

Running head: PLANT-POLLINATOR NETWORK ASSEMBLY

Major network reorganizations punctuate the assembly of plant-pollinator communities

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Abstract

Species and interactions are being lost at alarming rates and it is imperative to understand how communities assemble if we are to prevent their collapse and restore lost interactions. Using an eight-year dataset comprising nearly 20,000 pollinator visitation records, we explore the assembly of plant-pollinator communities at native plant restoration sites in an agricultural landscape. We find that species occupy highly dynamic network positions through time, causing the assembly process to be punctuated by major network reorganizations. The most persistent and generalized pollinator species are also the most variable in their network positions, contrary to what preferential attachment — the most widely studied theory of network assembly — predicts. Our results fundamentally alter our understanding of how communities assemble and how species interactions change through time while helping to inform efforts to re-assemble robust communities through restoration.

community assembly, change points, robustness, nestedness, modularity, restoration, mutual-

¹⁴ ism, preferential attachment

15 **Introduction**

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

25 Preferential attachment, the most widely explored mechanism of network assembly, predicts
26 that species entering a network are more likely to interact with species that are already well-
27 connected [the “rich-get-richer” principle, 5]. In pollination systems — a particularly ubiquitous
28 mutualism [49, 36] — some studies have found support for this assembly mechanism. Investiga-
29 ting the day-to-day, temporal assembly of a plant-pollinator network within a season, [48] found
30 that phenologically new plant and pollinator species tended to interact with already well-connected
31 species, potentially because these species are either more abundant or temporally persistent. Using
32 a space-for-time substitution to study primary succession, [2] also found evidence that assembly
33 along a glacier foreland occurred through preferential attachment. Specifically, network nested-
34 ness (i.e, a core group of generalists interacts with both specialist and generalist species) increased
35 as the community aged [2]. An increase in nestedness could have occurred via the preferential
36 attachment process, whereby specialist species attach to the well-connected, generalist core.

37 Significant reorganizations of interactions — change points — can also punctuate assembly
38 [51]. A change point is caused by a merge, split, fragmentation or formation of modules within
39 a network. Such interaction reorganizations are observed in social networks responding to abrupt

40 shifts in the behavior of interactors [51]. In ecological communities, such shifts may occur if, as
41 new species colonize, resident species change their interaction partners to optimize their foraging
42 effort [54, 12, 63, 2, 62]. For preferential attachment to be at play, change points would need to
43 be driven primarily by peripheral, temporally variable species while a stable, well-connected core
44 of species remained stable in their interactions. No studies, however, have examined if network
45 changing points occur during ecological network assembly and/or how these changes relate to
46 species behavior.

47 Understanding network assembly is particularly relevant to ecological restoration, which is
48 essentially “applied succession” [e.g., 50]. In pollination systems, time has been shown to affect
49 the structure of networks in restored areas [25, 19], suggesting that interactions change as a com-
50 munity develops. Facilitating network restoration is especially imperative in areas where species
51 interactions provide essential ecosystem services, such as crop pollination in agricultural land-
52 scapes. To promote pollinator services in agriculture, some farmers plant strips of native plants
53 along farm edges (hedgerows). By providing habitat, hedgerows augment the richness, abundance
54 and trait diversity of pollinators in agricultural landscapes [44, 37, 53], and promote the persistence
55 and colonization of floral resource specialists [42]. As the community assembles, it is important to
56 understand how these new species are incorporated into the network as well as the consequences
57 of adding species for interaction patterns and robustness.

58 We explore the process of network development using a eight-year dataset of plant-pollinator
59 community assembly following hedgerow installment in the highly simplified and intensively man-
60 aged agricultural landscape of California’s Central Valley. We first determine whether network
61 assembly was punctuated by significant reorganizations of interactions. We next tested whether
62 the species that are most variable in their network position — and thus important contributors to
63 network reorganizations — are less persistent and connected species, as would be expected by
64 preferential attachment. To further explore the mechanisms underlying the temporal dynamics of

65 the networks, also we examine patterns in the species and interaction temporal turnover. Finally,
66 we investigate whether networks assemble toward predictable interaction patterns, and the ramifi-
67 cations for the robustness of the networks.

68 Materials & Methods

69 Study sites and collection methods

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

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

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

87 During each sampling round, flower-visitors to plants in assembling hedgerows and non-
88 assembling controls were netted for one hour of active search time (the timer was paused when
89 handling specimens). The identify of the plant being visited was recorded for each floral visitor.
90 Honeybees (*Apis mellifera*) were not collected because their abundance is determined largely by
91 hive placement by bee-keepers. All other insect flower visitors that touched the reproductive parts
92 of the flower were collected; however, here we focus only on wild bees and syrphids — the most
93 abundant and effective pollinators in the system (representing 49 and 19 percent of records, re-
94 spectively, C. Kremen, A. Klein and L. Morandin, unpublished data). Bee and syrphid specimens
95 were identified to species (or morpho-species for some bee specimens in the genera *Nomada* and
96 *Sphecodes*) by expert taxonomists.

