistic calculated across these communities from the observed value, and then dividing by the
237 standard deviation. To assemble random communities, we reshuffled the interactions between
238 species but fixed the total number of interactions, species and interaction frequency distributions
239 [25].

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

246 Network robustness

247 Lastly, we tested whether the changes in interaction patterns associated with network assembly
248 affect the robustness of the network to species loss and cascading perturbations. Following [38],
249 we simulated plant species extinction and the subsequent extinction cascades of pollinator species.
250 Because the reproduction of plant species is facilitated by active restoration efforts, it is unlikely the

251 extinction of pollinator species would affect plant populations in the hedgerows. However, plants
252 ceasing to bloom, for example in response to drought, will likely affect the pollinators that depend
253 on them. We eliminated plants species based on their degree or abundance, and then calculated
254 the number of pollinators that secondarily went extinct. The area below the extinction curve is an
255 estimate of network robustness [38, 19].

256 We also explored how the robustness to cascading perturbations changed as the community as-
257 sembled, using algebraic connectivity — the second smallest eigenvalue of the Laplacian matrix
258 [21] — as a proxy for network robustness. Algebraic connectivity relates to how difficult it is to
259 turn a network into completely disconnected groups of species [15, 26]. The larger the algebraic
260 connectivity, the more sensitive a network is to cascading perturbations. Perturbations, such as the
261 decrease in abundance of a plant or pollinator, can have negative consequences for the species in
262 the network. For example, a decrease in abundance of a pollinator will diminish the pollination
263 services it provides to plants. The affected plants would set less seeds, and decrease in abundance
264 the subsequent year. Consequently, other pollinators that depended on those plant species would
265 also be affected, and the effects of this perturbation would continue to propagate throughout the
266 network. Alternatively, perturbations could also have a positive effect if, for example, the increase
267 in the abundance of a plant species lead to an increase in resource availability for pollinators. The
268 examples of negative perturbations (e.g., resource collapse, disease spreading, parasites), however,
269 outnumber possible positive perturbations. It is important to note that both robustness and alge-
270 braic connectivity assume that the network is static. They do not account for the ability of species
271 to alter their interaction depending on circumstances and the resource availability.

272 In order to test whether hedgerows changed in robustness as the communities assembled, the three
273 measures of robustness were modeled as responses in a linear mixed model with site type as an
274 explanatory variable and site as a random effect [10, 36].

275 **Results**

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

279 **Change point analysis**

280 **Identifying change points**

281 The majority (76%) of the sites underwent at least one significant interaction reorganization (Fig. 1,
282 2). All five of the assembling hedgerows experienced network changing points, whereas only 40%
283 and 81% of non-assembling hedgerows and field margins, respectively, underwent significant in-
284 teraction reorganizations. Assembling hedgerows had significantly more changing points than the
285 non-assembling networks (estimate of the difference in the odds ratios between assembling and
286 non-assembling networks, 3.316, 95% CI [1.314, 8.572], p -value= 0.0117). Network assembly
287 following restoration is thus punctuated by more interaction reorganizations than would be ex-
288 pected by environmental shifts alone that would have affected all networks similarly.

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

290 In contradiction to the predictions of assembly by preferential attachment, both pollinator per-
291 sistence and degree were positively related to network position variability (Fig. 3, estimate of
292 the slope of closeness centrality variability and persistence \pm standard error of the estimate,
293 0.496 ± 0.182 , p -value=0.016; slope of closeness centrality variability and degree, 0.004 ± 0.002 ,
294 p -value=0.056). The slope of these relationships remained significant when the species with the
295 top 10 persistence and degree scores were dropped. In addition, plant persistence and degree were

296 not significantly related to network position variability (Fig. 3). The variability of species net-
297 work position was not the result of closeness linearly increasing through time, and, in fact, plant
298 and pollinator closeness decreased slightly through time (Fig. S2, estimate of the slope of close-
299 ness through time \pm SE, pollinators: -0.082 ± 0.021 , $p\text{-value}=0.003$; plants -0.089 ± 0.044 ,
300 $p\text{-value}=0.04$). Though statistically significant, the models seems to be a poor fit to the data.

