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Major interaction reorganizations punctuate the assembly of pollination networks

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Abstract

The ability of communities to maintain function in the face of species extinction is related to the structure of networks. 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. The most persistent and generalized species were 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.

¹⁴ community assembly, change points, specialization, nestedness, modularity, bipartite, preferential
¹⁵ attachment

¹⁶ Introduction

¹⁷ Global change has created a severe biodiversity crisis, and as species are lost, so are their interac-
¹⁸ tions [20, 6]. Because mutualistic interactions are essential for maintaining the diversity of their
¹⁹ component guilds, these systems are particularly at risk from coextinction cascades. The nature
²⁰ of these cascades will depend on the interaction patterns within a community [38, 55, 9, 59]. To
²¹ safeguard ecological function, it has become increasingly imperative to aid the recovery of lost
²² interactions and component biodiversity through ecological restoration, and a key restoration aim
²³ is to facilitate assembly of robust interaction networks [39]. We know little, however, about how
²⁴ to re-assemble interacting communities through restoration, or the process of ecological network
²⁵ assembly more generally.

²⁶ Preferential attachment, the most widely explored mechanism of network assembly, [5], predicts
²⁷ that species entering a network are more likely to interact with species that are already well-
²⁸ connected [”the rich-get-richer” principle, 5]. In pollination systems — a particularly ubiquitous
²⁹ mutualism [47, 34] — some studies have found support for this assembly mechanism. Investigating
³⁰ the day-to-day, temporal assembly of a plant-pollinator network within a season, [46] found that
³¹ phenologically new plant and pollinator species tended to interact with already well-connected
³² species, potentially because these species are either more abundant or more temporally persis-
³³ tent. In addition, using a space-for-time substitution to study primary succession along a glacier
³⁴ foreland, [2] also found some evidence that assembly occurred through preferential attachment.
³⁵ Specifically, network nestedness (i.e, a core group of generalists interacts with both specialist and
³⁶ generalist species) increased as the community aged [2]. An increase in nestedness could result
³⁷ from the preferential attachment process where specialist species attach to the well-connected,
³⁸ generalist core.

³⁹ In contrast to the network build-up described by preferential attachment, significant reorganiza-

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

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

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

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

76 Materials & Methods

77 Study sites and collection methods

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

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

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

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

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

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

¹⁰⁹ **Change point analysis**

¹¹⁰ **Identifying change points**

¹¹¹ We employed a change point detection method [49] to identify fundamental reorganizations in
¹¹² large-scale interaction patterns. A change point is caused by a merge, split, fragmentation or
¹¹³ formation of modules (also called compartments). Change point detection methods have yet to
¹¹⁴ be generalized to quantitative networks, so for this analysis we focused on qualitative (binary)
¹¹⁵ networks. Following [49], we first defined a probability distribution over the networks using the
¹¹⁶ generalized hierarchical random graph model (GHRG). The GHRG model is able to capture both
¹¹⁷ assortative and disassortative structure patterns at all scales in the network [49]. A network G is
¹¹⁸ composed of vertices V and edges E . The GHRG model decomposes the N vertices into a series
¹¹⁹ of nested groups, the relationships among which are represented by the dendrogram T . The tips
¹²⁰ of T are the vertices of G , and the probability that two vertices u and v connect is given by the
¹²¹ parameter p_r . The probability distribution of the network G is thus defined as:

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

¹²² Where E_r is the observed number of edges between vertices with the common ancestor r , and N_r
¹²³ is the total possible edges.

¹²⁴ Using Bayesian posterior inference and techniques from phylogenetic tree reconstruction, we fit
¹²⁵ the GHRG model to the networks [49]. This is accomplished by using a Markov chain Monte
¹²⁶ Carlo (MCMC) procedure to first sample the posterior distribution of bipartitions, from which a
¹²⁷ consensus tree is derived [49]. We use β distributions with the hyperparameters $\alpha = \beta = 1$ to
¹²⁸ define priors for p_r .

