

Running head: PLANT-POLLINATOR NETWORK ASSEMBLY

Major interaction reorganizations punctuate the assembly of pollination networks

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Abstract

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

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

17 **Introduction**

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

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

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

41 tions of interactions can punctuate assembly [49]. Such significant reorganizations of interactions,
42 or network changing points, are observed in social networks that respond to abrupt shifts in the
43 behavior of interactors [49]. In ecolo

44 To estimate the temporal species and interaction turnover, we use an approach similar to calcu-
45 lating spatial β -diversity. Instead of calculating the variation in community composition across
46 sites within a year, we estimated turnover across years at a site. We first calculated the pairwise
47 dissimilarity of plants, pollinators and interactions between years within each site using the Chao
48 dissimilarity estimator that incorporates abundances, while also accounting for unobserved records
49 [14]. Dissimilarity estimates can be affected by the total number of species and individuals sam-
50 pled at a site [e.g., 51]. For example, the probability that two sites do not share any species is
51 higher when there are few individuals at those sites. Following [51], we use null models that con-
52 strained species richness to estimate the deviation of the observed dissimilarity from that which
53 would be expected under a random community assembly process. With the corrected dissimilarity
54 values, we then calculated the multivariate dispersion of community composition across years [4].
55 In order to test whether assembling hedgerows had more species and interactions turnover than
56 non-assembling communities, the species and interaction temporal turnover estimates were mod-
57 eled as responses in a linear mixed model with site type as an explanatory variable and site as a
58 random effect [10, 36].

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

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

73 **Temporal changes in interaction patterns**

74 **Network structure**

75 Any changing points in network structure may contribute to the reorganization of the assembling
76 networks into predictable interaction patterns. Pollination networks exhibit two main structural
77 patterns — modularity [e.g., 45] and nestedness [e.g., 8, 7]. In modular networks, interactions are
78 insular, occurring within separate groups or “modules” more often than between modules. Modules
79 in the network may fragment as the network assembles, enhancing modularity. Conversely, nested
80 networks are like a pyramid of interactions, where there are some species that interact with many
81 species, other species that interact with a subset of those species, and so on. If species entering
82 the network tend to interact with the generalist base of the network pyramid as would be expected
83 with preferential attachment, nestedness would increase through time. The connectance — the
84 proportion of observed out of possible interactions — would decrease as new, specialist species,
85 preferentially attach to the core. Lastly, the overall level of network specialization may change
86 as the community assembles. Network-level specialization will increase if specialist species colo-
87 nize the network or species begin to limit their interaction niche breadth as the network assembles
88 [11].

89 To evaluate network nestedness, we used the estimator weighted NODF [3]. NODF evaluates
90 whether species with fewer partners interact with subsets of partners with which more connected
91 species interact [3]. To estimate modularity, we use a hierarchical clustering algorithm [43, 16]. We
92 evaluate network specialization with the metric H2, which estimates the deviation of the observed
93 interaction frequency between plants and pollinators from a null expectation where all partners
94 interact in proportion to their abundances [11]. It ranges from zero for generalized networks to
95 one for specialized networks. We calculated standardized z-scores so that nestedness, modularity
96 and specialization metrics could be compared across communities. The z-scores were calculated
97 by generating an ensemble of 999 randomly assembled communities, subtracting the mean of the
98 statistic calculated across these communities from the observed value, and then dividing by the
99 standard deviation. To assemble random communities, we reshuffled the interactions between
100 species but fixed the total number of interactions, species and interaction frequency distributions
101 [25].

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

108 Network robustness

109 Lastly, we tested whether the changes in interaction patterns associated with network assembly
110 affect the robustness of the network to species loss and cascading perturbations. Following [38],
111 we simulated plant species extinction and the subsequent extinction cascades of pollinator species.
112 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.