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

100 **Change point analysis**

101 **Identifying change points**

102 We employed a change point detection method [51] to identify fundamental reorganizations in
103 large-scale interaction patterns. Change point detection methods have yet to be generalized to
104 quantitative networks, so for this analysis we focused on qualitative (binary) networks. Following
105 [51], we first defined a probability distribution over the networks using the generalized hierarchi-
106 cal random graph model (GHRG). The GHRG model captures both assortative and disassortative
107 structure patterns at all scales in the network [51]. A network G is composed of vertices V and
108 edges E . The GHRG model decomposes the N vertices into a series of nested groups, the rela-
109 tionships among which are represented by the dendrogram T . The tips of T are the vertices of G ,

110 and the probability that two vertices u and v connect is given by the parameter p_r . The probability
111 distribution of the network G is thus defined as:

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

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

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

119 Once the GHRG model was fit to the networks, we determined whether a change point oc-
120 curred between two time slices. To detect a change point, we used Bayes factors to compare the
121 fit of two models — one where a change point occurred between two networks, and one where no
122 change occurred. We chose a sliding window of length, w , of four years to detect change points.
123 Larger windows allow for more gradual changes, and four was the maximum possible with our
124 eight years of data. Lastly, to calculate a p -value for the Bayes factors, we used parametric boot-
125 strapping to numerically estimate the null distribution [51]. We employed code published online
126 by L. Peel for the change point analysis. Analyses were conducted in Python 3.4.

127 We next tested whether the change points occurring in maturing hedgerows were a component
128 of the assembly process or a product of environmental shifts that lead to network reorganizations
129 in all types of communities. We modeled the number of change points as successes and the total
130 number of sample years at each site as trials, and used a generalized linear model with Binomial
131 error to test whether the probability of a change point occurrence varied by site type. We used
132 standard techniques to determine whether the assumptions of the models were met for this and all

133 subsequent models. For the non-assembling controls, only sites with five or greater survey years
134 were included in this analysis ($N = 11$). All statistical analyses were conducted in R 3.2.3 [55].

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

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

140 We calculated species persistence as the proportion of surveys in which a plant or pollinator is
141 observed. Species observed consistently within and between years were thus maximally persistent.
142 Species degree was calculated from interaction observations from an extensive dataset from Yolo
143 County (approx. 18000 interaction records) that included both the data included in this study and
144 additional data from sites where we collected flower visitors using the same methods [42, 53].

145 To represent network position variability, we computed the coefficient of variation of weighted
146 closeness centrality [26] at each site through time. Closeness centrality represents the importance
147 of a species by calculating the path lengths to other vertices (species) in the network [26]. The
148 shorter the mean path length to other species, the higher the closeness centrality. We used linear
149 mixed models to test whether the species closeness variability (log) is related to the persistence
150 or degree of that species [10, 38]. We included random effects for species and site. Because
151 the degree and persistence of pollinators were strongly correlated, ($\rho = 0.071$, $p\text{-value} < 2 * 10^{-16}$), we included each explanatory variable in separate models. Plant degree and persistence
152 were not significantly correlated, but we used the same models as we did for the pollinators for
153 consistency. Because an approximately logarithmic increase in closeness centrality — as would
154 be expected with assembly by preferential attachment — we also tested whether log closeness
155 centrality increased through time.

157 **Species and interaction turnover**

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

168 To estimate the temporal species and interaction turnover, we used an approach similar to cal-
169 culating spatial β -diversity. Instead of calculating the variation in community composition across
170 sites within a year, we estimated turnover across years at a site. We first calculated the pairwise
171 dissimilarity of plants, pollinators and interactions between years within each site using the Chao
172 dissimilarity estimator that incorporates abundances, while also accounting for unobserved records
173 [16]. Dissimilarity estimates can be affected by the total number of species and individuals sam-
174 pled at a site [e.g., 53]. For example, the probability that two sites do not share any species is
175 higher when there are few individuals at those sites. Following [53], we used null models that con-
176 strained species richness to estimate the deviation of the observed dissimilarity from that which
177 would be expected under a random community assembly process. With the corrected dissimilarity
178 values, we then calculated the multivariate dispersion of community composition across years [4].
179 In order to test whether assembling hedgerows had more species and interactions turnover than
180 non-assembling communities, the species and interaction temporal turnover estimates were mod-
181 eled as responses in a linear mixed model with site type as an explanatory variable and site as a

182 random effect [10, 38].

