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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.

<sup>15</sup> community assembly, change points, specialization, nestedness, modularity, bipartite, preferential  
<sup>16</sup> 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-

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

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

We explore the process of network development using a nine year dataset of plant-pollinator community assembly following hedgerow restoration in the highly simplified and intensively managed 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 km<sup>2</sup>. 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  $\beta$  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. 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 shorter  
162 the mean path length to other species, the higher is the closeness centrality. We use linear mixed  
163 models to test whether the species closeness variability (log) is related to the persistence or degree  
164 of that species [10, 36]. We included random effects for species and site. Because the degree and  
165 persistence of pollinators were strongly correlated, ( $\rho = 0.84$ ,  $p$ -value  $< 2 * 10^{-16}$ ), we include  
166 each explanatory variable in separate models. Plant degree and persistence were not significantly  
167 correlated, but we use the same models as we did for the pollinators for consistency. Because an  
168 approximately logarithmic increase in closeness centrality, as would be expected with assembly  
169 by preferential attachment, would also lead to high variability in closeness scores, we also test  
170 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  $\beta$ -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 models to test whether the weighted turnover  
209 of interactions varied between assembling and non-assembling networks [10, 36].

## 210 **Temporal changes in interaction patterns**

### 211 **Network structure**

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

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

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

## 245 Network robustness

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

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

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

<sup>271</sup> **Results**

<sup>272</sup> Over eight years and 747 samples, we collected and identified 19,547 wild bees and syrphids  
<sup>273</sup> comprising 173 species from 50 genera. We observed 1,521 unique interactions between plants  
<sup>274</sup> and pollinators.

<sup>275</sup> **Change point analysis**

<sup>276</sup> **Identifying change points**

<sup>277</sup> The majority (76%) of the sites underwent at least one significant interaction reorganization (Fig. 1,  
<sup>278</sup> 2). All five of the assembling hedgerows experienced network changing points, whereas only 40%  
<sup>279</sup> and 81% of non-assembling hedgerows and field margins, respectively, underwent significant in-  
<sup>280</sup> teraction reorganizations. Assembling hedgerows had significantly more changing points than the  
<sup>281</sup> non-assembling networks (estimate of the difference in the odds ratios between assembling and  
<sup>282</sup> non-assembling networks, 3.316, 95% CI [1.314, 8.572], *p*-value= 0.0117). Network assembly  
<sup>283</sup> following restoration is thus punctuated by more interaction reorganizations than would be ex-  
<sup>284</sup> pected by environmental shifts alone that would effect all networks similarly.

<sup>285</sup> **Characteristics of species that contribute to change points**

<sup>286</sup> In contradiction to the predictions of assembly by preferential attachment, both pollinator per-  
<sup>287</sup> sistence and degree were positively related to network position variability (Fig. 3, estimate of  
<sup>288</sup> the slope of closeness centrality variability and persistence  $\pm$  standard error of the estimate,  
<sup>289</sup>  $0.653 \pm 0.225$ , *p*-value=0.009; slope of closeness centrality variability and degree,  $0.008 \pm 0.002$ ,  
<sup>290</sup> *p*-value=0.002). The slope of these relationships remained significant when the species with the  
<sup>291</sup> top 10 persistence and degree scores were dropped. In addition, plant persistence and degree were

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

## 298 Species and interaction turnover

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

## 309 Temporal changes in interaction patterns

### 310 Network structure

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

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

321 Both plant and pollinator species richness increased through time (Fig. 5, estimate of the slope  
322 of richness through time  $\pm$  SE, pollinators:  $0.193 \pm 0.0729$ ,  $p$ -value=0.008; plants:  $0.212 \pm$   
323  $0.0653$ ,  $p$ -value=0.001). Unsurprisingly, pollinator species are colonizing and persisting at the  
324 assembling hedgerows. Plant species richness in the networks is based on the flowers actually  
325 visited by pollinators and not the presence of a particular plant species at a site. Thus, though  
326 some new plant species may establish themselves in the hedgerows, the increase in plant richness  
327 in the networks is likely due to previously unvisited plants attracting visitors as they mature and  
328 offer 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,  $0.6814 \pm 0.272$ ,  $p$ -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