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

137 **Results**

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

141 **Change point analysis**

142 **Identifying change points**

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

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

152 In contradiction to the predictions of assembly by preferential attachment, both pollinator per-
153 sistence and degree were positively related to network position variability (Fig. 4, estimate of
154 the slope of closeness centrality variability and persistence \pm standard error of the estimate,
155 0.496 ± 0.182 , p -value=0.016; slope of closeness centrality variability and degree, 0.004 ± 0.002 ,
156 p -value=0.056). The slope of these relationships remained significant when the species with the
157 top 10 persistence and degree scores were dropped. In addition, plant persistence and degree were

not significantly related to network position variability (Fig. 4). The variability of species network position was not the result of closeness linearly increasing through time, and, in fact, plant and pollinator closeness decreased slightly through time (Fig. S2, estimate of the slope of closeness through time \pm SE, pollinators: -0.082 ± 0.021 , $p\text{-value}=0.003$; plants -0.089 ± 0.044 , $p\text{-value}=0.04$). Though statistically significant, the models seems to be a poor fit to the data.

Species and interaction turnover

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

Temporal changes in interaction patterns

Network structure

Nestedness and modularity did not change in any predictable pattern with assembly (Fig. 6). All of the networks were significantly nested ($z\text{-scores} > 1.96$), but not modular ($z\text{-scores} <$

¹⁷⁹ 2, Fig. 6).

¹⁸⁰ Connectance decreased as the community assembled (Fig. 6, estimate of the slope of connectance
¹⁸¹ through time \pm standard error of the estimate, -0.023 ± 0.008 , $p\text{-value}=0.007$). Specialization
¹⁸² also decreased, though the slope was not significantly different from zero. Most communities were
¹⁸³ more generalized than expected when interactions were randomized (Fig. 6).

¹⁸⁴ Both plant and pollinator species richness increased through time (Fig. 6, estimate of the slope of
¹⁸⁵ richness through time \pm SE, pollinators: 0.136 ± 0.064 , $p\text{-value}=0.034$; plants: 0.140 ± 0.060 ,
¹⁸⁶ $p\text{-value}=0.012$). Unsurprisingly, pollinator species are colonizing and persisting at the assembling
¹⁸⁷ hedgerows. Plant species richness in the networks is based on the flowers actually visited by
¹⁸⁸ pollinators and not the presence of a particular plant species at a site. Thus, though some new
¹⁸⁹ plant species may establish themselves in the hedgerows, the increase in plant richness in the
¹⁹⁰ networks is likely due to previously unvisited plants attracting visitors as they mature and offer
¹⁹¹ better rewards.

¹⁹² Network robustness

¹⁹³ Assembly did not affect network robustness to species extinction when species were removed
¹⁹⁴ incrementally by degree or abundance In contrast, the sensitivity of networks to cascading per-
¹⁹⁵ turbations, as measured by the algebraic connectivity of the network, increased as the network
¹⁹⁶ assembled (Fig. 7, estimate of the slope of sensitivity to cascading perturbations through time \pm
¹⁹⁷ SE, 0.6814 ± 0.272 , $p\text{-value}=0.042$).

198 **Discussion**

199 We show that the temporal assembly of plant-pollinator networks following restoration is a highly
200 dynamic process where interactions often undergo significant reorganizations, the so called chang-
201 ing points. If these network reorganizations were a product of environmental forces alone, we
202 would expect to observe the same changing points at the same periods, consistently across all
203 sites. However, network changing points in non-assembling communities are less frequent, and
204 there are few consistent trends in when change points occurred across all sites. Several sites had
205 network changing points between years 2009 and 2011 (Fig. 2). In California, 2011 marked the
206 beginning of a multi-year drought. The assembling hedgerows were not sampled in 2010, so dis-
207 entangling whether the changing points are due to skipping a year of monitoring the assembly
208 process or the drought is not possible. Interestingly, most assembling hedgerows did not undergo
209 a significant interaction reorganization immediately after a hedgerow was planted (i.e., the transi-
210 tion from weedy field margin to hedgerow). This result is consistent with the finding that in our
211 study system, hedgerow restoration takes several years to have an impact on the plant-pollinator
212 communities, and with the observation that hedgerows do not begin to produce many flowers until
213 3–5 years following planting [35].

