Major interaction reorganizations punctuate the assembly of pollination networks

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Abstract

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

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

Introduction

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

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

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

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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 chose 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

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

Materials & Methods

Study sites and collection methods

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

between sites sampled in the same year was 1 km. The entire area surveyed spanned almost 300 km^2. The crop fields adjacent to all sites were similarly managed as intensive, high-input mono-culture.

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

Flower-visitors to plants in hedgerows and unrestored controls were netted for one hour of active search time (the timer was paused when handling specimens). Honeybees (*Apis mellifera*) were not collected because their abundance is determined largely by hive placement by bee-keepers. All other insect flower visitors that touched the reproductive parts of the flower were collected; however, here we focus only on wild bees and syrphids — the most abundant and effective polli-nators in the system (representing 49 and 19 percent of records, respectively, C. Kremen, A. Klein and L. Morandin, unpublished data). Bee and syrphid specimens were identified to species (or morpho-species for some bee specimens in the genera *Nomada* and *Sphecodes*) by expert tax-onomists.

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

Change point analysis

Identifying change points

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

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

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

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

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

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

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

Characteristics of species that contribute to change points

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

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

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

Species and interaction turnover

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

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

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

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

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

Temporal changes in interaction patterns

Network structure

Any changing points in network structure may contribute to the reorganization of the assembling networks into predictable interaction patterns. Pollination networks exhibit two main structural patterns — modularity [e.g., 45] and nestedness [e.g., 8, 7]. In modular networks, interactions are insular, occurring within separate groups or "modules" more often than between modules. Modules in the network may fragment as the network assembles, enhancing modularity. Conversely, 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 decrease as new, specialist species, preferentially attach to the core. Lastly, the overall level of network specialization may change as the community assembles. Network-level specialization will increase if specialist species colonize the network or species begin to limit their interaction niche breath as the network assembles [11].

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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 use a hierarchical clustering algorithm [43, 16]. We evaluate 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 [25].

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 employ generalized linear mixed models with Poisson error to model richness. We scaled explanatory variables.

Network robustness

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

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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. For example, the increase in abundance of a plant species would lead to an increase in resource availability for the 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.

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Results

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

Change point analysis

Identifying change points

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

Characteristics of species that contribute to change points

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

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not significantly related to network position variability (Fig. 3). 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: -0.0003 ± 0.00005, p-value=$2.7 * 10^{-12}$; plants -0.007 ± 0.001, p-value=$1.4 * 10^{-6}$). Through statistically significant, the slopes are so slight they may not be biologically significant.

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. 4, estimate $\pm$ SE of the difference in turnover between field margins and mature hedgerows, -0.0498 ± 0.026, p-value=0.058). When interactions where weighted by their similarity, both assembling and mature hedgerows had higher rates of turnover than field margins (Fig. 4, estimate $\pm$ SE of the difference in turnover between field margins and assembling hedgerows, 0.115 ± 0.027, p-value=0.0002; field margins and mature hedgerows, 0.082 ± 0.024, p-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

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

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

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

Network robustness

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

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Discussion

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

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

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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

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

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

Contrary to the general restoration goals, the susceptibility of the networks to cascading perturbations increased as the communities assembled. Because network vulnerability to cascading perturbations, as measured by algebraic connectivity, is correlated with species richness, the increase in and plant and pollinator richness following restoration is at least partially responsible for the

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increase in response to cascading effects. Connectance is also positively related to algebraic connectivity [26], but because we observed a decrease in connectance, topological characteristics of the networks beyond 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. 5). 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 2 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 models of mutualistic network assembly [60, 44, 29]. In addition, the few developed models often borrow their mechanisms from competitive interactions, leading to inaccurate biological assump-