301 Species and interaction turnover

302 The rates of plant, pollinator and interaction temporal turnover were similar across assembling
303 hedgerows, non-assembling hedgerows and field margins, though mature hedgerows has marginally
304 significantly less pollinator turnover than field margins (Fig. 4, estimate \pm SE of the difference in
305 turnover between field margins and mature hedgerows, -0.051 ± 0.026 , $p\text{-value}=0.049$). The
306 turnover of plants and interactions was not significantly different between site types. When inter-
307 actions where weighted by their similarity, both assembling and mature hedgerows had higher
308 rates of turnover than field margins (Fig. 4, estimate \pm SE of the difference in turnover be-
309 tween field margins and assembling hedgerows, 0.115 ± 0.027 , $p\text{-value}=0.0002$; field margins
310 and mature hedgerows, 0.082 ± 0.024 , $p\text{-value}=0.002$). The weighted interaction turnover at
311 assembling hedgerows, however, was not significantly higher than in non-assembling, mature
312 hedgerows.

313 Temporal changes in interaction patterns

314 Network structure

315 Nestedness and modularity did not change in any predictable pattern with assembly (Fig. 5). All of
316 the networks were significantly nested (z -scores > 2), but not modular (z -scores < 2 , Fig. 5).

317 Connectance decreased as the community assembled (Fig. 5, estimate of the slope of connectance
318 through time \pm standard error of the estimate, -0.023 ± 0.008 , $p\text{-value}=0.007$). Specialization
319 also decreased, though the slope was not significantly different from zero. Most communities were
320 more generalized than expected when interactions were randomized (Fig. 5).

321 Both plant and pollinator species richness increased through time (Fig. 5, estimate of the slope of
322 richness through time \pm SE, pollinators: 0.136 ± 0.064 , $p\text{-value}=0.034$; plants: 0.140 ± 0.060 ,
323 $p\text{-value}=0.012$). Unsurprisingly, pollinator species are colonizing and persisting at the assembling
324 hedgerows. Plant species richness in the networks is based on the flowers actually visited by
325 pollinators and not the presence of a particular plant species at a site. Thus, though some new
326 plant species may establish themselves in the hedgerows, the increase in plant richness in the
327 networks is likely due to previously unvisited plants attracting visitors as they mature and offer
328 better rewards.

329 **Network robustness**

330 Assembly did not affect network robustness to species extinction when species were removed
331 incrementally by degree or abundance. In contrast, the sensitivity of networks to cascading per-
332 turbations, as measured by the algebraic connectivity of the network, increased as the network
333 assembled (Fig. 6, estimate of the slope of sensitivity to cascading perturbations through time \pm
334 SE, 0.6814 ± 0.272 , $p\text{-value}=0.042$).

335 **Discussion**

336 We show that the temporal assembly of plant-pollinator networks following restoration is a highly
337 dynamic process where interactions often undergo significant reorganizations, the so called chang-

338 ing points. If these network reorganizations were a product of environmental forces alone, we
339 would expect to observe the same changing points at the same periods, consistently across all
340 sites. However, network changing points in non-assembling communities are less frequent, and
341 there are few consistent trends in when change points occurred across all sites. Several sites had
342 network changing points between years 2009 and 2011 (Fig. 1). In California, 2011 marked the
343 beginning of a multi-year drought. The assembling hedgerows were not sampled in 2010, so dis-
344 entangling whether the changing points are due to skipping a year of monitoring the assembly
345 process or the drought is not possible. Interestingly, most assembling hedgerows did not undergo
346 a significant interaction reorganization immediately after a hedgerow was planted (i.e., the transi-
347 tion from weedy field margin to hedgerow). This result is consistent with the finding that in our
348 study system, hedgerow restoration takes several years to have an impact on the plant-pollinator
349 communities, and with the observation that hedgerows do not begin to produce many flowers until
350 3–5 years following planting [35].