214 In addition to finding multiple network organization changing points during assembly, the way
215 in which these reorganizations occur was different from what would be expected from preferential
216 attachment. In a preferential attachment process, we expect that the most persistent and high degree
217 species would remain stable in the network core during assembly [5]. Surprisingly, however, we
218 encountered the opposite pattern. For example, the four most ubiquitous species in our study
219 landscape — *Halictus ligatus*, *Halictus tripartitus*, *Lasioglossum (Dialictus) incompletum*, and
220 *Toxomerus marginatus* — were the only species that changed which module they were a member
221 in across years in all the assembling hedgerows. Because species degree and persistence were
222 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

248 species preferentially attached to a central, generalist core [2]. In addition, connectance decreased,
249 as would be expected if the network is being colonized by specialist species and the overall mean
250 number of interactions per species did not change. However, the frequent changing points in
251 network organization, dynamic nature of species positions in the networks, and turnover of species
252 and interactions all point to an assembly mechanism other than preferential attachment. The stable
253 level of network-level specialization through the assembly process may be due to the increased
254 colonization of specialized species [40] accompanied by an increase in the diet breath of resident
255 species. This would be expected if resident species were able to minimize their foraging time
256 by expanding their diet breath as plant diversity increases with hedgerow maturation [65, 52, 12,
257 2]. Such a change in pollinator behavior would also explain the increase in network nestedness.
258 Because so many mechanisms give rise to the same patterns of interaction, additional tests are
259 necessary to assess the contribution of different mechanisms to community assembly.

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

268 Contrary to the general restoration goals, networks' susceptibility to cascading perturbations in-
269 creased as the communities assembled. We measured vulnerability to cascading perturbations as
270 the algebraic connectivity of the network: the greater the algebraic connectivity, the more vulnera-
271 ble a community is to cascading perturbations. Algebraic connectivity is positively related to both
272 the number of species and connectance of a network [26]. The increase in and plant and pollinator

richness following restoration is thus at least partially responsible for the increase in response to cascading effects. Algebraic connectivity is also positively correlated with the number in interactions, or connectance of a network [26], We, however, observed a decrease in connectance, suggesting topological characteristics of the networks beyond just species richness and connectance are needed to explain the increased sensitivity to perturbations spreading. These hedgerows were designed to provide floral resources to the largest number of pollinators across the growing season [39]. The generalized nature of the floral community may explain why the networks tended to be more generalized than expected if interactions were randomly distributed across species (Fig. 6). In addition, the design of the hedgerow plantings may have facilitated the emergence of a single, highly connected module in all of the networks (see 3 for examples). This network configuration results in short path lengths (the distance between species in a network based on their shared partners), and thus, a perturbation in one species can more easily spread to other species. In order to promote more resilient communities, future restoration efforts should explore designing floral communities to promote more interaction partitioning using, for example, algorithms to optimize different network properties based on prior knowledge of pollinator floral preferences [41], and on desired network architectures that renders them more robust both to species loss and to cascading effects.

Plant-pollinator networks, in general, are highly dynamic, with high turnover of species and interactions both within and between seasons [13]. Though our non-assembling communities experience fewer network reorganizations than the assembling hedgerows, 82% of field margins and 40% of mature hedgerows underwent at least one changing point in network structure. Pollinators are also highly opportunistic [50, 62, 2], though trait complementarity such as tongue length and corolla depth impose some biophysical limits to the interactions between plants and pollinators [64, 63, 57, 58, 56]. Such opportunism may buffer plant-pollinator communities from global change [e.g., 54, 31], but our limited understanding of the assembly of these communities impedes making such predictions [63, 13]. Unlike in the broader food web literature, we have few assembly

299 models of mutualistic network assembly [60, 44, 29]. In addition, the few developed models often
300 borrow their mechanisms from competitive interactions, leading to inaccurate biological assump-
301 tions [30]. We need further development of mechanistic models of mutualistic systems to generate
302 testable predictions, along with empirical exploration of network assembly. Plant-pollinator com-
303 munities and mutualisms broadly are vital for biodiversity maintenance and essential ecosystem
304 service provision. We must therefore understand the processes underlying their assembly to facili-
305 tate restoration and conservation.