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

197 **Temporal changes in interaction patterns**

198 **Network structure**

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

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

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

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

230 eralized linear mixed models with Poisson error to model richness [10]. We scaled explanatory
231 variables.

232 Network robustness

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

242 We also explored how the robustness to cascading perturbations changed as the community
243 assembled, using algebraic connectivity — the second smallest eigenvalue of the Laplacian matrix
244 [23] — as a proxy for network robustness. Algebraic connectivity relates to how difficult it is to
245 turn a network into completely disconnected groups of species [17, 28]. The larger the algebraic
246 connectivity, the more sensitive a network is to cascading perturbations. Perturbations, such as the
247 decrease in abundance of a plant or pollinator, can have negative consequences for the species in
248 the network. For example, a decrease in abundance of a pollinator will diminish the pollination
249 services it provides to plants. The affected plants would set less seeds, and decrease in abundance
250 the subsequent year. Consequently, other pollinators that depended on those plant species would
251 also be affected, and the effects of this perturbation would continue to propagate throughout the
252 network. Alternatively, perturbations could also have a positive effect if, for example, the increase
253 in the abundance of a plant species lead to an increase in resource availability for pollinators. The

254 examples of negative perturbations (e.g., resource collapse, disease spreading, parasites), however,
255 outnumber possible positive perturbations. It is important to note that both robustness and algebraic
256 connectivity assume that the network is static — they do not account for the ability of species to
257 alter their interaction depending on circumstances and the resource availability.

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

261 **Results**

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

265 **Change point analysis**

266 **Identifying change points**

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

275 or non-assembling) similarly.

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

277 In contradiction to the predictions of assembly by preferential attachment, both pollinator per-
278 sistence and degree were positively related to network position variability (Fig. 4, estimate of
279 the slope of closeness centrality variability and persistence \pm standard error of the estimate,
280 0.496 ± 0.182 , $p\text{-value}=0.016$; slope of closeness centrality variability and degree, 0.004 ± 0.002 ,
281 $p\text{-value}=0.056$). The slope of these relationships remained significant when the species with the
282 top 10 persistence and degree scores were dropped. In addition, plant persistence and degree were
283 not significantly related to network position variability (Fig. 4). The variability of species net-
284 work position was not the result of closeness linearly increasing through time, and, in fact, plant
285 and pollinator closeness decreased slightly through time (Fig. S2, estimate of the slope of close-
286 ness through time \pm SE, pollinators: -0.082 ± 0.021 , $p\text{-value}=0.003$; plants -0.089 ± 0.044 ,
287 $p\text{-value}=0.04$).

288 **Species and interaction turnover**

289 The rates of plant, pollinator and interaction temporal turnover were similar across assembling
290 hedgerows, non-assembling hedgerows and field margins, though mature hedgerows had marginally
291 less pollinator turnover than field margins (Fig. 5, estimate \pm SE of the difference in turnover be-
292 tween field margins and mature hedgerows, -0.051 ± 0.026 , $p\text{-value}=0.049$). The turnover of
293 plants and interactions was not significantly different between site types. When interactions were
294 weighted by their similarity, both assembling and mature hedgerows had higher rates of turnover
295 than field margins (Fig. 5, estimate \pm SE of the difference in turnover between field margins
296 and assembling hedgerows, 0.115 ± 0.027 , $p\text{-value}=0.0002$; field margins and mature hedgerows,
297 0.082 ± 0.024 , $p\text{-value}=0.002$). The weighted interaction turnover at assembling hedgerows, how-

298 ever, was not significantly higher than in non-assembling, mature hedgerows.

299 **Temporal changes in interaction patterns**

300 **Network structure**

301 Nestedness, modularity and specialization did not change predictably assembly (Fig. 6). All of the
302 networks were significantly nested (z -scores > 2), but not modular (z -scores < 2 , Fig. 6). Most
303 communities were more generalized than expected when interactions were randomized (Fig. 6).
304 Connectance decreased as the community assembled (Fig. 6, estimate of the slope of connectance
305 through time \pm standard error of the estimate, -0.023 ± 0.008 , p -value=0.007).