¹²⁹ Once the GHRG model has been fit to the networks, we determine whether a change point occurred

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

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

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

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

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

¹⁵⁴ observed. Species observed consistently within and between years are thus maximally persistent.
¹⁵⁵ Weighted species degree is calculated from interaction observations from an extensive dataset from
¹⁵⁶ Yolo County (approx. 18000 interaction records) that included both the data included in this study
¹⁵⁷ and additional data from sites where we collected flower visitors using the same methods [40, 51].
¹⁵⁸ To represent network position variability, we computed the coefficient of variation of weighted
¹⁵⁹ closeness centrality [24] at each site through time. Closeness centrality represents the importance
¹⁶⁰ of a space by calculating the path lengths to other vertices (species) in the network [24]. The shorter
¹⁶¹ the mean path length to other species, the higher is the closeness centrality. We use linear mixed
¹⁶² models to test whether the species closeness variability (log) is related to the persistence or degree
¹⁶³ of that species [10, 36]. We included random effects for species and site. Because the degree and
¹⁶⁴ persistence of pollinators were strongly correlated, ($\rho = 0.84$, p -value $< 2 * 10^{-16}$), we include
¹⁶⁵ each explanatory variable in separate models. Plant degree and persistence were not significantly
¹⁶⁶ correlated, but we use the same models as we did for the pollinators for consistency. Because an
¹⁶⁷ approximately logarithmic increase in closeness centrality, as would be expected with assembly
¹⁶⁸ by preferential attachment, would also lead to high variability in closeness scores, we also test
¹⁶⁹ whether log closeness centrality increases through time.

¹⁷⁰ Species and interaction turnover

¹⁷¹ Reorganizations of network structure can be the result of species turnover or species changing
¹⁷² their interaction partners (i.e., re-wiring). To better understand the mechanisms underlying the
¹⁷³ temporal dynamics of the assembling networks, we examined patterns of species and interac-
¹⁷⁴ tion turnover. For example, assembling networks may have higher rates of pollinator turnover
¹⁷⁵ than non-assembling communities because new pollinator species are colonizing and establishing
¹⁷⁶ themselves [40]. Similarly, because species are turning over and pollinators are trying to maximize
¹⁷⁷ their foraging efficiency based on the species present, interactions may turnover more quickly than

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

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

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

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

209 **Temporal changes in interaction patterns**

210 **Network structure**

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

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

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

244 Network robustness

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

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

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

270 **Results**

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

274 **Change point analysis**

275 **Identifying change points**

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

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

285 In contradiction to the predictions of assembly by preferential attachment, both pollinator per-
286 sistence and degree were positively related to network position variability (Fig. 3, estimate of
287 the slope of closeness centrality variability and persistence \pm standard error of the estimate,
288 0.653 ± 0.225 , p -value=0.009; slope of closeness centrality variability and degree, 0.008 ± 0.002 ,
289 p -value=0.002). The slope of these relationships remained significant when the species with the
290 top 10 persistence and degree scores were dropped. In addition, plant persistence and degree were

291 not significantly related to network position variability (Fig. 3). The variability of species net-
292 work position was not the result of closeness linearly increasing through time, and, in fact, plant
293 and pollinator closeness decreased slightly through time (Fig. S2, estimate of the slope of closeness
294 through time \pm SE, pollinators: -0.0003 ± 0.00005 , $p\text{-value}=2.7 * 10^{-12}$; plants -0.007 ± 0.001 ,
295 $p\text{-value}=1.4 * 10^{-6}$). Through statistically significant, the slopes are so slight they may not be bi-
296 ologically significant.

297 Species and interaction turnover

298 The rates of plant, pollinator and interaction temporal turnover were similar across assembling
299 hedgerows, non-assembling hedgerows and field margins, though mature hedgerows has marginally
300 significantly less pollinator turnover than field margins (Fig. 4, estimate \pm SE of the difference
301 in turnover between field margins and mature hedgerows, -0.0498 ± 0.026 , $p\text{-value}=0.058$).
302 When interactions where weighted by their similarity, both assembling and mature hedgerows had
303 higher rates of turnover than field margins (Fig. 4, estimate \pm SE of the difference in turnover
304 between field margins and assembling hedgerows, 0.115 ± 0.027 , $p\text{-value}=0.0002$; field mar-
305 gins and mature hedgerows, 0.082 ± 0.024 , $p\text{-value}=0.002$). The weighted interaction turnover
306 at assembling hedgerows, however, was not significantly higher than in non-assembling, mature
307 hedgerows.