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 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  
407 as the algebraic connectivity of the network: the greater the algebraic connectivity, the harder it  
408 is to turn a network into completely disconnected groups of species, and the more vulnerable a  
409 community is to cascading perturbations. However, algebraic connectivity is positively related

410 not only to the number of species— species richness— but also to the number of interactions—  
411 connectance [26]. because algebraic connectivity is correlated with species richness, the increase  
412 in in plant and pollinator richness following restoration is at least partially responsible for the  
413 increase in response to cascading effects. Connectance is also positively related to algebraic con-  
414nectivity [26], but because we observed a decrease in connectance, topological characteristics of  
415 the networks beyond species richness and connectance are needed to explain the increased sensi-  
416 tivity to perturbations spreading. These hedgerows were designed to provide floral resources to the  
417 largest number of pollinators across the growing season [39]. The generalized nature of the floral  
418 community may explain why the networks tended to be more generalized than expected if inter-  
419 actions were randomly distributed across species (Fig. 5). In addition, the design of the hedgerow  
420 plantings may have facilitated the emergence of a single, highly connected module in all of the  
421 networks (see 2 for examples). This network configuration results in short path lengths (the dis-  
422 tance between species in a network based on their shared partners), and thus, a perturbation in one  
423 species can more easily spread to other species. In order to promote more resilient communities,  
424 future restoration efforts should explore designing floral communities to promote more interaction  
425 partitioning using, for example, algorithms to optimize different network properties based on prior  
426 knowledge of pollinator floral preferences [41], and on desired network architectures that renders  
427 them more robust both to species loss and to cascading effects.

428 Plant-pollinator networks, in general, are highly dynamic, with high turnover of species and in-  
429 teractions both within and between seasons [13]. Though our non-assembling communities expe-  
430 rience fewer network reorganizations than the assembling hedgerows, 82% of field margins and  
431 40% of mature hedgerows underwent at least one changing point in network structure. Pollina-  
432 tors are also highly opportunistic [50, 62, 2], though trait complementarity such as tongue length  
433 and corolla depth impose some biophysical limits to the interactions between plants and pollina-  
434 tors [64, 63, 57, 58, 56]. Such opportunism may buffer plant-pollinator communities from global  
435 change [e.g., 54, 31], but our limited understanding of the assembly of these communities impedes

436 making such predictions [63, 13]. Unlike in the broader food web literature, we have few assembly  
437 models of mutualistic network assembly [60, 44, 29]. In addition, the few developed models often  
438 borrow their mechanisms from competitive interactions, leading to inaccurate biological assump-  
439 tions [30]. We need further development of mechanistic models of mutualistic systems to generate  
440 testable predictions, along with empirical exploration of network assembly. Plant-pollinator com-  
441 munities and mutualisms broadly are vital for biodiversity maintenance and essential ecosystem  
442 service provision. We must therefore understand the processes underlying their assembly to facili-  
443 tate restoration and conservation.