306 Both plant and pollinator species richness increased through time (Fig. 6, estimate of the
307 slope of richness through time \pm SE, pollinators: 0.136 ± 0.064 , p -value=0.034; plants: 0.140
308 ± 0.060 , p -value=0.012). Unsurprisingly, pollinator species are colonizing and persisting at the
309 assembling hedgerows. Plant species richness in the networks is based on the flowers actually
310 visited by pollinators and not the presence of a particular plant species at a site. Thus, though
311 some new plant species may establish themselves in the hedgerows, the increase in plant richness
312 in the networks is likely due to previously unvisited plants attracting visitors as they mature and
313 offer better rewards.

314 **Network robustness**

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

319 **Discussion**

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

334 In a preferential attachment process, we expect that the most persistent and high degree
335 species (the species with the most unique interaction partners) would remain stable in the net-
336 work core during assembly [5]. Surprisingly, however, we encountered the opposite pattern. For
337 example, the four most ubiquitous species in our study landscape — *Halictus ligatus*, *Halictus*
338 *tripartitus*, *Lasioglossum (Dialictus) incompletum*, and *Toxomerus marginatus* — were the only
339 species that changed which module they were a member in across years in all the assembling
340 hedgerows. Because species degree and persistence were strongly correlated, it is difficult to dis-
341 entangle the causal mechanism for why species with those characteristics are so variable in their
342 network position. Species that can interact with a relatively high number of partners may be better
343 able to exploit the limited floral resources in the intensively managed agriculture landscape, and

thus also be the most persistent [in ant-plant mutualisms, 20]. More persistent species usually have longer phenologies, so they can visit many different flowers, resulting in a higher degree [65, 24]. 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 [67, 29, 39]. Thus given the opportunity and ability to use different resources, species will often change their network positions [39].

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 generally be 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 therefore both support more stable pollinator communities, while also providing resources for rare and/or specialized species [37, 42].

When we explored how network-level interaction patterns changed through time, we found few patterns. The connectance decreased, as would be expected if the network is being colonized by specialist species [42]. Network specialization, however, did not change predictably with as-

369 sembly. Decreasing connectance without an accompanying increase in specialization would be
370 possible if the increased colonization of specialized species was accompanied by an increase in
371 the diet breath of resident species. This would be expected if resident species were able to mini-
372 mize their foraging time by expanding their diet breath as plant diversity increases with hedgerow
373 maturation [54, 67, 12, 2].

374 Interestingly, however, the changes in network patterns associated with assembly did not
375 affect the hedgerow network robustness to species extinction or susceptibility to cascading per-
376 turbations. The hedgerows were designed to provide floral resources for the largest number of
377 pollinators across the growing season [41]. The generalized nature of the floral community may
378 explain why the networks tended to be more generalized than expected if interactions were ran-
379 domly distributed across species (Fig. 6). In addition, the design of the hedgerow plantings may
380 have facilitated the emergence of a single, highly connected module in all of the networks (see
381 3 for examples). This network configuration results in short path lengths (the distance between
382 species in a network based on their shared partners), and thus, a perturbation in one species can
383 more easily spread to other species. These networks are also vulnerable to the extinction of highly
384 connected species [13]. In order to promote more resilient communities, future restoration efforts
385 should explore designing floral communities to promote more interaction partitioning using, for
386 example, algorithms to optimize different network properties based on prior knowledge of polli-
387 nator floral preferences [43], and on desired network architectures that renders them more robust
388 both to species loss and to cascading effects.

389 In general, plant-pollinator networks are highly dynamic, with high turnover of species and
390 interactions both within and between seasons [14]. Though our non-assembling communities ex-
391 perienced fewer network reorganizations than the assembling hedgerows, 82% of field margins
392 and 40% of mature hedgerows underwent at least one changing point in network structure. Pol-
393 linators are highly opportunistic [52, 64, 2], though trait complementarity such as tongue length

394 and corolla depth impose some biophysical limits to the interactions between plants and pollina-
395 tors [60, 58, 66, 65, 59]. Such opportunism may buffer plant-pollinator communities from global
396 change [e.g., 56, 33], but our limited understanding of the assembly of these communities impedes
397 making such predictions [65, 14]. Unlike in the broader food web literature, we have few assembly
398 models of mutualistic network assembly [62, 46, 31]. In addition, the few developed models often
399 borrow their mechanisms from competitive interactions, leading to inaccurate biological assump-
400 tions [32]. We need further development of mechanistic models of mutualistic systems to generate
401 testable predictions, along with empirical exploration of network assembly. Plant-pollinator com-
402 munities and mutualisms are vital for biodiversity maintenance and essential ecosystem service
403 provision. We must therefore understand the processes underlying their assembly to facilitate
404 restoration and conservation.