351 In addition to finding multiple network organization changing points during assembly, the way
352 in which these reorganizations occur was different from what would be expected from preferential
353 attachment. In a preferential attachment process, we expect that the most persistent and high degree
354 species would remain stable in the network core during assembly [5]. Surprisingly, however, we
355 encountered the opposite pattern. For example, the four most ubiquitous species in our study
356 landscape — *Halictus ligatus*, *Halictus tripartitus*, *Lasioglossum (Dialictus) incompletum*, and
357 *Toxomerus marginatus* — were the only species that changed which module they were a member
358 in across years in all the assembling hedgerows. Because species degree and persistence were
359 strongly correlated, it is difficult to disentangle the causal mechanism for why species with those
360 characteristics are so variable in their network position. Generalized species may be better able to
361 exploit the limited floral resources in the intensively managed agriculture landscape, and thus also
362 be the most persistent [in ant-plant mutualisms, 18]. More persistent species usually have longer
363 phenologies, so they can visit many different flowers, resulting in a higher degree [63, 22]. Either

364 way, our result suggests that adaptable species can change their network position to utilize the most
365 advantageous floral resources available, which may depend on both the other pollinator species that
366 are present and the state of the plant community [37, 27, 65]. Thus given the opportunity and ability
367 to use different resources, species will often change their network positions [37].

368 Interestingly, though assembling hedgerows had more network reorganizations than non-assembling
369 communities, pollinator species and interaction turnover occurred at similar rates across site types.
370 Assembling hedgerows have higher turnover than non-assembling field margins only when inter-
371 actions were weighted by their similarity. This is likely because though species and interactions
372 are turning over at the field margins, species and interactions that fill similar roles in the network
373 are replacing each other. In contrast, at the assembling hedgerows, unique interactions are turn-
374 ing over as the networks continually reorganize. Non-assembling mature hedgerow communities,
375 however, had similar rates of weighted interaction turnover as assembling hedgerows but also the
376 lowest pollinator turnover. Pollinator communities at mature hedgerows may be generally more
377 stable, but rare and/or specialized pollinators could generate this pattern if they entered a commu-
378 nity, formed unique interactions with plants that did not previously share pollinators, but did not
379 persist in the networks. These species would not contribute strongly to network reorganization or
380 species turnover, but would enhance weighted interaction turnover. Mature hedgerows may thus
381 both support more stable pollinator communities, while also providing resources for rare and/or
382 specialized species [35, 40].

383 When we explore the how network-level interaction patterns changed through time, we found that
384 nestedness did increase as the community assembled, as would be expected if colonizing, specialist
385 species preferentially attached to a central, generalist core [2]. In addition, connectance decreased,
386 as would be expected if the network is being colonized by specialist species and the overall mean
387 number of interactions per species did not change. However, the frequent changing points in
388 network organization, dynamic nature of species positions in the networks, and turnover of species

389 and interactions all point to an assembly mechanism other than preferential attachment. The stable
390 level of network-level specialization through the assembly process may be due to the increased
391 colonization of specialized species [40] accompanied by an increase in the diet breath of resident
392 species. This would be expected if resident species were able to minimize their foraging time
393 by expanding their diet breath as plant diversity increases with hedgerow maturation [65, 52, 12,
394 2]. Such a change in pollinator behavior would also explain the increase in network nestedness.
395 Because so many mechanisms give rise to the same patterns of interaction, additional tests are
396 necessary to assess the contribution of different mechanisms to community assembly.

397 Interestingly, however, the changes in network patterns associated with assembly did not affect
398 the robustness of hedgerow communities to species loss. This is particularly surprising given
399 the observed increase in nestedness, which is often associated with an increase in robustness to
400 extinction [38]. Perhaps assembling hedgerows have yet to reach sufficient levels of nestedness
401 to realize the benefits nestedness confers. Nestedness of the assembling hedgerows, however,
402 did not asymptote within the eight years following restoration that the sites were surveyed, so
403 hedgerow networks may eventually reach sufficient levels of nestedness to gain the robustness
404 advantage.