308 Temporal changes in interaction patterns

309 Network structure

310 Network nestedness significantly increased with assembly (Fig. 5, estimate of the slope of nest-
311 edness through time \pm SE, 1.834 ± 0.6142 , $p\text{-value}=0.022$). All of the networks were signifi-

312 cantly nested (z -scores > 2 , Fig. 5). Modularity decreased (Fig. 5), though the slope was not
313 significantly different from zero. In addition, none of the networks were significantly modular
314 (z -scores < 2 , Fig. 5). Connectance decreased as the community assembled (Fig. 5, estimate of
315 the slope of connectance through time \pm standard error of the estimate, -0.0434 ± 0.0152 , p -
316 value=0.03). Specialization also decreased, though the slope was only marginally significantly
317 different from zero (estimate of the slope of specialization through time \pm SE, -0.926 ± 0.450 ,
318 p -value=0.078). Most communities were more generalized than expected when interactions were
319 randomized (Fig. 5).

320 Both plant and pollinator species richness increased through time (Fig. 5, estimate of the slope
321 of richness through time \pm SE, pollinators: 0.193 ± 0.0729 , p -value=0.008; plants: $0.212 \pm$
322 0.0653 , p -value=0.001). Unsurprisingly, pollinator species are colonizing and persisting at the
323 assembling hedgerows. Plant species richness in the networks is based on the flowers actually
324 visited by pollinators and not the presence of a particular plant species at a site. Thus, though
325 some new plant species may establish themselves in the hedgerows, the increase in plant richness
326 in the networks is likely due to previously unvisited plants attracting visitors as they mature and
327 offer better rewards.

328 Network robustness

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

334 **Discussion**

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

350 In addition to finding multiple network organization changing points during assembly, the way in
351 which these reorganizations occur was different from what would be expected from preferential
352 attachment. With a preferential attachment process, we expect that the most persistent and high
353 degree species would remain stable in the network core during assembly [5]. Surprisingly, how-
354 ever, we encountered the opposite pattern. For example, the four most ubiquitous species in our
355 study landscape — *Halictus ligatus*, *Halictus tripartitus*, *Lasioglossum (Dialictus) incompletum*,
356 and *Toxomerus marginatus* — were the only species that changed which module they were a mem-
357 ber in across years in all the assembling hedgerows. Because species degree and persistence were
358 strongly correlated, it is difficult to disentangle the causal mechanism for why species with those

characteristics are so variable in their network position. Generalized species may be better able to exploit the limited floral resources in the intensively managed agriculture landscape, and thus also be the most persistent [in ant-plant mutualisms, 18]. More persistent species usually have longer phenologies, so they can visit many different flowers, resulting in a higher degree [63, 22]. Either way, our result suggests that adaptable species can change their network position to utilize the most advantageous floral resources available, which may depend on both the other pollinator species that are present and the state of the plant community [37, 27, 65]. Thus given the opportunity and ability to use different resources, species will often change their network positions [37].

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

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 effect
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 enhanced 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, the susceptibility of the networks to cascading perturba-
406 tions increased as the communities assembled. Because network vulnerability to cascading per-
407 turbations, as measured by algebraic connectivity, is correlated with species richness, the increase
408 in and plant and pollinator richness following restoration is at least partially responsible for the

409 increase in response to cascading effects. Connectance is also positively related to algebraic con-
410nectivity [26], but because we observed a decrease in connectance, topological characteristics of
411the networks beyond species richness and connectance are needed to explain the increased sensi-
412tivity to perturbations spreading. These hedgerows were designed to provide floral resources to the
413largest number of pollinators across the growing season [39]. The generalized nature of the floral
414community may explain why the networks tended to be more generalized than expected if inter-
415actions were randomly distributed across species (Fig. 5). In addition, the design of the hedgerow
416plantings may have facilitated the emergence of a single, highly connected module in all of the
417networks (see 2 for examples). This network configuration results in short path lengths (the dis-
418tance between species in a network based on their shared partners), and thus, a perturbation in one
419species can more easily spread to other species. In order to promote more resilient communities,
420future restoration efforts should explore designing floral communities to promote more interaction
421partitioning using, for example, algorithms to optimize different network properties based on prior
422knowledge of pollinator floral preferences [41], and on desired network architectures that renders
423them more robust both to species loss and to cascading effects.