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

Acknowledgments

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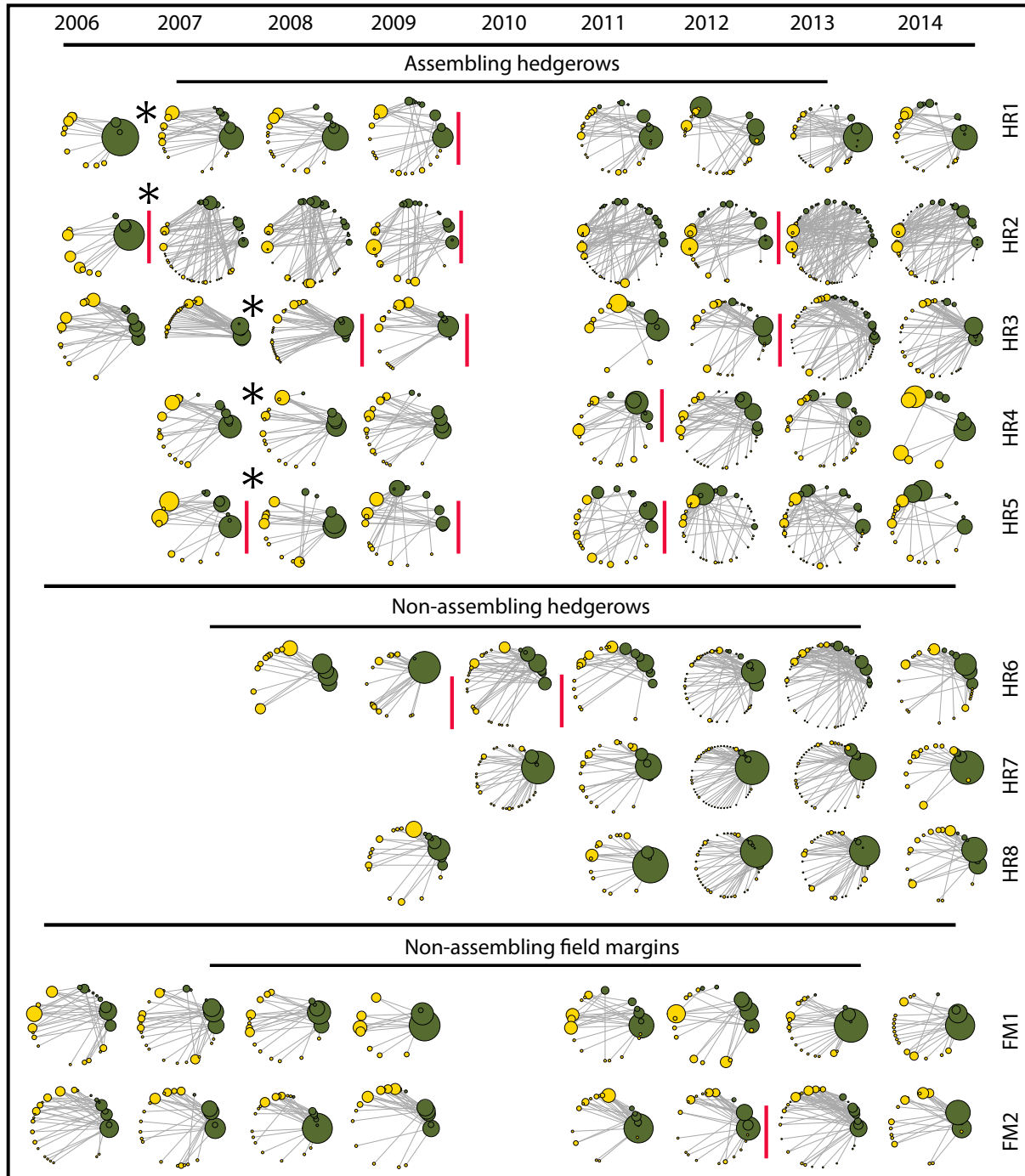
Figure 1: Assembling hedgerow networks had more changing points (vertical red lines) than non-assembling hedgerows and weedy field margins (a representative sample of non-assembling sites are depicted here). In each network, plants and pollinators are represented by green and yellow circles, respectively, weighted by their degree. Each species has a consistent position in the perimeter of the network across years. In the assembling hedgerows, colored squares in the corner of each network represent