405 Contrary to the general restoration goals, networks' susceptibility to cascading perturbations in-
406 creased as the communities assembled. We measured vulnerability to cascading perturbations as
407 the algebraic connectivity of the network: the greater the algebraic connectivity, the more vulnera-
408 ble a community is to cascading perturbations. Algebraic connectivity is positively related to both
409 the number of species and connectance of a network [26]. The increase in and plant and pollinator
410 richness following restoration is thus at least partially responsible for the increase in response to
411 cascading effects. Algebraic connectivity is also positivly correlated with the number in interac-
412 tions, or connectance of a network [26], We, however, observed a decrease in connectance, sug-
413 gesting topological characteristics of the networks beyond just species richness and connectance

414 are needed to explain the increased sensitivity to perturbations spreading. These hedgerows were
415 designed to provide floral resources to the largest number of pollinators across the growing season
416 [39]. The generalized nature of the floral community may explain why the networks tended to be
417 more generalized than expected if interactions were randomly distributed across species (Fig. 5).
418 In addition, the design of the hedgerow plantings may have facilitated the emergence of a single,
419 highly connected module in all of the networks (see 2 for examples). This network configuration
420 results in short path lengths (the distance between species in a network based on their shared part-
421 ners), and thus, a perturbation in one species can more easily spread to other species. In order
422 to promote more resilient communities, future restoration efforts should explore designing floral
423 communities to promote more interaction partitioning using, for example, algorithms to optimize
424 different network properties based on prior knowledge of pollinator floral preferences [41], and on
425 desired network architectures that renders them more robust both to species loss and to cascading
426 effects.

427 Plant-pollinator networks, in general, are highly dynamic, with high turnover of species and in-
428 teractions both within and between seasons [13]. Though our non-assembling communities expe-
429 rience fewer network reorganizations than the assembling hedgerows, 82% of field margins and
430 40% of mature hedgerows underwent at least one changing point in network structure. Pollina-
431 tors are also highly opportunistic [50, 62, 2], though trait complementarity such as tongue length
432 and corolla depth impose some biophysical limits to the interactions between plants and pollina-
433 tors [64, 63, 57, 58, 56]. Such opportunism may buffer plant-pollinator communities from global
434 change [e.g., 54, 31], but our limited understanding of the assembly of these communities impedes
435 making such predictions [63, 13]. Unlike in the broader food web literature, we have few assembly
436 models of mutualistic network assembly [60, 44, 29]. In addition, the few developed models often
437 borrow their mechanisms from competitive interactions, leading to inaccurate biological assump-
438 tions [30]. We need further development of mechanistic models of mutualistic systems to generate
439 testable predictions, along with empirical exploration of network assembly. Plant-pollinator com-

440 munities and mutualisms broadly are vital for biodiversity maintenance and essential ecosystem
441 service provision. We must therefore understand the processes underlying their assembly to facilitate
442 restoration and conservation.

