The temporal assembly of plant-pollinator networks following restoration

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Abstract

TO BE RE-WRITTEN The structure of networks is related to ability of communities to maintain function in the face of species extinction. Understanding network structure and how it relates to network disassembly, therefore, is a priority for system-level conservation biology. We explore the assembly of plant-pollinator communities on native plant restorations in the Central Valley of California.

Keywords: changing points, temporal networks, hedgerows, species interactions, preferential attachment, mutualisms

Introduction

Global change has created a severe biodiversity crisis, and as species are lost, so are their interactions (Dunn *et al.*, 2009; Barnosky *et al.*, 2011). Because mutualistic interactions are essential for maintaining the diversity their component guilds of species, these systems are particularly at risk from coextinction cascades. The nature of these coextinction cascades depends on the interaction patterns within a community (Memmott *et al.*, 2004; Rezende *et al.*, 2007; Bascompte & Stouffer, 2009). Recovering the lost biodiversity and interactions through ecological restoration has become increasingly imperative, and a key restoration aim is to facilitate assembly of robust interaction networks (Menz *et al.*, 2010). We know little, however, about how to re-assemble interacting communities through restoration, or the process of ecological network assembly more generally.

The mostly widely explored mechanism of network assembly, preferential attachment (Barabási & Albert, 1999), predicts that a new species is more likely to interact with species that are already well-connected ("the rich-get-richer" principle, Barabási & Albert, 1999). In pollination systems — a particularly ubiquitous mutualism (Ollerton *et al.*, 2011; Klein *et al.*, 2007) — some studies have found support for this mechanism of assembly. Investigating the day-to-day, temporal assembly of a plant-pollinator network within a season, Olesen *et al.* (2008) found that new species tended to interact with already well-connected species, likely because these species are either more abundant or more temporally persistent (Olesen *et al.*, 2008). In addition, using a space-for-time substitution to study primary succession along a glacier foreland, Albrecht *et al.* (2010) found some indication assembly was occurring through preferential attachment. Network nestedness, a pattern of interactions where a generalist core interacts with both specialist and generalist species, increased as the community aged (Albrecht *et al.*, 2010). Increasing nestedness could result from a process like preferential attachment where specialist species attach to the well-connected, generalist core.

In contrast to the ordered network build-up described by preferential attachment, assembly can be punctuated by significant reorganizations of interactions (Peel & Clauset, 2014). For example, as new species are added, resident species change their interaction partners to minimize competition, or become extinct. Such significant reorganizations of interactions, or changing points, have been observed in networks responding to abrupt shifts in the behavior of interacters (Peel & Clauset, 2014). No studies, however, have examined whether changing points occur during ecological network assembly.

Understanding network assembly is particularly relevant to ecological restoration, which is essentially 'applied succession' (Parker, 1997, e.g.,). In pollination systems, the time since an area was restored has been shown to effect the structure of networks (Forup *et al.*, 2008a,b; Devoto *et al.*, 2012), suggesting interactions are evolving as the community develops. Understanding the mechanisms of network assembly will help to guide the restoration of particular communities.

Facilitating effective restoration of networks is particularly imperative in areas where species interactions provide essential ecosystem services, such as crop pollination. In intensively managed agricultural landscapes, the demand for pollination services is the greatest (Kremen, 2008). However, honey bees, managed extensively around the world to provide crop pollination, are in global decline (Neumann & Carreck, 2010; van Engelsdorp *et al.*, 2009). In addition, native pollinators, which have the capacity to provide sufficient crop pollination (Kremen *et al.*, 2002; Winfree *et al.*, 2007; Kremen *et al.*, 2004), are in short supply because these landscapes make poor habitats for pollinator populations (Kremen *et al.*, 2002). To ensure provision the continued provision of ecosystem services and curb biodiversity loss, effective restoration of pollinators and their interactions in agricultural landscapes is critical.