424 Plant-pollinator networks, in general, are highly dynamic, with high turnover of species and in-
425teractions both within and between seasons [13]. Though our non-assembling communities expe-
426rience fewer network reorganizations than the assembling hedgerows, 82% of field margins and
42740% of mature hedgerows underwent at least one changing point in network structure. Pollina-
428tors are also highly opportunistic [50, 62, 2], though trait complementarity such as tongue length
429and corolla depth impose some biophysical limits to the interactions between plants and pollina-
430tors [64, 63, 57, 58, 56]. Such opportunism may buffer plant-pollinator communities from global
431change [e.g., 54, 31], but our limited understanding of the assembly of these communities impedes
432making such predictions [63, 13]. Unlike in the broader food web literature, we have few assembly
433models of mutualistic network assembly [60, 44, 29]. In addition, the few developed models often
434borrow their mechanisms from competitive interactions, leading to inaccurate biological assump-

435 tions [30]. We need further development of mechanistic models of mutualistic systems to generate
436 testable predictions, along with empirical exploration of network assembly. Plant-pollinator com-
437 munities and mutualisms broadly are vital for biodiversity maintenance and essential ecosystem
438 service provision. We must therefore understand the processes underlying their assembly to facili-
439 tate restoration and conservation.

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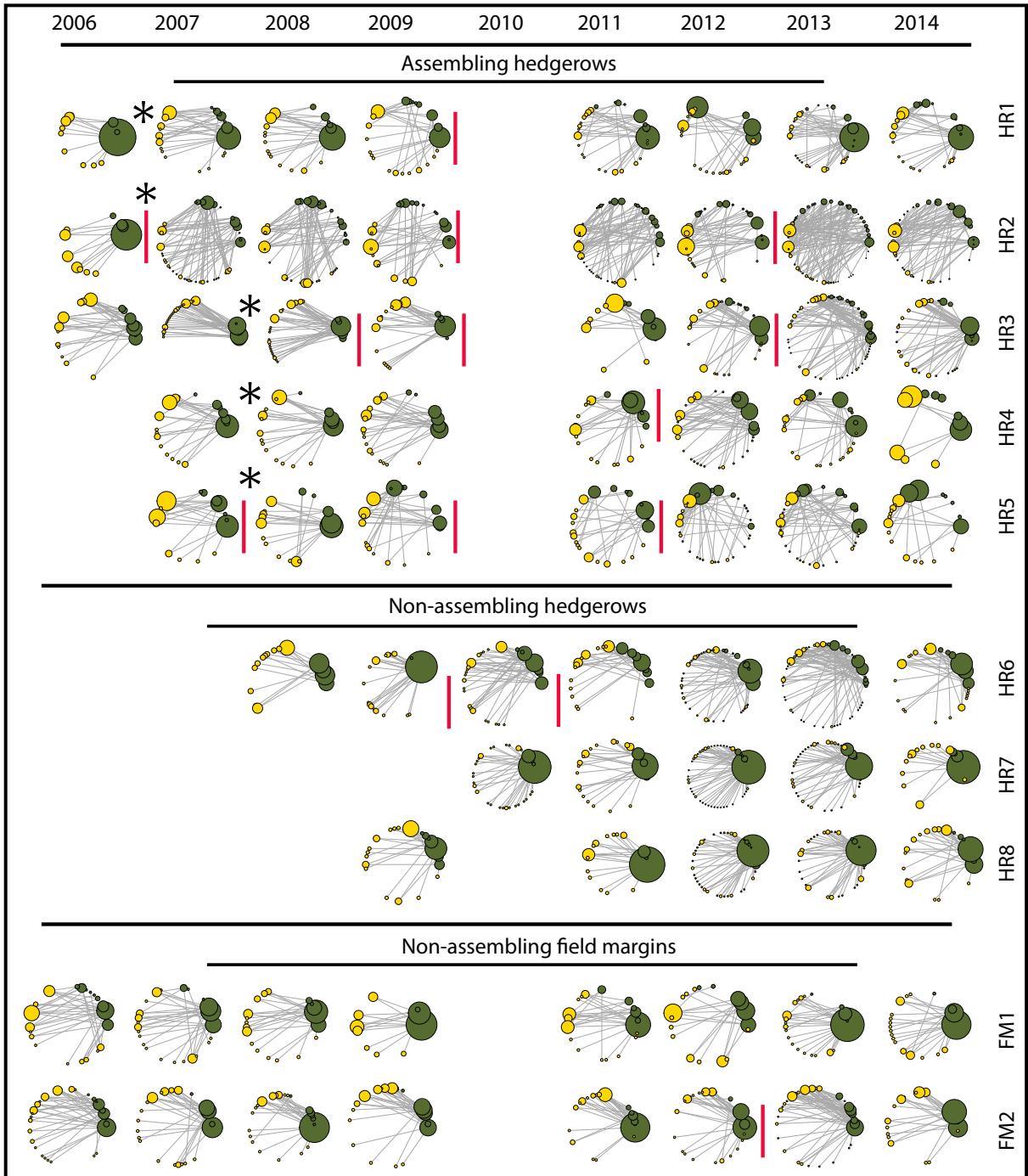