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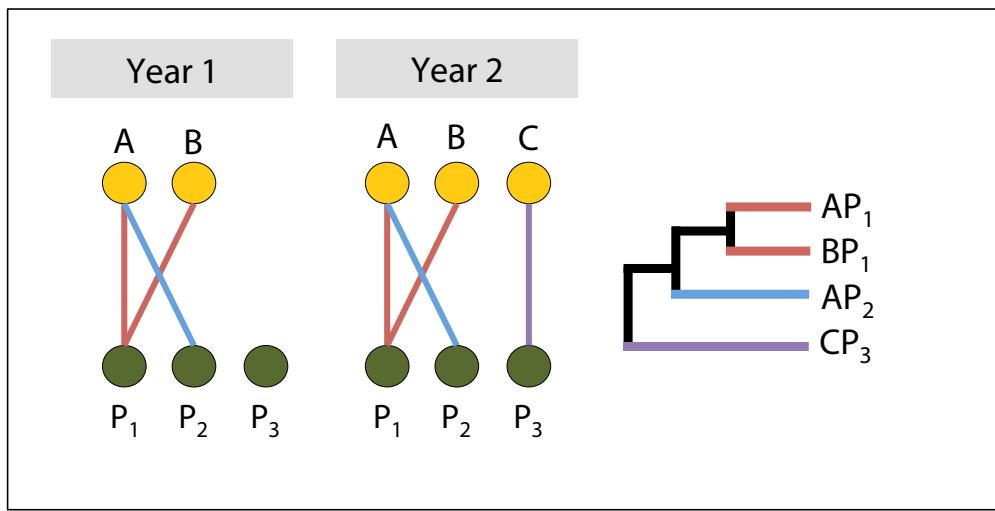


Figure 1: Diagram illustrating the analysis to examine the temporal turnover of interactions weighted based on their similarity. A, B and C are animal species, and Ps are plant species. The dendrogram depicts the interaction similarity across years based on the number of shared constituent species.