the year of assembly. Asterisks indicate the year the hegdgerow was planted. Before that, the sites were weedy field margins. 29
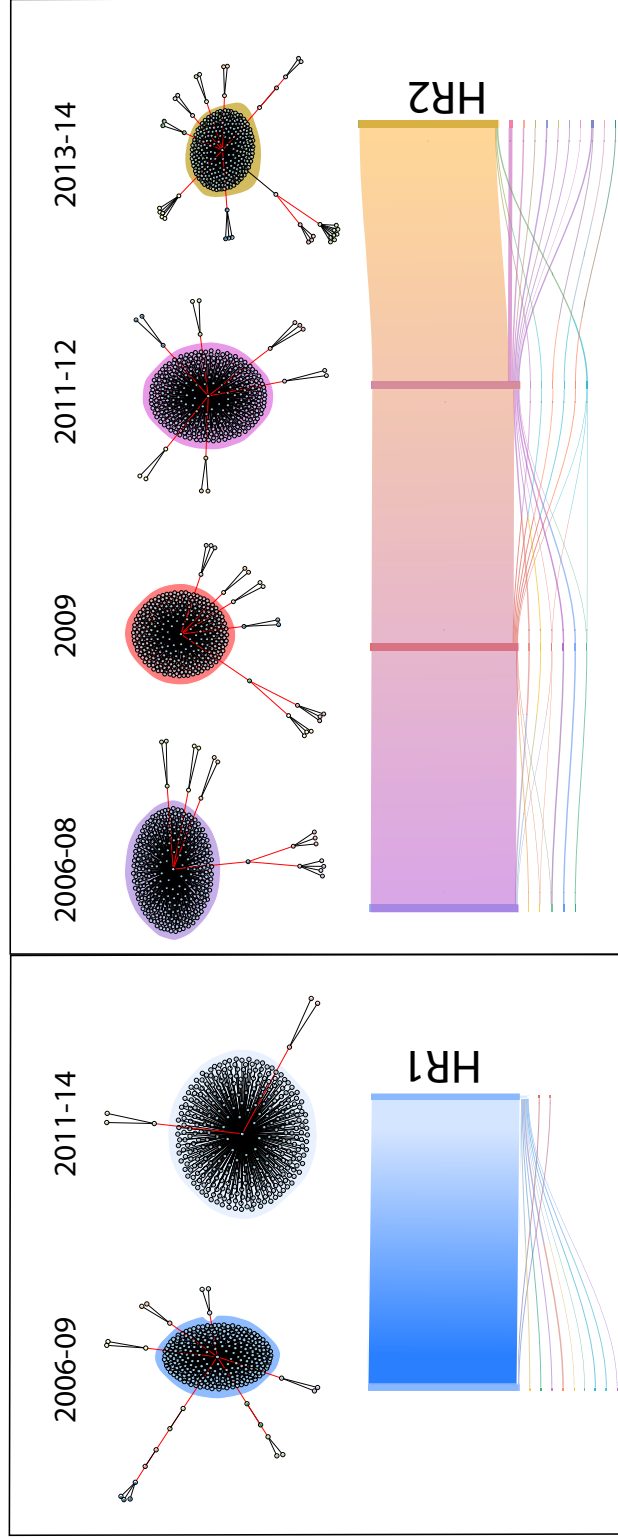
Figure 2: The module membership between network changing points. Two representative assembling hedgerows are depicted. In the top panel, species are grouped by module. The bottom panels visualize the flow of species between modules between changing points.
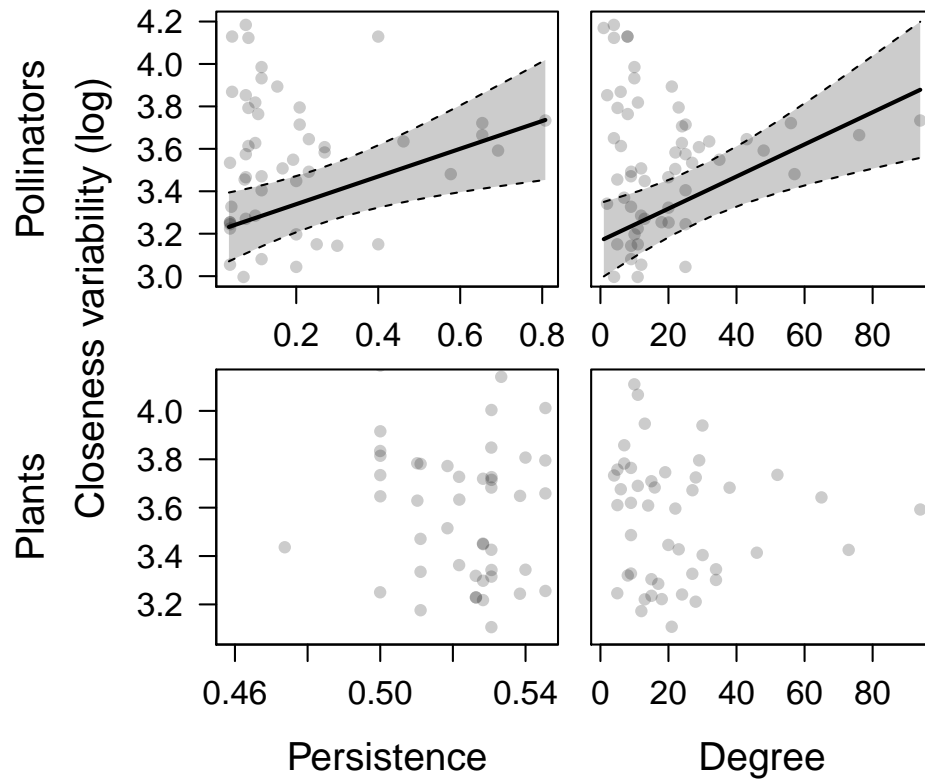
Figure 3: The variation coefficient of network position, as represented by closeness, plotted against pollinator persistence and degree. Persistence and degree were positively related to network