Figure 1: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, weighted by their degree. Each species has a consistent position in the perimeter of the network across years. In the assembling hedgerows, colored squares in the corner of each network represent the year of assembly. Asterisks indicate the year the hedge was planted. Before that, the sites were weedy field margins. 29

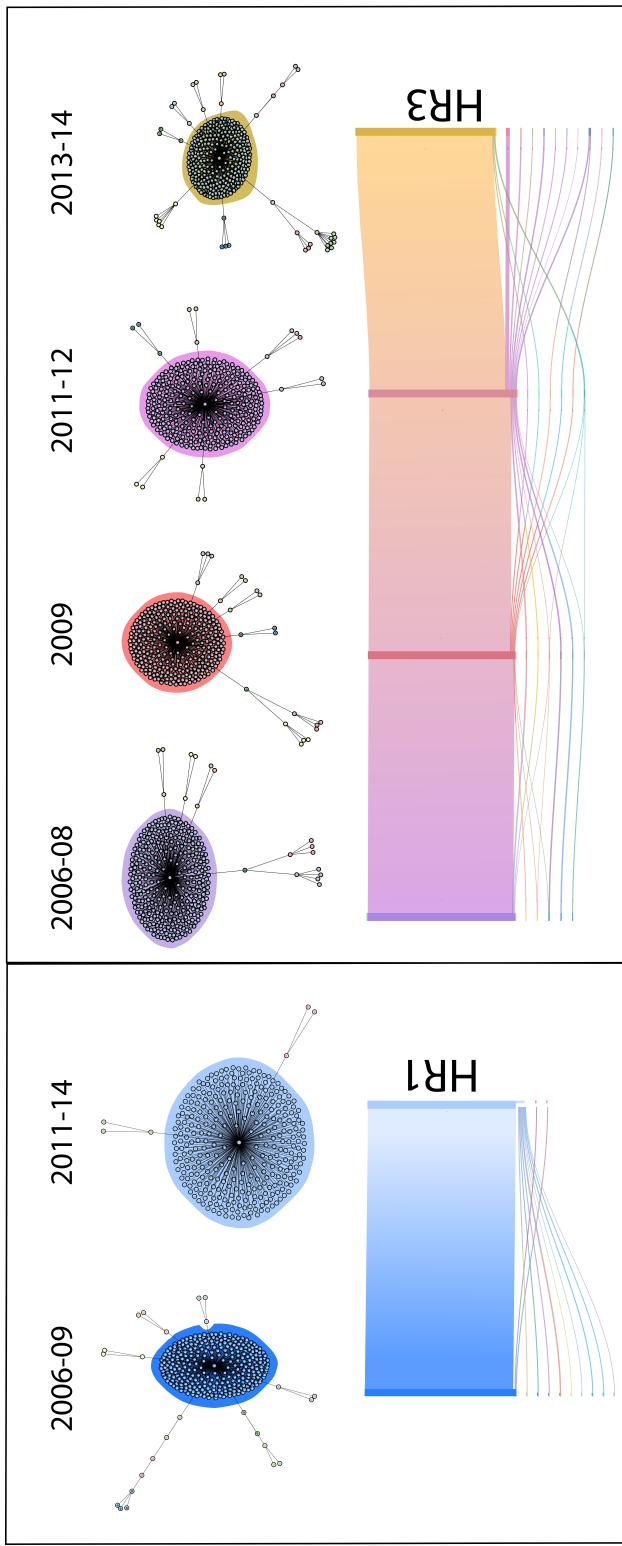


Figure 2: The module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species between modules between changing points.

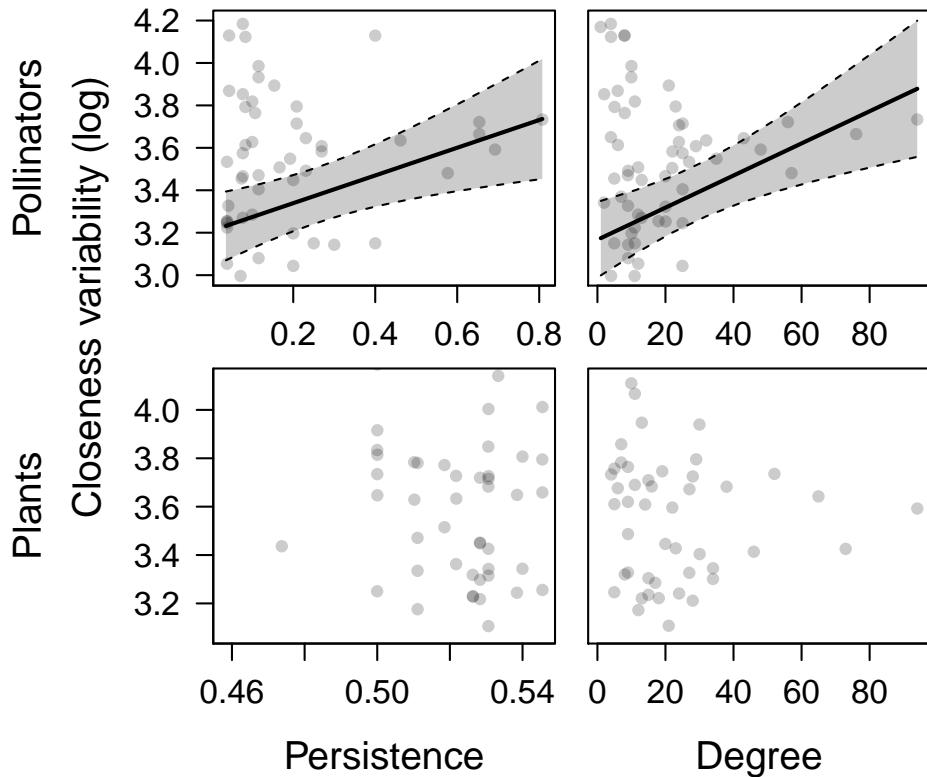


Figure 3: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across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