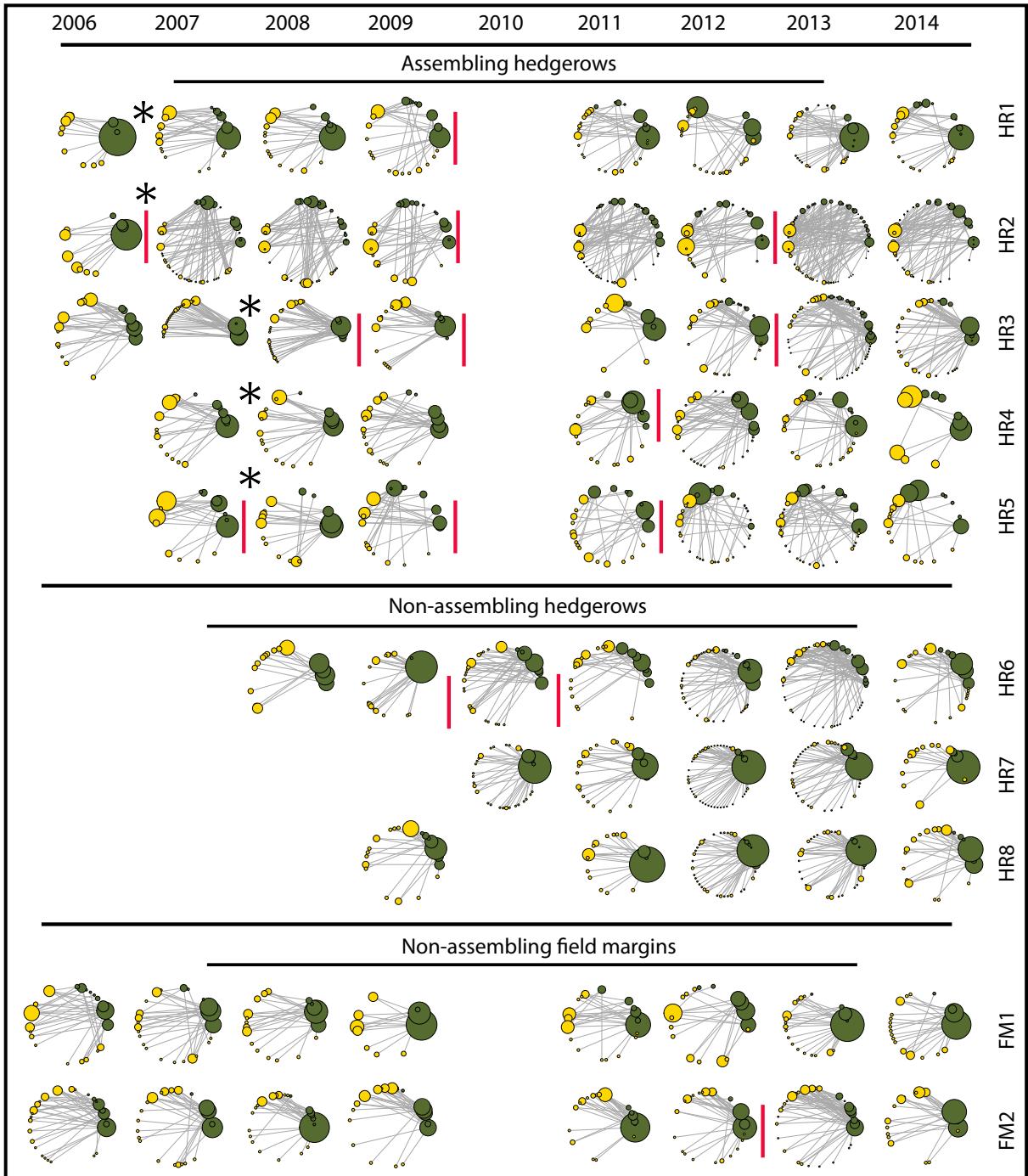


Figure 2: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, respectively, weighted by their degree. Each species has a consistent position in the perimeter of the network across years. Asterisks indicate the year the hedgerow was planted. Before that, the sites were weedy field margins.