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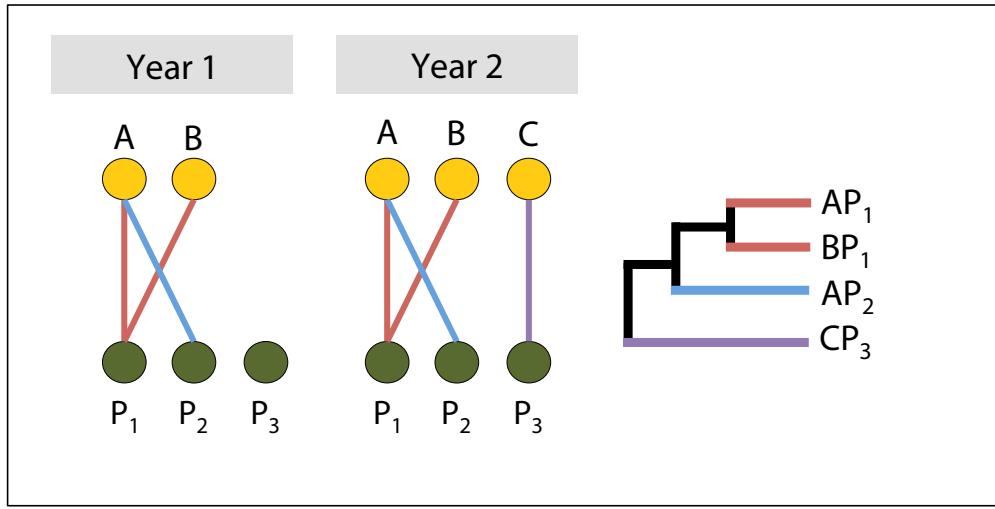


Figure 1: Diagram illustrating the analysis to examine the temporal turnover of interactions weighted based on their similarity. A, B and C are animal species, and Ps are plant species. The dendrogram depicts the interaction similarity across years based on the number of shared constituent species.