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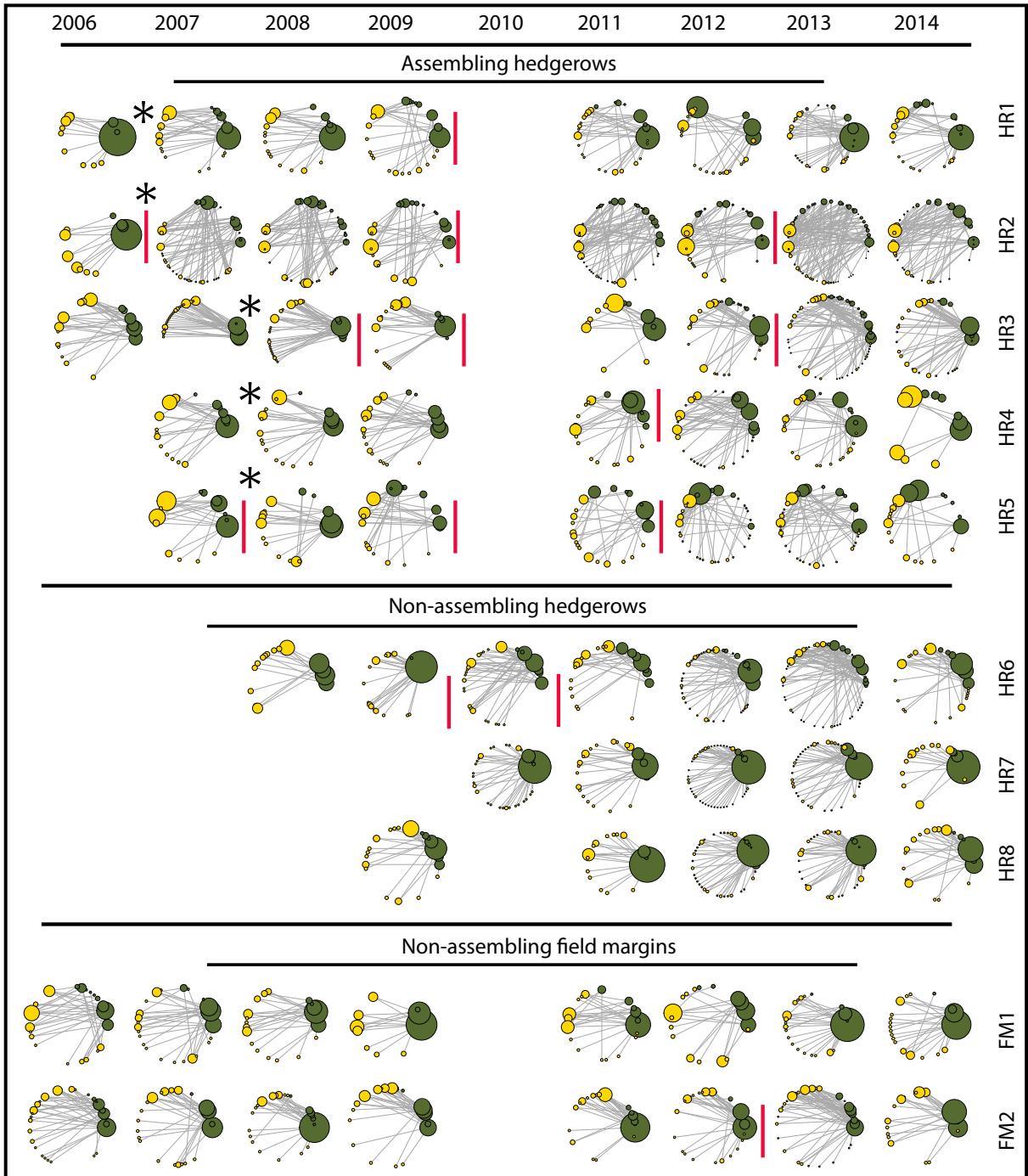


Figure 1: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, respectively, 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.