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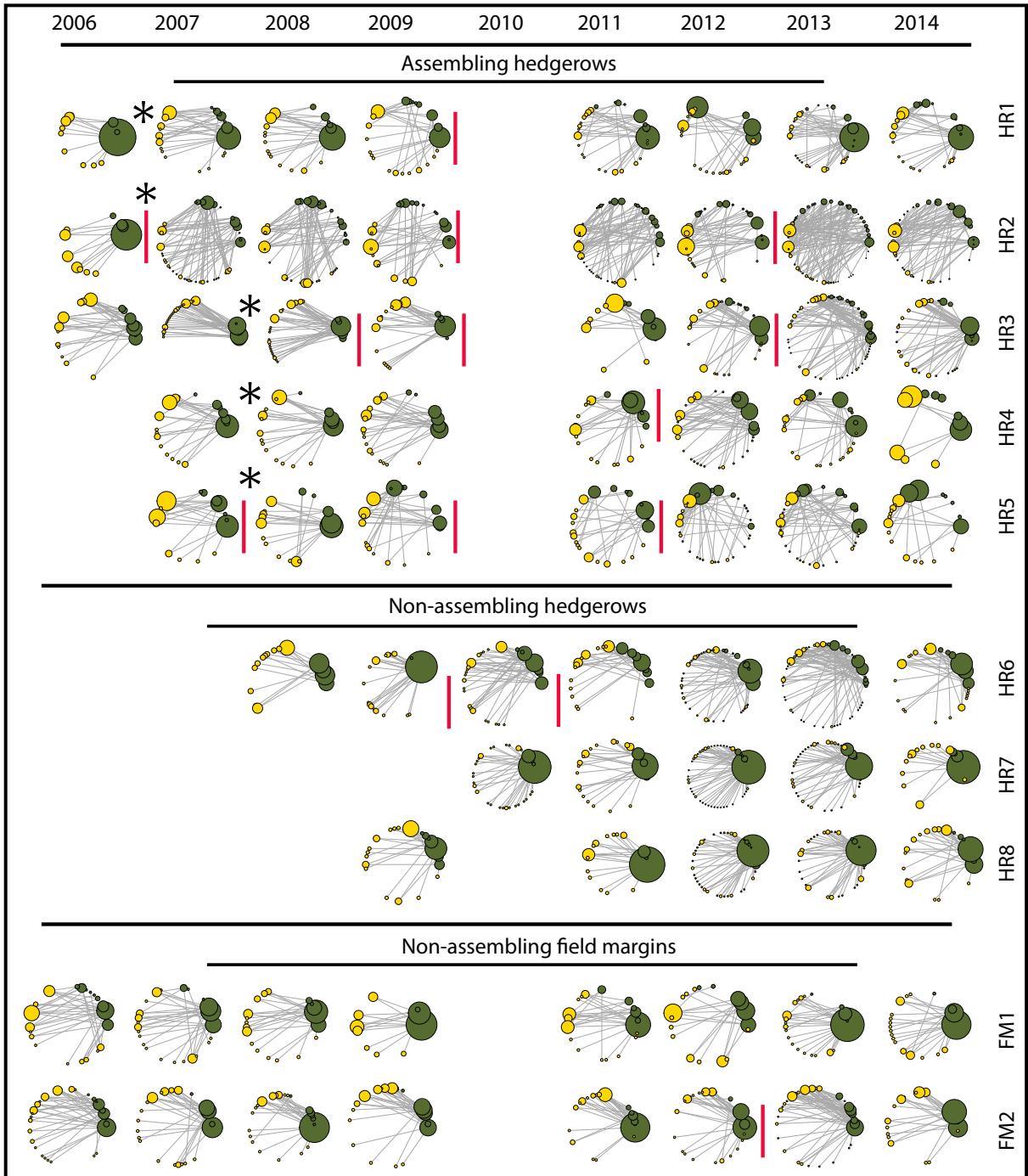


Figure 1: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, weighted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