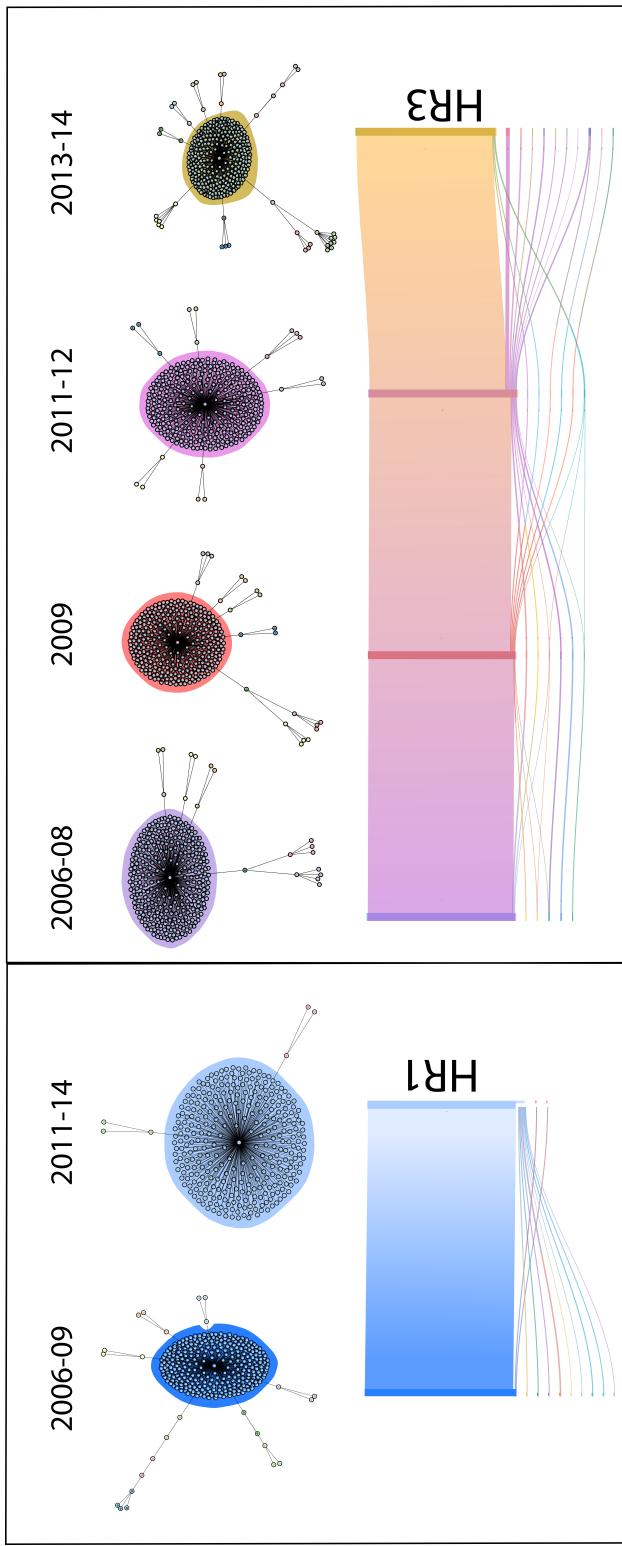


Figure 3: The species module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species between modules between changing points. Each line represents the change of s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

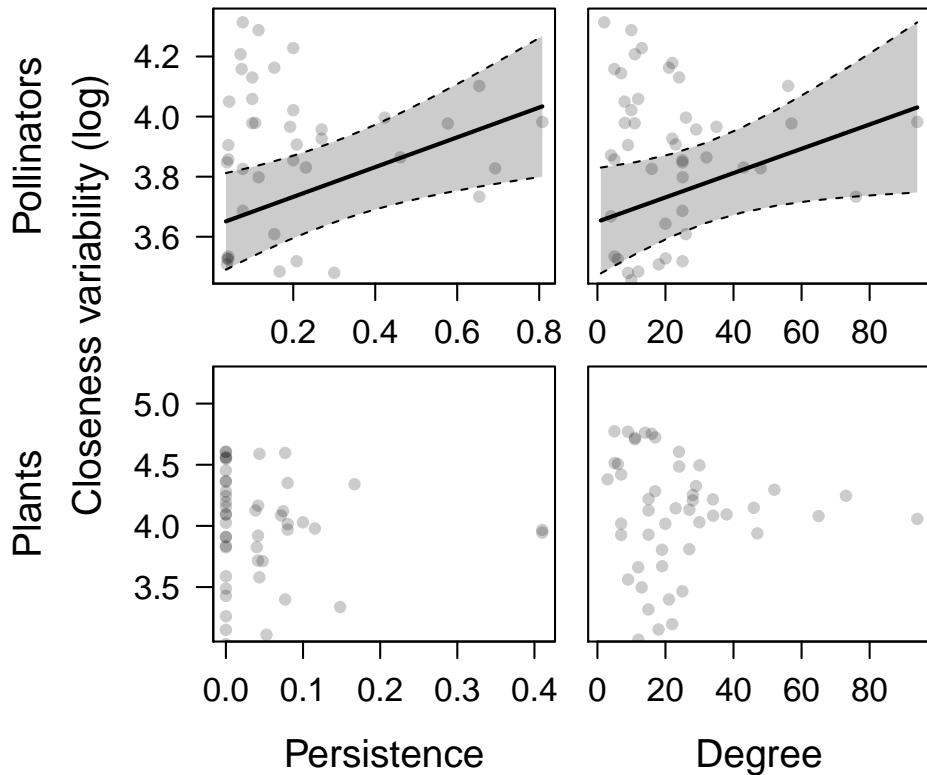


Figure 4: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across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