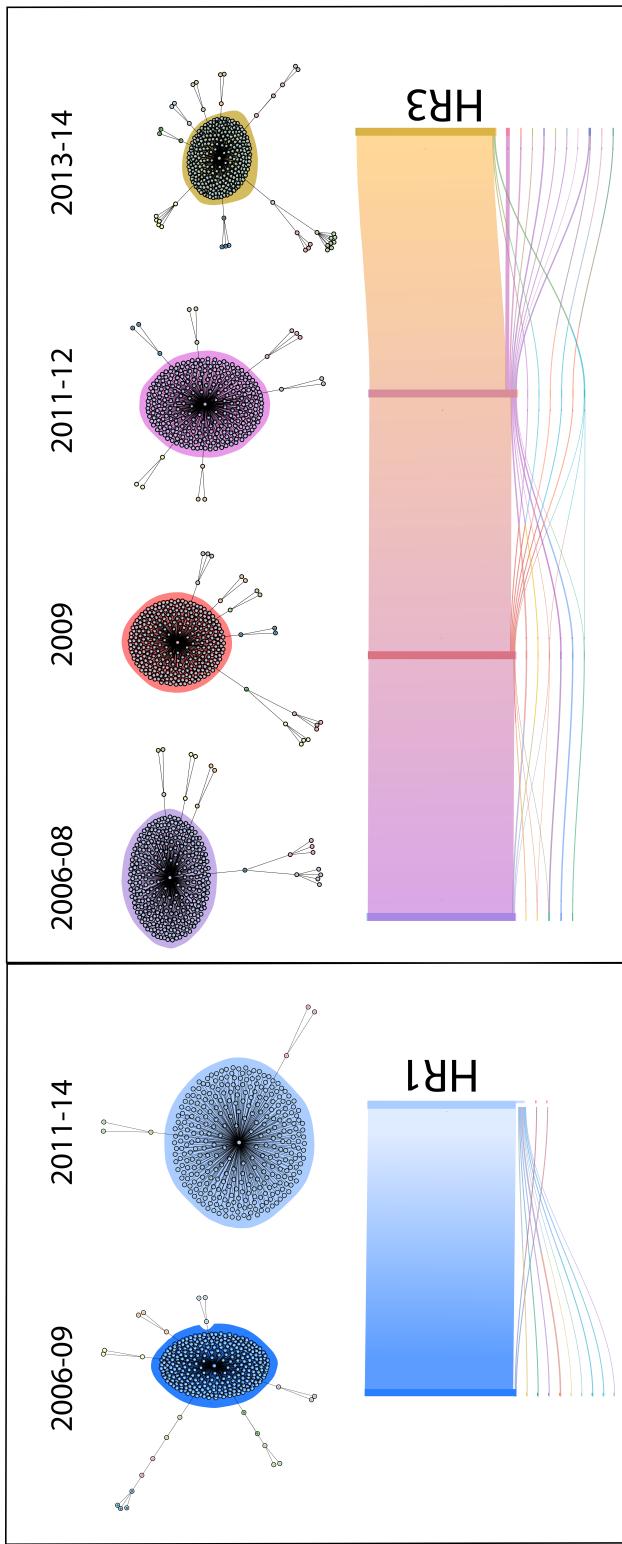


Figure 2: The species module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species between modules between changing points. Each line represents the change of species from one module to another.

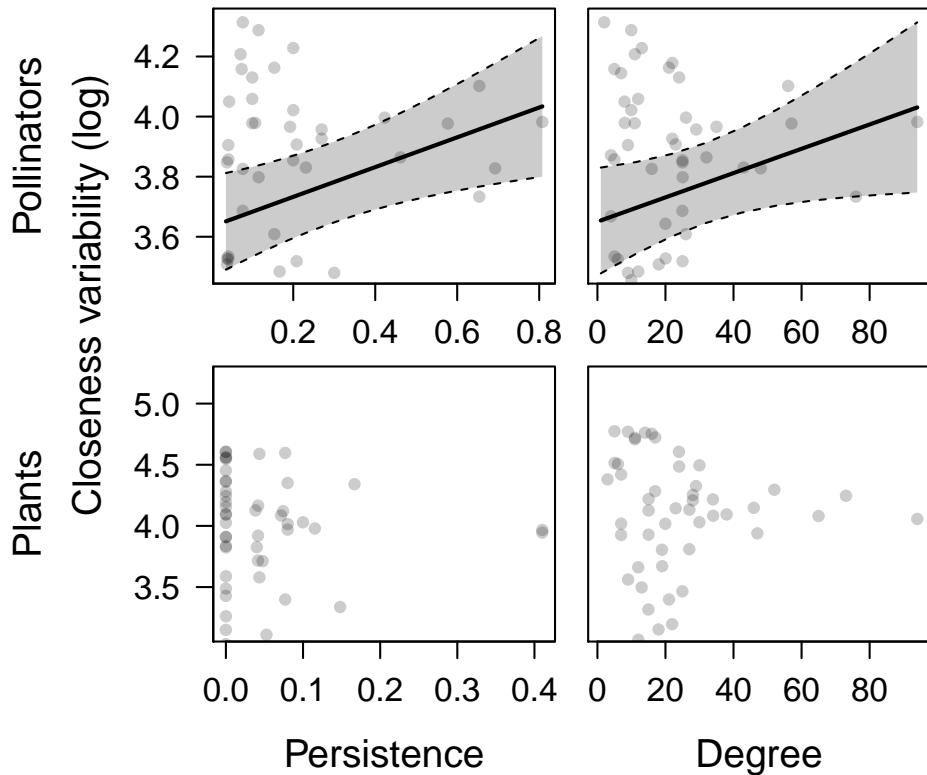


Figure 3: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across sites. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