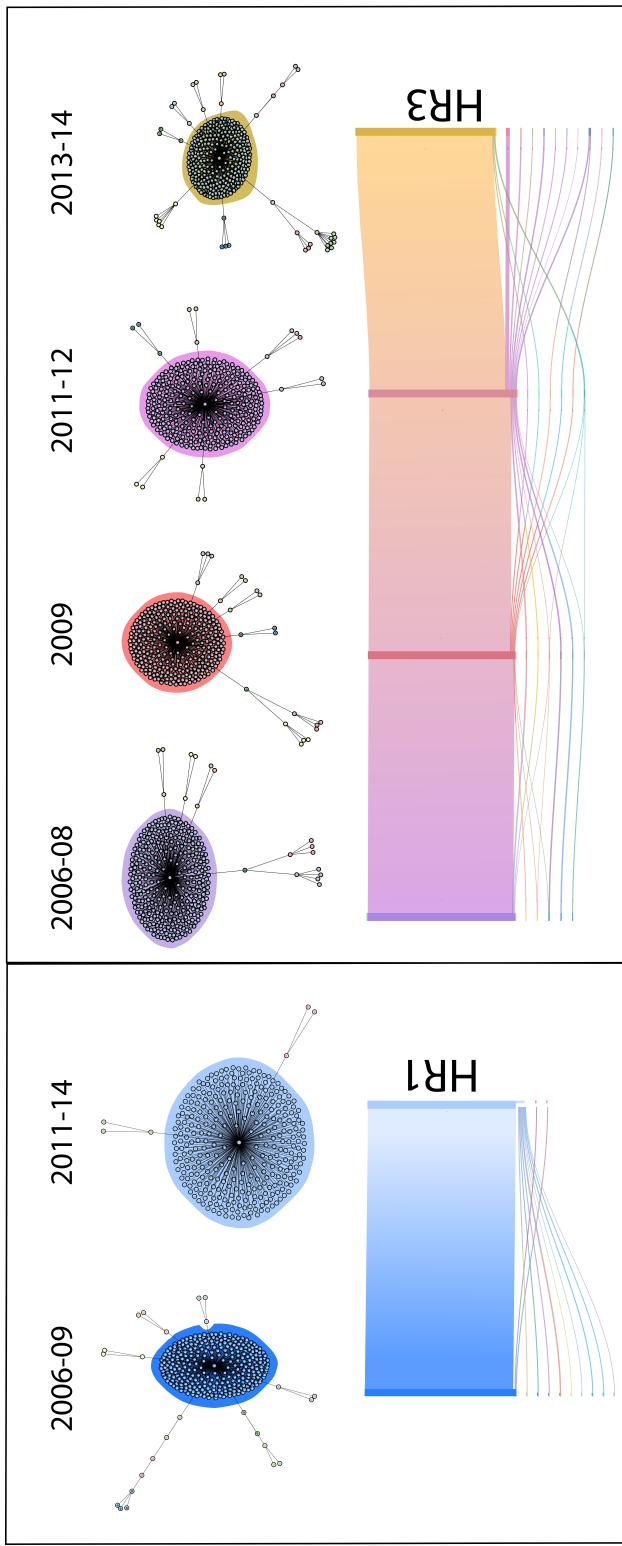


Figure 2: The module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species between modules between changing points.

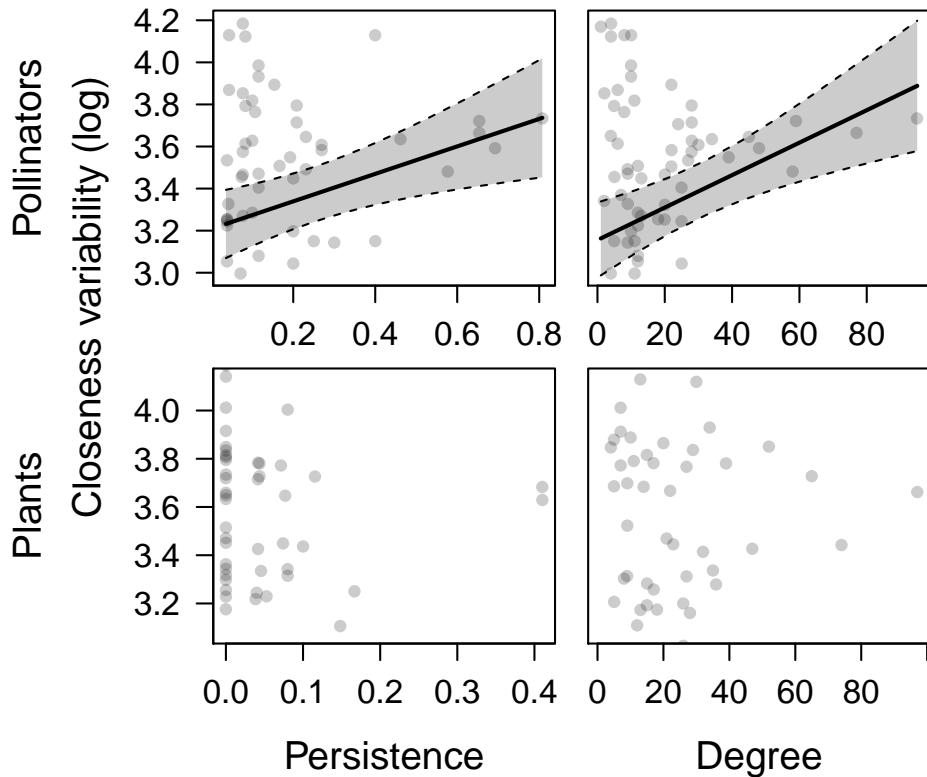


Figure 3: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across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