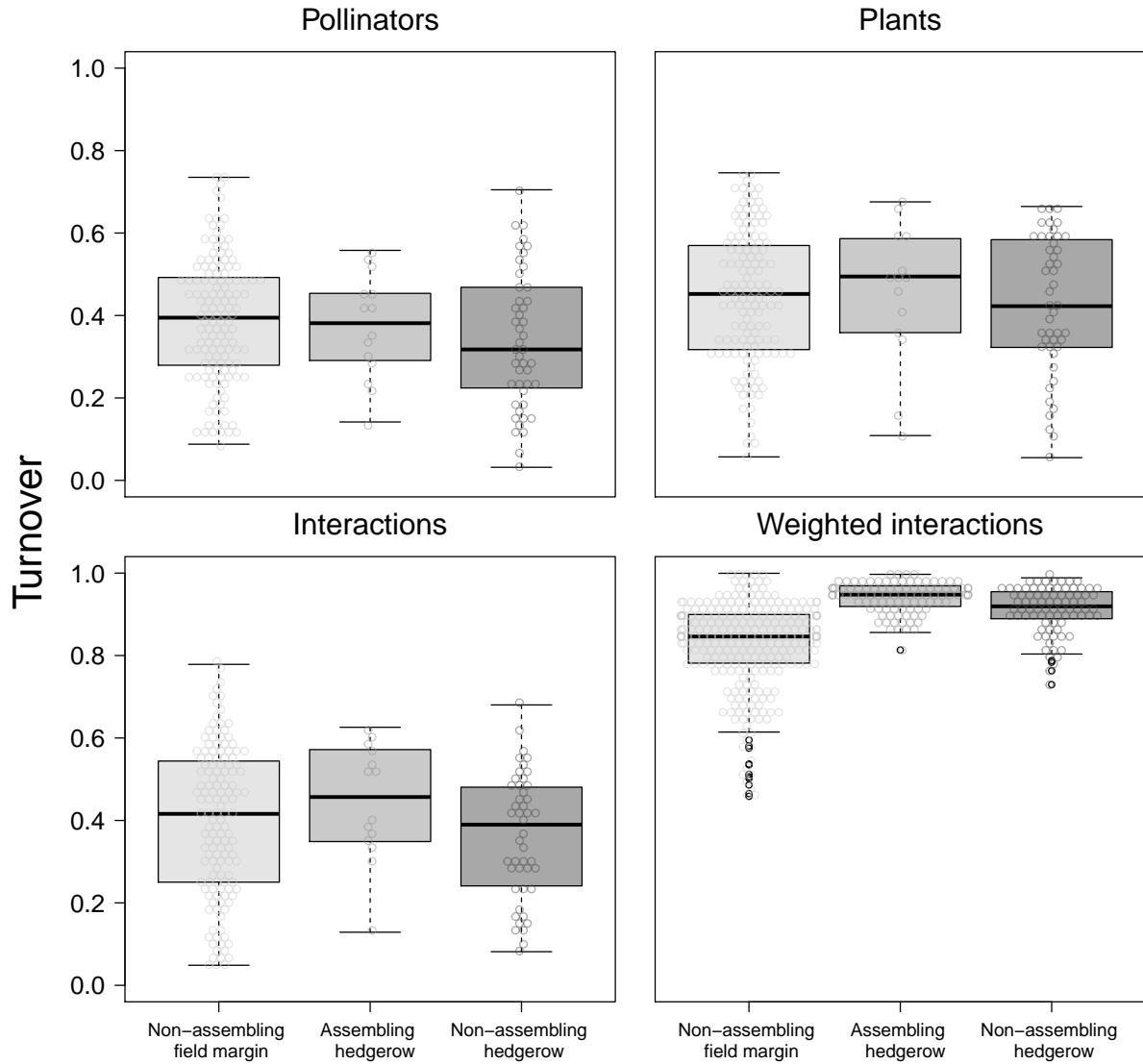


Figure 4: The species, interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally significantly less pollinator turnover. However, when interactions where weighted by their similarity, both hedgerow types had higher turnover that unrestored field margins. Boxplots represent medians (black horizontal line) first and third quartiles (box perimeter) and extremes (whiskers).