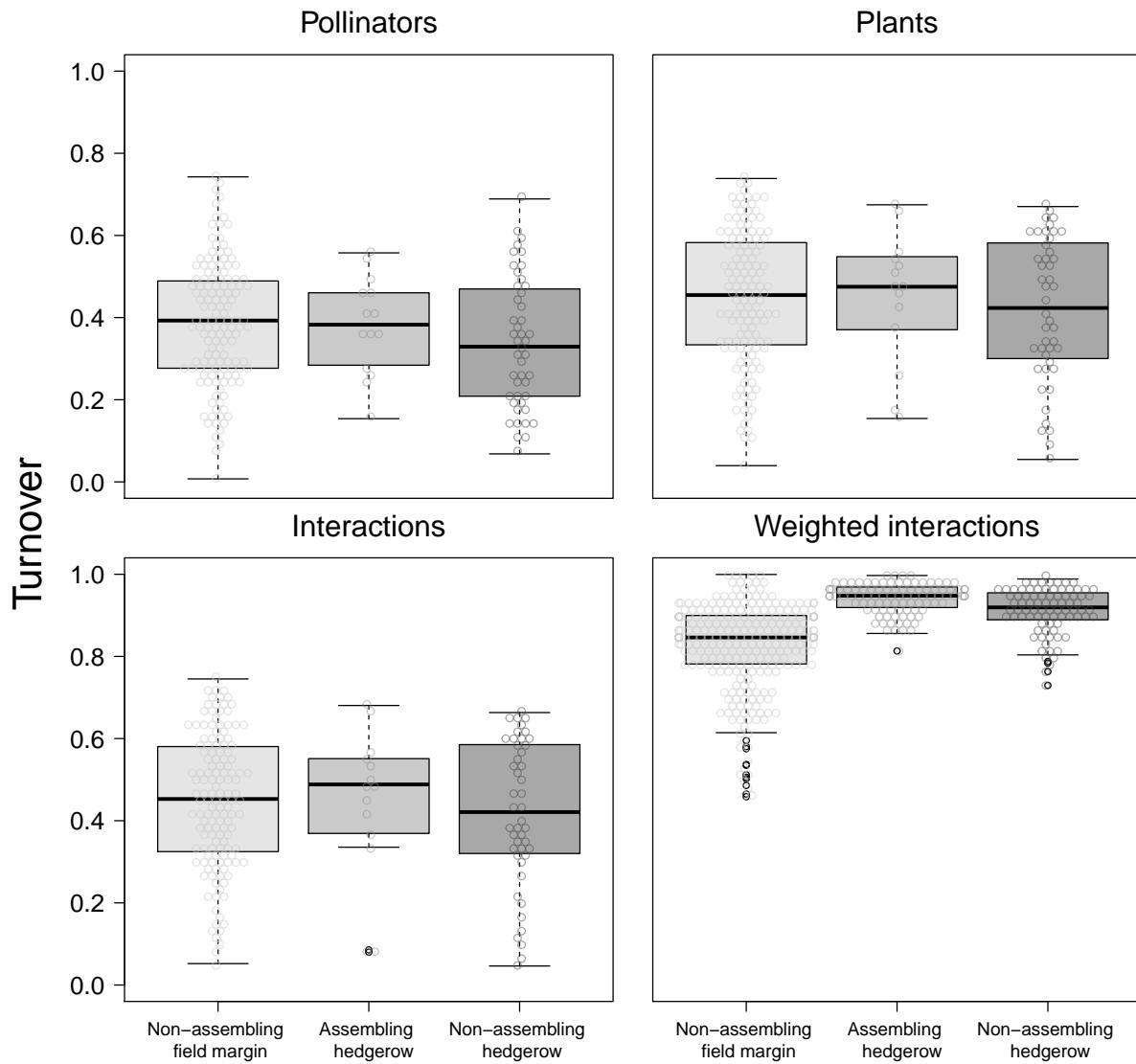


Figure 5: Species interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally significantly less pollinator turnover. However, when interactions were weighted by their similarity, both hedgerow types had higher turnover than unrestored field margins. Boxplots represent medians (black horizontal line) first and third quartiles (box perimeter) and extremes (whiskers).