position variability in pollinators, but unrelated in plants. Points represent means for each species across sites. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.
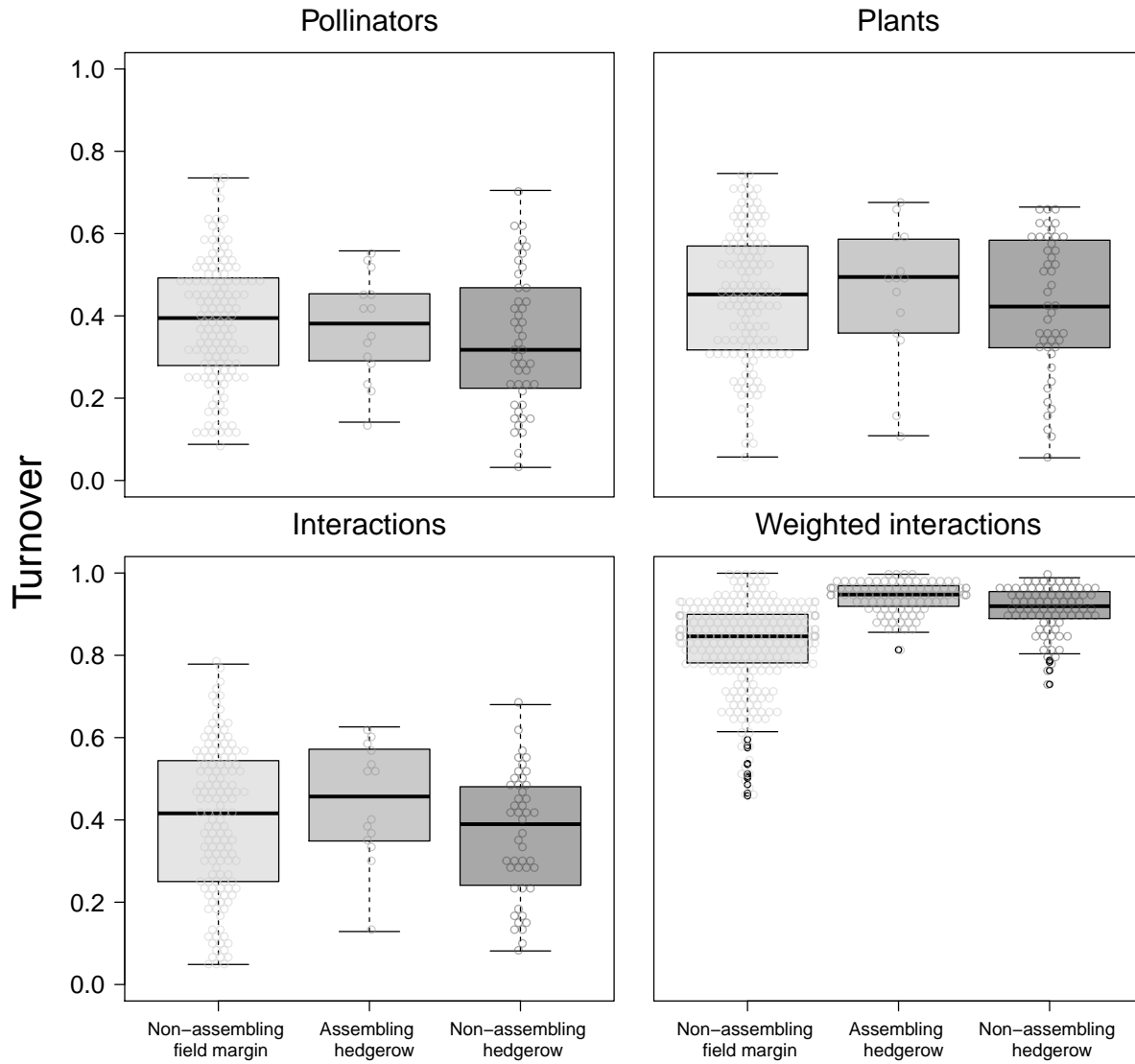
Figure 4: The species, interaction and weighted interactions turnover of plant-pollinator networks at non-assembling field margins sites, assembling hedgerows, and non-assembling, mature hedgerows. Rates of species and interaction turnover were similar between site types, though mature hedgerows has marginally significantly less pollinator turnover. However, when interactions where weighted by their similarity, both hedgerow types had higher turnover