To promote pollinator services in agriculture, farmers are increasingly turning to the habitat restoration technique of planting strips of native plants along farm edges (hedgerows) to help provide habitat for pollinators without removing arable land from production. Hedgerows have been shown to augment the richness, abundance and trait diversity of pollinators in agricultural landscapes(Morandin & Kremen, 2013; M'Gonigle *et al.*, 2015; Kremen & M'Gonigle, 2015; Ponisio *et al.*, 2015). In addition, hedgerows promote the persistence and colonization of floral resource specialists (M'Gonigle *et al.*, 2015). Little is known however, about the assembly of the network following hedgerow restoration.

Using a long-term data-set of plant-pollinator communities assembling following hedgerow restoration in the highly simplified and intensively managed agricultural landscape of California's Central Valley, we explore the process of network development. We first determine whether the mechanism underlying network assembly is a smooth build up of interactions as would be predicted by preferential attachment, or punctuated by significant reorganizations of interactions (i.e., changing points). Even with changing points in interaction organization, networks could still be assembling via preferential attachment if the network reorganizations were primarily driven the by peripheral, temporally variable species while a stable, well-connected core of species still persists. We thus examine whether the species are most variable in their network position — and thus important contributors network reorganizations — are less persistent and connected species. Lastly, we examine whether networks are assembling toward predictable interaction patterns, and the ramifications for the robustness of the networks to species extinction and perturbation.

Materials & Methods

Study sites and collection methods

We surveyed plant-pollinator interaction networks of assembling hedgerows (N=5), as well as in two types of non-assembling communities to serve as controls: unrestored, weedy field margins (N=19) and established 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 comprised of intensively managed agriculture – primarily monocultures of conventional row crops, vineyards and orchards. Hedgerows we planted along field margins where they do not remove valuable land from production, and are ca. 3–6m wide and approximately 350m long and border 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 (Kremen & M'Gonigle, 2015; M'Gonigle *et al.*, 2015). The mean distance between monitoring sites was 15 km, and the minimum distance between sites of the same type sampled in the same year was 2 km. The entire area surveyed spanned almost 300 km^2. The crop fields adjacent to all sites were similarly managed as intensive, high-input monoculture.

Monitoring began in 2006 and continued through 2015. Sampling of the assembling hedgerows 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). 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 the placement of hives throughout the region 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 (representing 49 and 19 percent of records, respectively), the most abundant and effective pollinators in the system (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 taxonomists.

Quantitative networks were generative for each site through time. To account for the unequal number of surveys between years, the mean of the interactions between a pair of plants and pollinators across surveys within a year was used as a representation of the frequency of interactions.

Change point analysis

Identifying change points

We employed a change point detection method (Peel & Clauset, 2014) to identify fundamental changes in large-scale pattern of interactions of plants and pollinators. A change point is caused by a merge, split, fragmentation or formation of communities (also called modules or compartments). Change point detection methods have yet to be generalized to quantitative networks, so for this analysis we focused on qualitative (binary) networks. Following Peel & Clauset (2014), 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 community structure patterns at all scales in the network (Peel & Clauset, 2014). A network G is composed of vertices V and edges $E \subseteq VV$. 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 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 (Peel & Clauset, 2014). 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 (Peel & Clauset, 2014). We used 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 compare the fit of two models – one where a change point had occurred between two networks, and one where no change occurred – using posterior Bayes factors. 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 maximum of nine years of data. Lastly, to calculate a p-value for the Bayes factors, we use parametric bootstrapping to numerically estimate the null distribution (Peel & Clauset, 2014). The change point analysis was carried out using code published online by L. Peel. Analyses we 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 trails, and use a generalized linear model with Binomial error to test whether the probability of a change point occurring varied by site type. For the non-assembling hedgerows and weedy field margins, only sites with five or greater years of sampling was included in this analysis. All statistical analysis were conducted in R 3.2.3 (R Core Team, 2015).

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 the reorganization of interactions. Some species remain in relatively similar network positions through time, whereas others are more variable in their role and thus contribute more strongly to network reorganization. We test the that more persistent species with the highest degree are the most stable in their network position, as would be expected is the networks were assembling via preferential attachment.