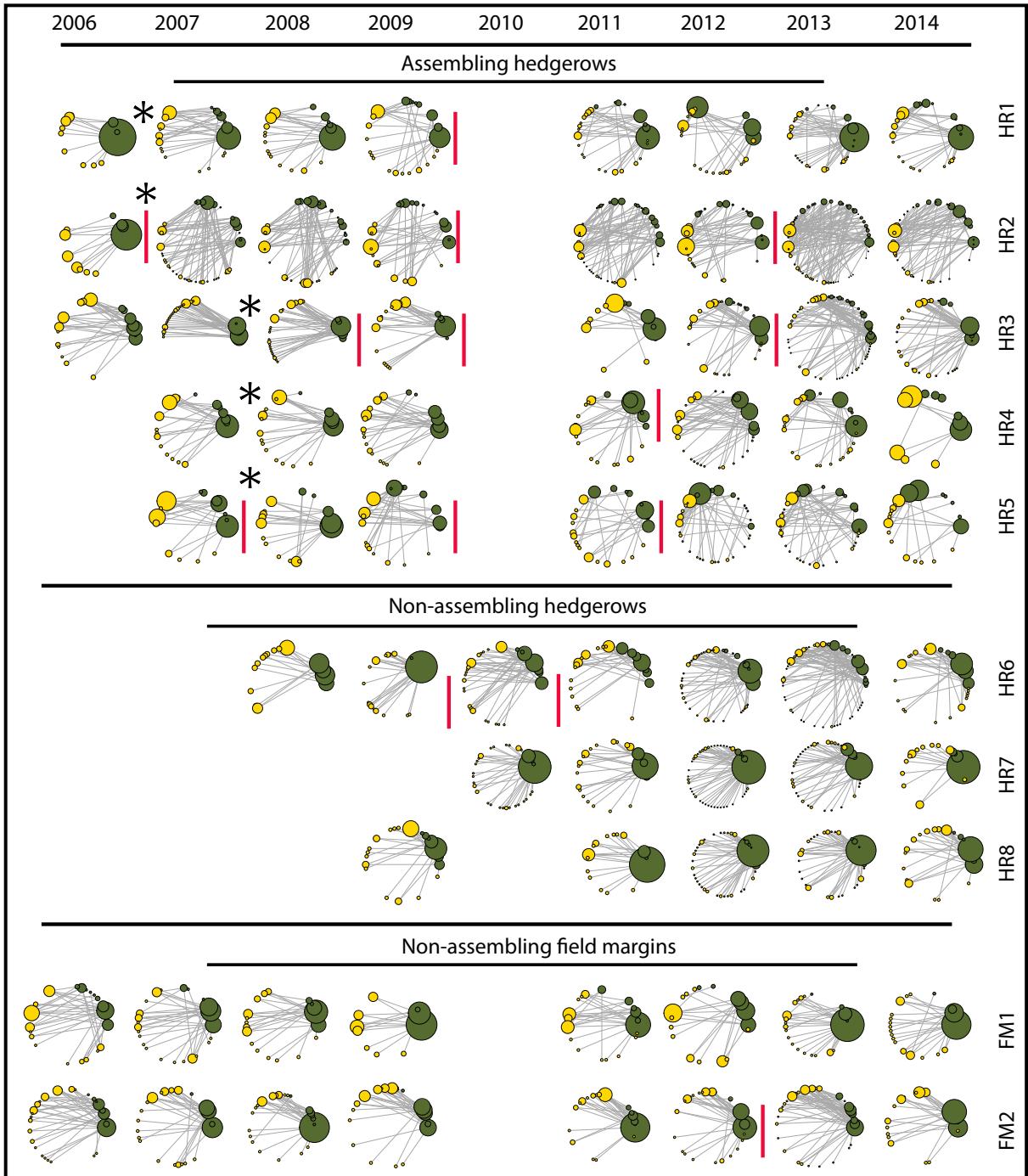


Figure 2: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, respectively,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

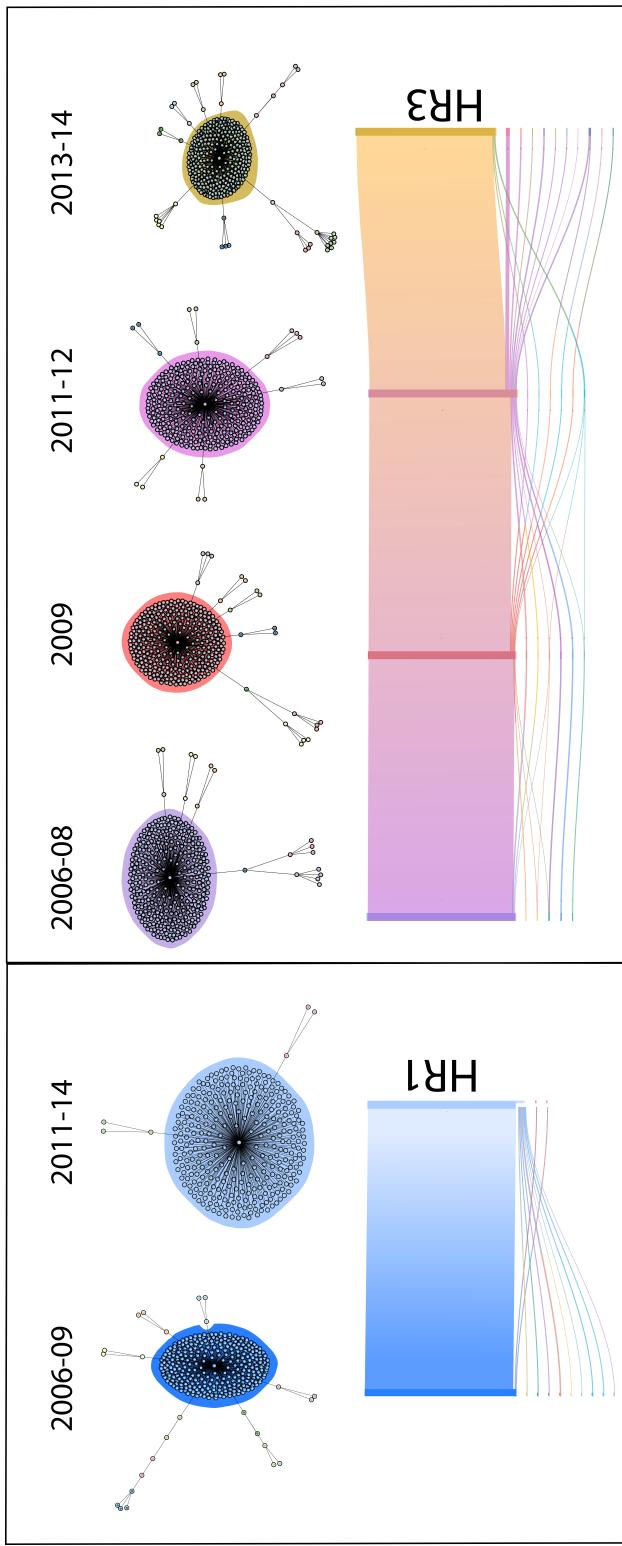


Figure 3: The species module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species to different modules between change points.