that unrestored field margins. Boxplots represent medians (black horizontal line) first and third quartiles (box perimeter) and extremes (whiskers).
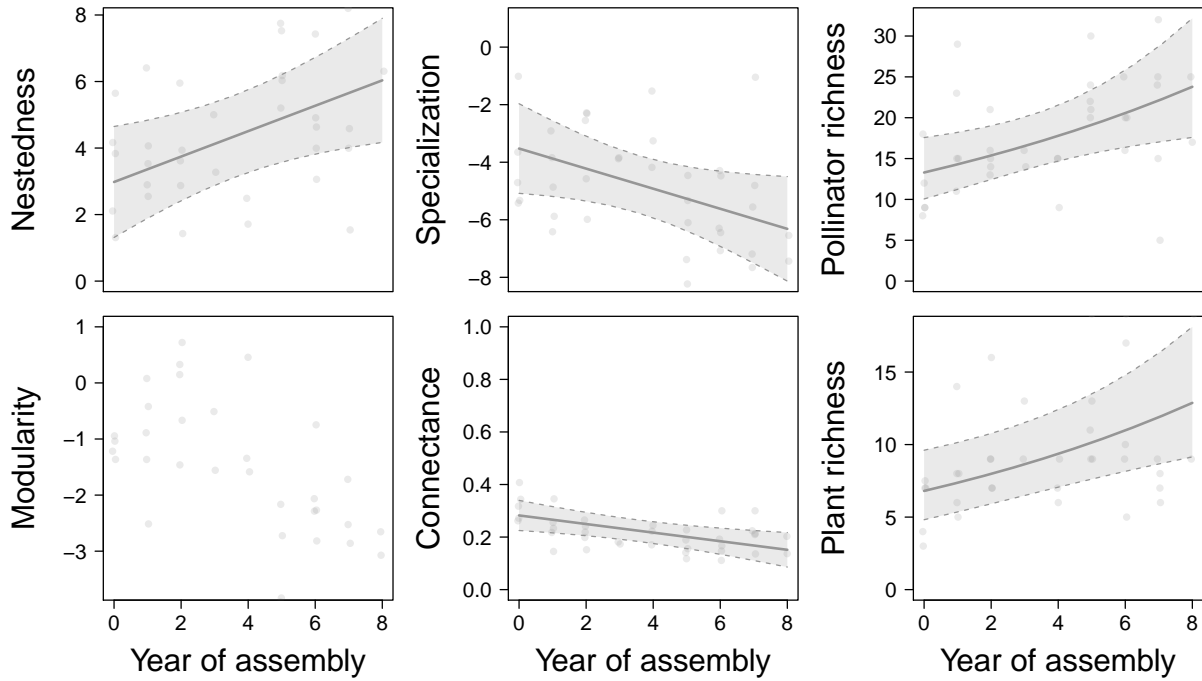
Figure 5: Nestedness, plant richness and pollinator richness increased as the networks assembled. Specialization and modularity remained consistent across years, while connectance decreased. The nestedness, modularity and specialization scores represent z-scores. Scores greater than ~ 2 or less than ~ -2 are significantly more or less structured than randomly assembled networks. Points are the metric value for each site at each year of assembly. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.