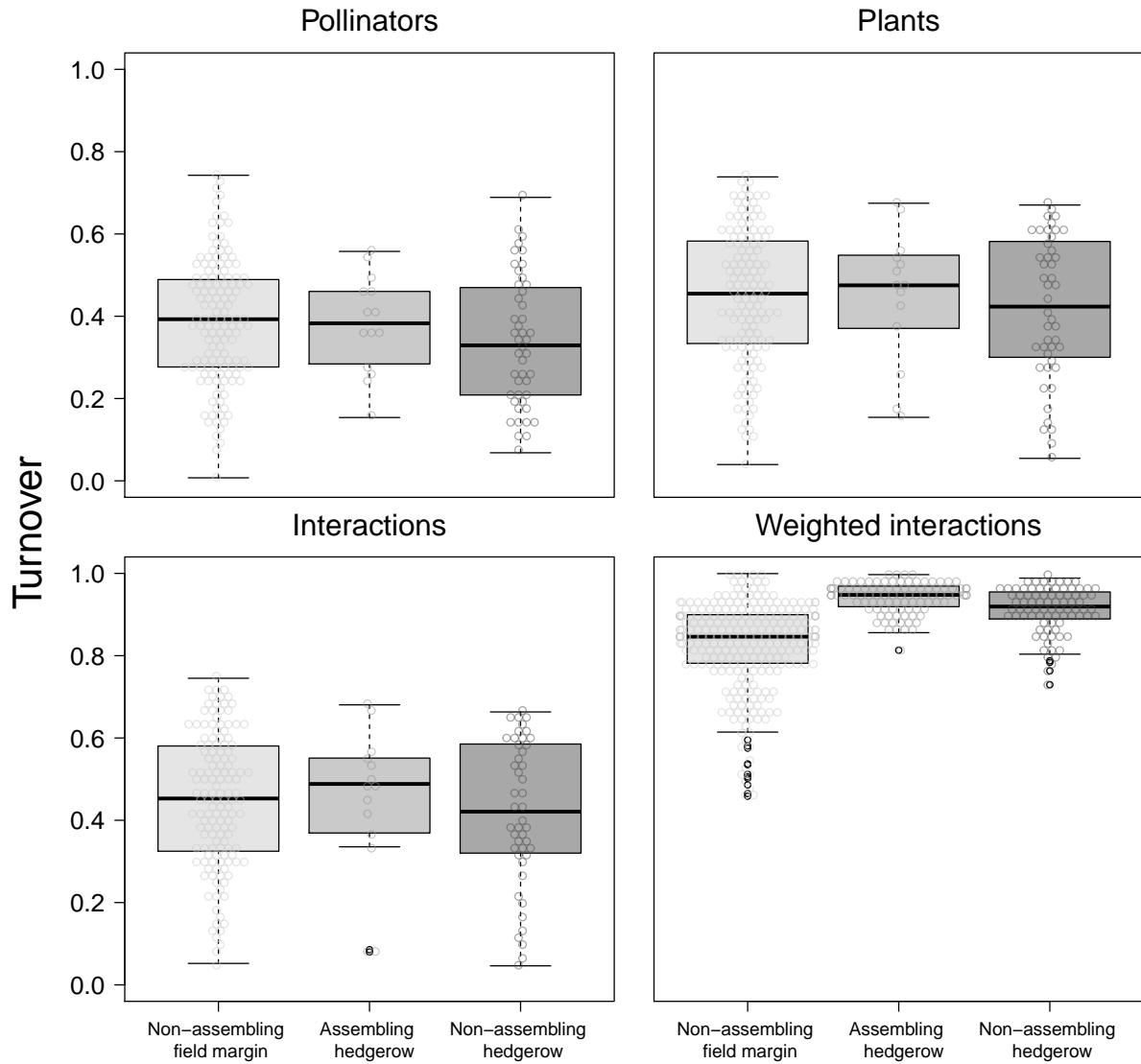


Figure 4: Species interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally 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).