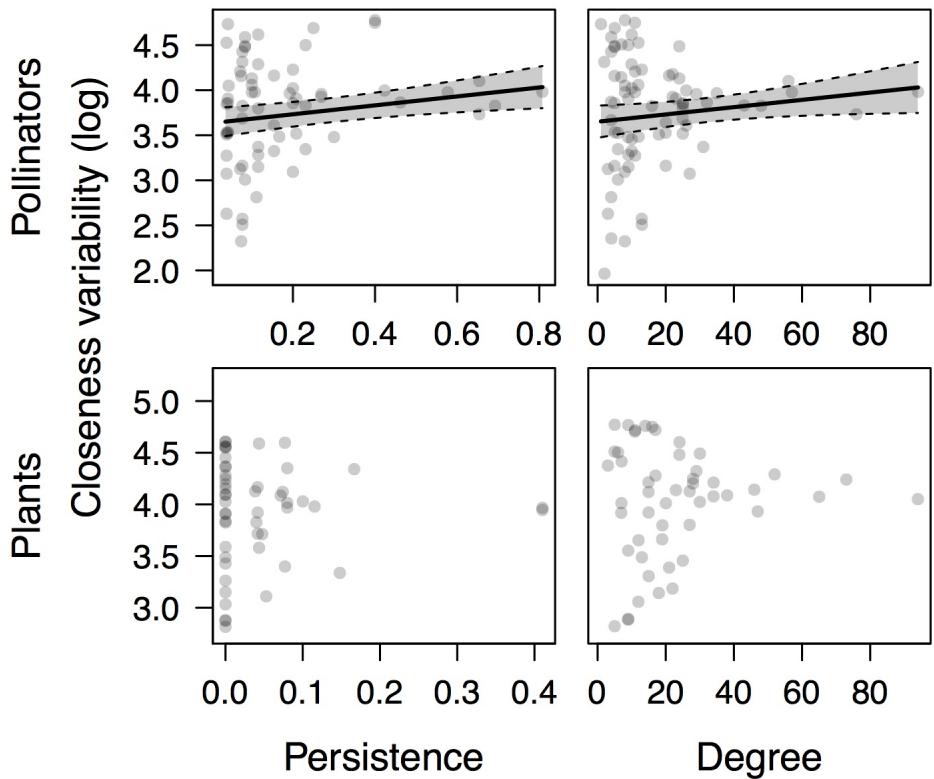


Figure 4: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across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