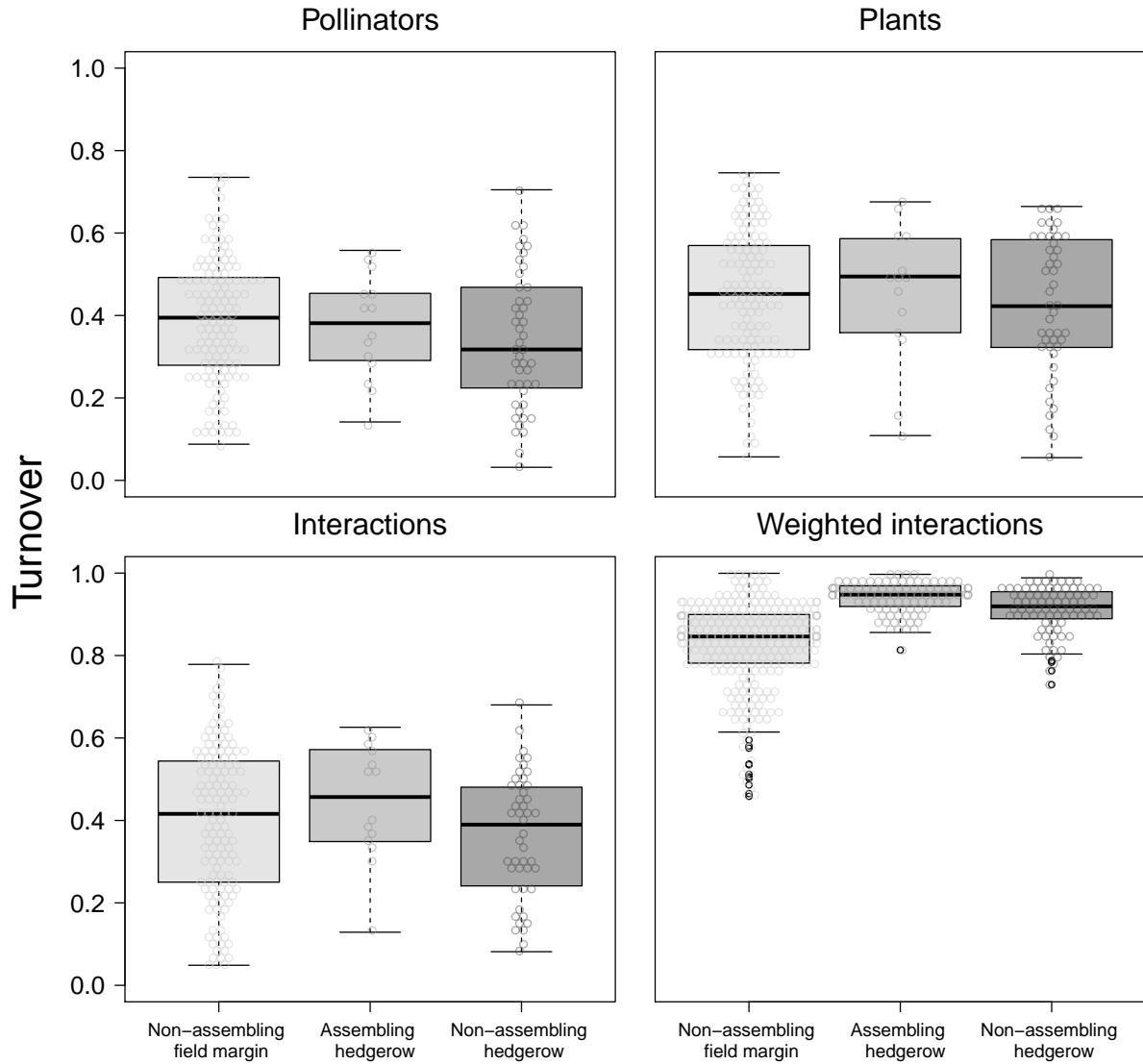


Figure 4: The species, interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has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