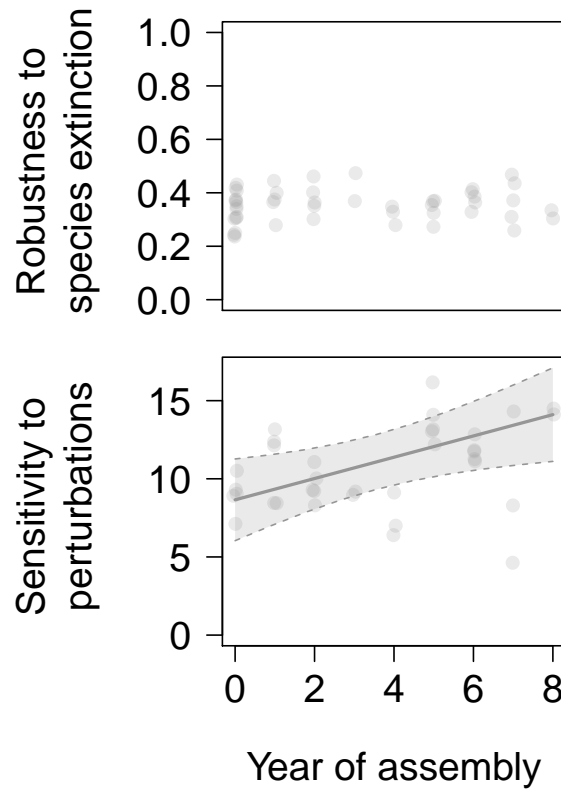
Figure 6: The robustness of networks to species extinction did not change with network assembly, but the sensitivity to cascading perturbations increased. The robustness to species extinction is measured by incrementally removing species by degree, though removing species by abundance did not yield qualitatively different results. The robustness of networks to cascading perturbations is measured as the algebraic connectivity, the second smallest eigenvalue of the Laplacian matrix. Points are the value for each site at each year of assembly. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.