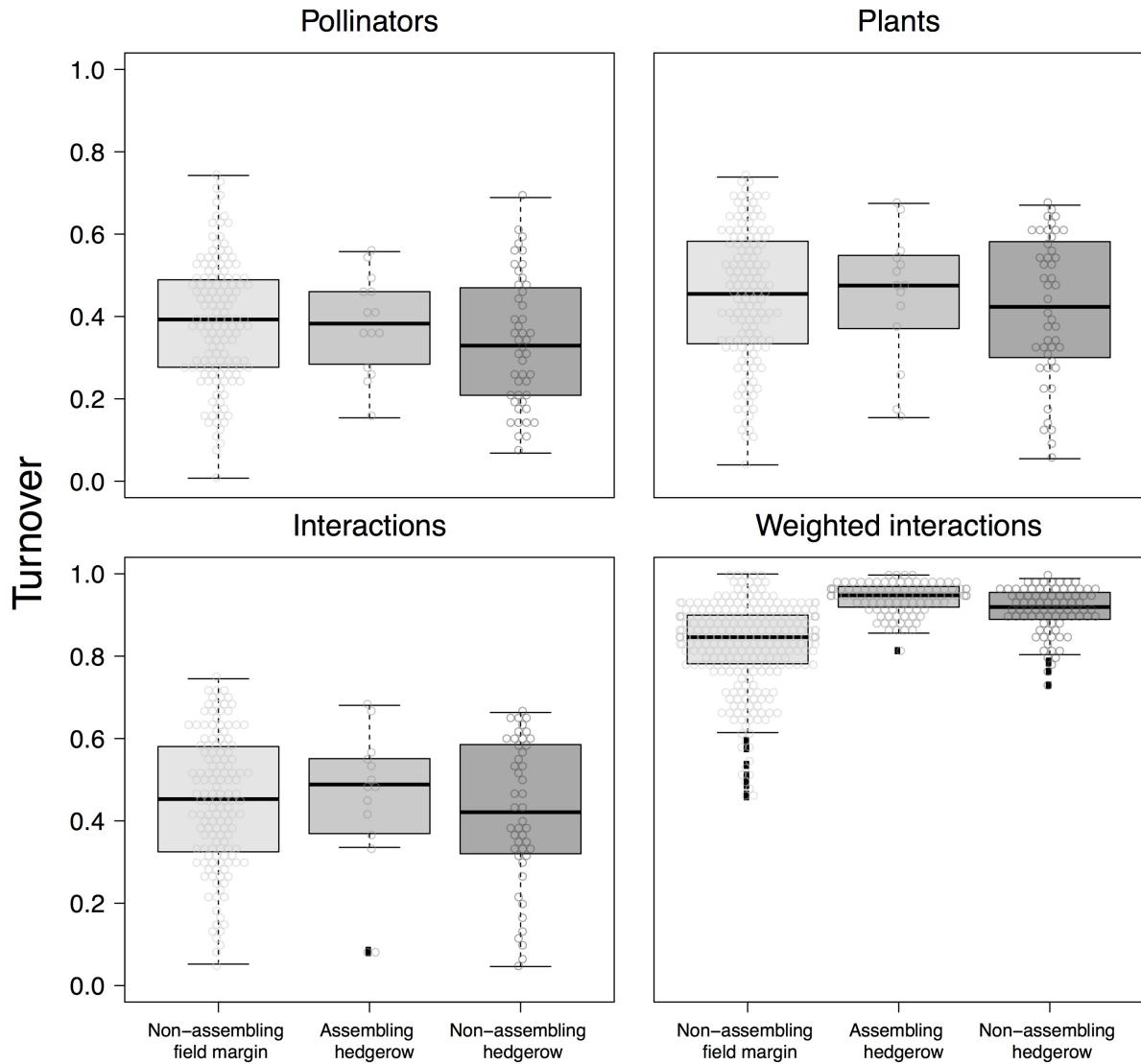


Figure 5: Species interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally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

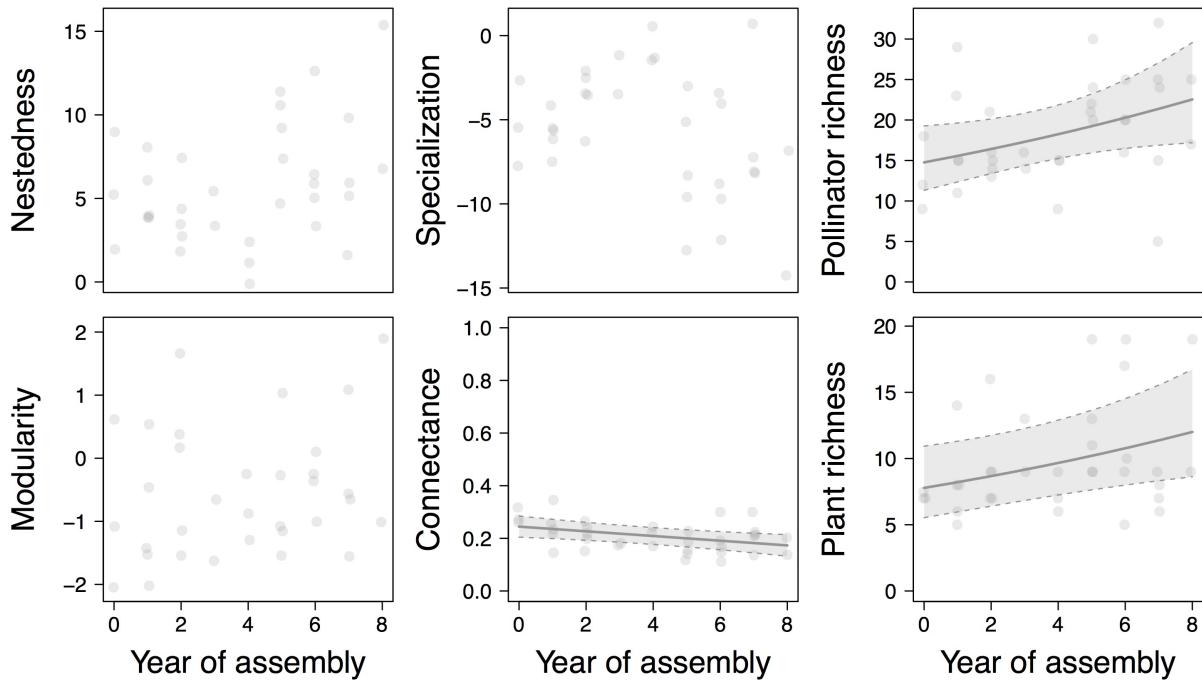


Figure 6: Plant richness and pollinator richness increased as the networks assembled. Nestedness, modularity and specialization did not change predictable across years, while connectance decreased. The nestedness, modularity and specialization scores represent z-scores. Scores greater than ~ 2 or less than ~ -2 are significantly more or less structured than randomly assembled networks. Points are the metric value for each site at each year of assembly. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.