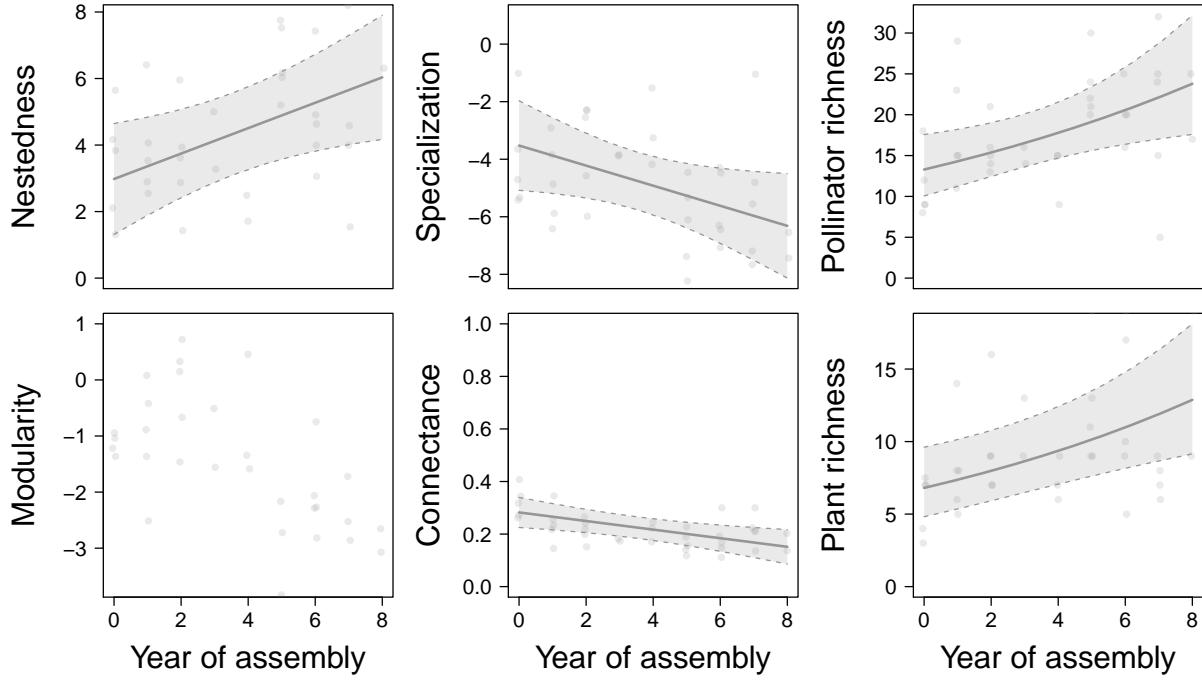


Figure 5: Nestedness, plant richness and pollinator richness increased as the networks assembled. Specialization and modularity remained consistent across years, while connectance decreased. The nestedness, modularity and specialization scores represent z-scores. Scores greater than  $\sim 2$  or less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

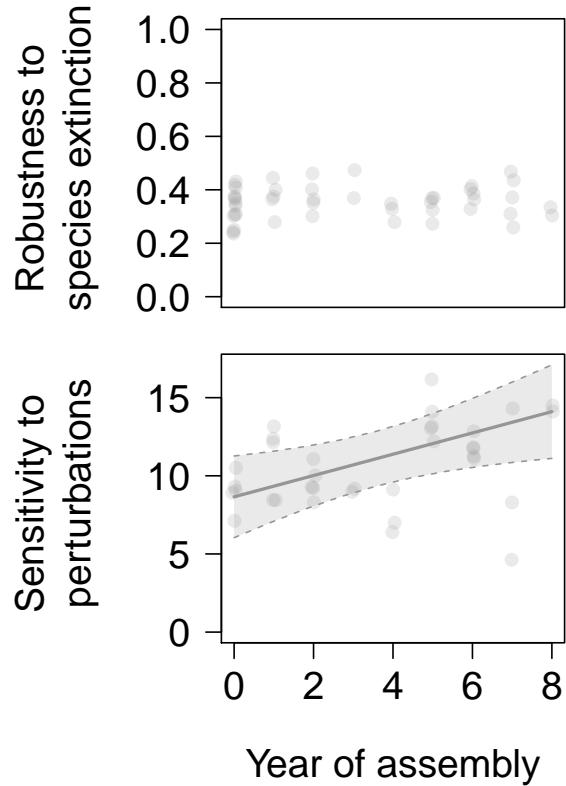


Figure 6: The robustness of networks to species extinction did not change with network assembly, but the sensitivity to cascading perturbations increased. The robustness to species extinction is measured by incrementally removing species by degree, though removing species by abundance did not yield qualitatively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