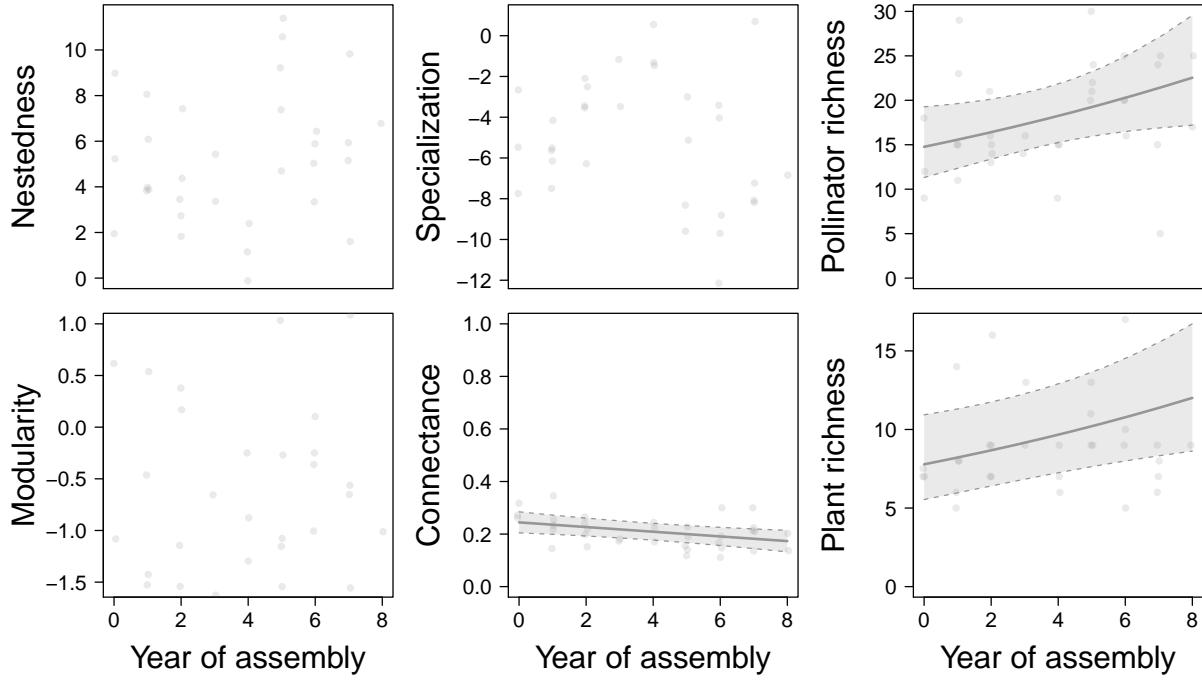


Figure 6: Nestedness, plant richness and pollinator richness increased as the networks assembled. Specialization and modularity remained consistent across years, while connectance decreased. The nestedness, modularity and specialization scores represent z-scores. Scores greater than ~ 2 or less than ~ -2 are significantly more or less structured than randomly assembled networks. Points are the metric value for each site at each year of assembly. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

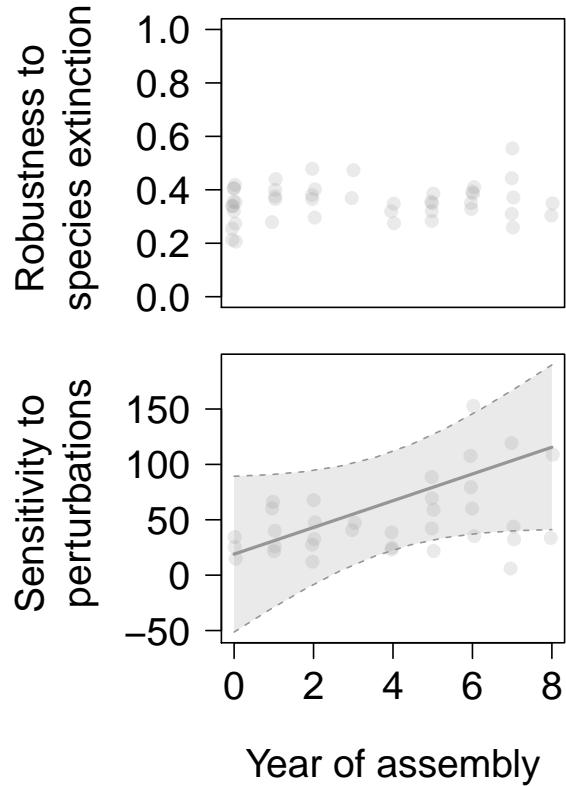


Figure 7: The robustness of networks to species extinction did not change with network assembly, but the sensitivity to cascading perturbations increased. The robustness to species extinction is measured by incrementally removing species by degree, though removing species by abundance did not yield qualitatively 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.