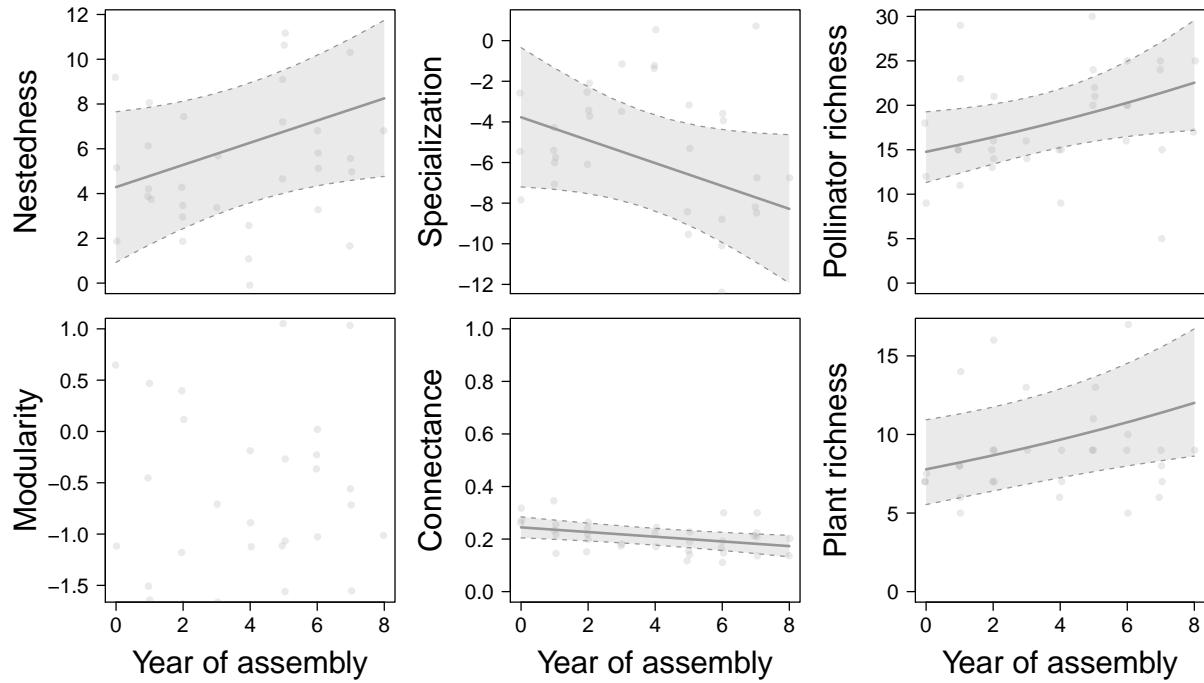


Figure 5: Nestedness, plant richness and pollinator richness increased as the networks assembled. Specialization and modularity remained consistent across years, while connectance decreased. The nestedness, modularity and specialization scores represent z-scores. Scores greater than ~ 2 or less than ~ -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.

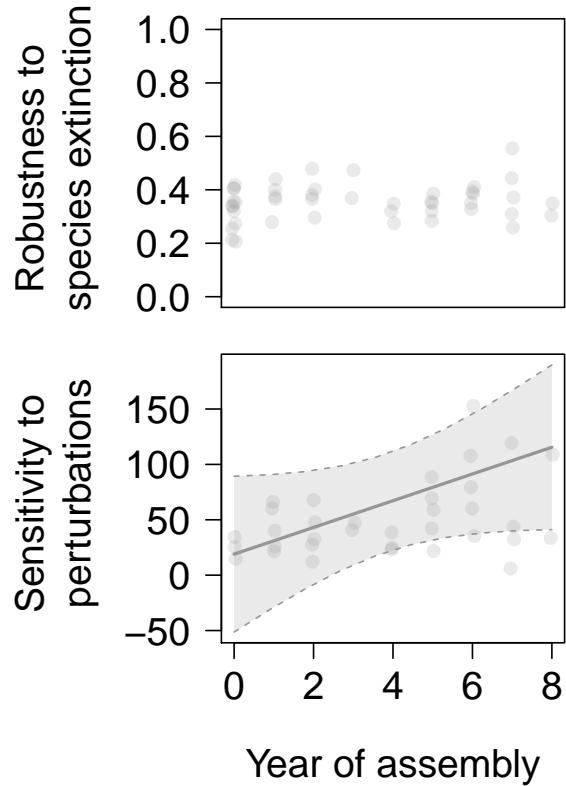


Figure 6: The robustness of networks to species extinction did not change with network assembly, but the sensitivity to cascading perturbations increased. The robustness to species extinction is measured by incrementally removing species by degree, though removing species by abundance did not yield qualitatively different results. The robustness of networks to cascading perturbations is measured as the algebraic connectivity, the second smallest eigenvalue of the Laplacian matrix. Points are the 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.