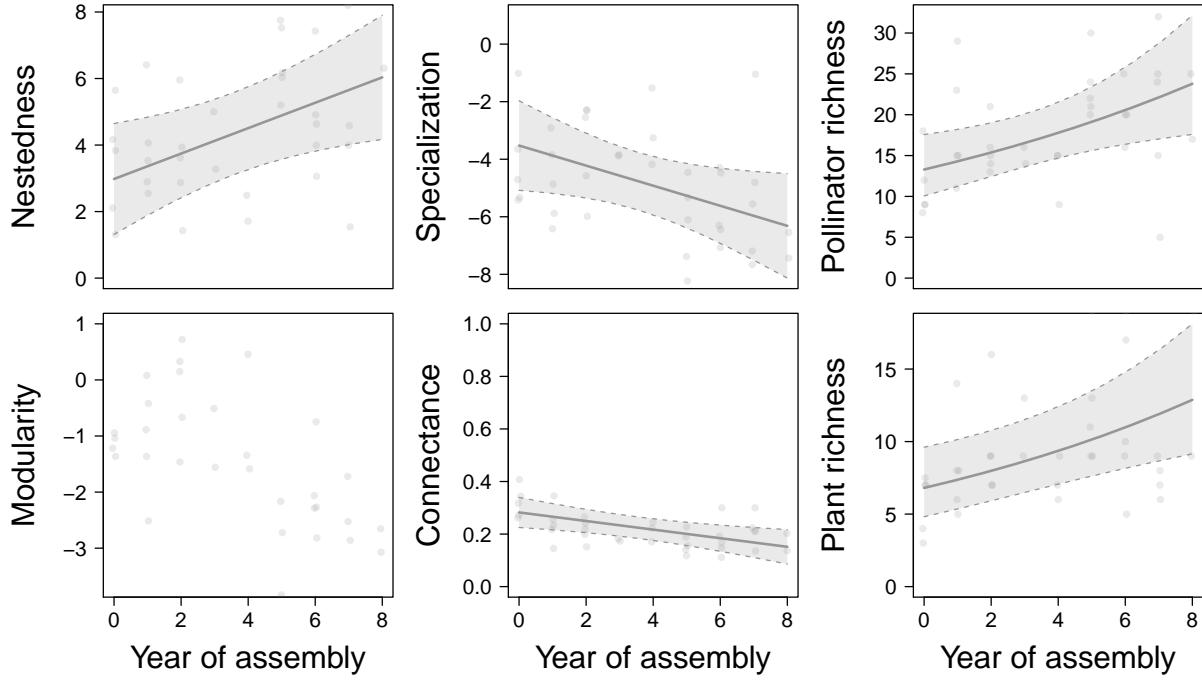


Figure 5: Nestedness, plant richness and pollinator richness increased as the networks assembled. Specialization and modularity remained consistent across years, while connectance decreased. The nestedness, modularity and specialization scores represent z-scores. Scores greater than ~ 2 or less than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

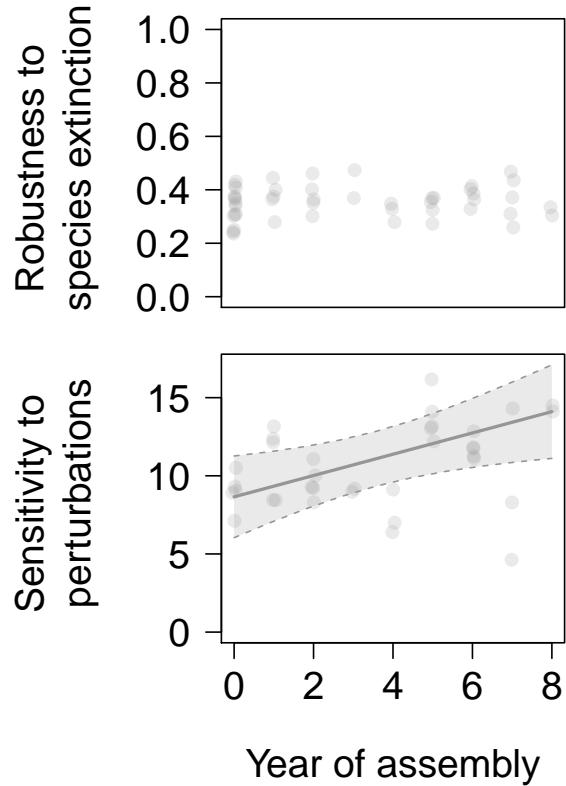


Figure 6: The robustness of networks to species extinction did not change with network assembly, but the sensitivity to cascading perturbations increased. The robustness to species extinction is measured by incrementally removing species by degree, though removing species by abundance did not yield qualitatively 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.