We calculate species persistence as the proportion of the surveys a pollinator was observed. Species observed consistently within and between years are thus maximally persistent. Weighted species degree is calculated from interaction observations observed in more extensive data-set 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 (M'Gonigle *et al.*, 2015; Ponisio *et al.*, 2015). To represent the the variability of species within networks, we computed the coefficient of variation of weighted closeness at each site through time. Closeness describes the centrality of a species in the network by calculating path lengths to other vertices (species) in the graph. We used linear mixed models to test whether the variability of species closeness values was related to the persistence or degree of that species (Bates *et al.*, 2014; Kuznetsova *et al.*, 2014). We included random effects for species, as well as site. We focused on the pollinator species because the hedgerow flowers are planted and thus are not directly assembling. Because degree and persistence were strongly correlated, ($\rho = 0.84$, p-value $< 2 * 10^{-16}$), each explanatory variable was included in the model separately. Because a linear increase in closeness, as might be expected with assembly by preferential attachment, would lead to a high variability in closeness scores, we also test whether closeness increases through time.

Temporal changes in interaction patterns

Network structure

The 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., Olesen *et al.*, 2007) and nestedness (e.g., Bascompte *et al.*, 2006, 2003). In modular networks, interactions are insular, occurring within separate groups or "modules" more often than between modules. Communities in the network may fragment as the network assembles, enhancing modularity. Conversely, nested networks are like 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 (i.e., via preferential attachment), nestedness would increase through time. Lastly, if the network is accumulating specialist species or species are beginning to limit their interaction niche breath as the network assembles, this would lead to an increase in the network-level specialization (Blüthgen *et al.*, 2006). To test whether network modularity, nestedness 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.

We use NODF (weighted or unweighted) to evaluate network nestedness (Almeida-Neto *et al.*, 2008). NODF evaluates whether species with fewer partners interact with subsets of partners with which more connected species interact (Almeida-Neto *et al.*, 2008). To estimate modularity, we use a hierarchical clustering algorithm (Newman & Girvan, 2004; Csardi & Nepusz, 2006). We calculated standardized z-scores so that nestedness and modularity metrics could be compared between 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 the distribution of the interaction frequencies (Galeano *et al.*, 2009). Lastly, Network specialization was measured using H2, which estimate the deviation of the observed interaction frequency between plants and pollinators from a null expectation where all partners interact in proportion to their abundances (Blüthgen *et al.*, 2006). It ranges from 0 for generalized networks to 1 for specialized networks.

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Network robustness

Lastly, we test the changes in interaction patterns associated with network assembly affect the robustness of the network to species loss and to cascading effects. Following Memmott *et al.* (2004), we simulate the extinction of plant species the subsequent extinction cascades of pollinator species. Because the reproduction of plant species if facilitated by active restoration efforts, it is unlikely the extinction of pollinators 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. Plants species were eliminated based on their degree or abundance, and the number of pollinators that secondarily went extinct is calculated. The area below the extinction curve is used as a measure of network robustness (Dormann *et al.*, 2008).

We also explored how the robustness to cascading effects changed as community assembled, using algebraic connectivity— the second smallest eigenvalue of the Laplacian matrix (Fiedler, 1973)— as a proxy for network robustness (e.g. Gaiarsa et al., submitted). Algebraic connectivity was first used to describe spectral properties of complex graphs other than ecological networks, and it is related to how difficult it is to turn a network into completely disconnected groups of nodes, or species (Fiedler, 1973; Costa *et al.*, 2007), and also to flows in . The larger the algebraic connectivity, the more robust a network is to perturbations (e.g. Gaiarsa et al., submitted).

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 tests underwent at least one significant reorganization of interactions (Fig. 1). There were no consistent trends as to when change points occurred within assembling hedgerows or across all sites, except many site had changing points between year 2009 and 2011 (Fig. 1). In California, 2011 marked the beginning of a multi year drought. In the assembling hedgerows were not sampled in 2010, so disentangling whether the changing points are due to skipping a year of assembly or the drought is not impossible.

All five of the assembling hedgerows experienced changing points, whereas only 40% and 81% of non-assembling hedgerows and field margins, respectively, underwent significant interaction reorganizations. Assembling hedgerows experienced significantly more changing points than the non-assembling networks (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 that would effect assembling and non-assembling networks equally.

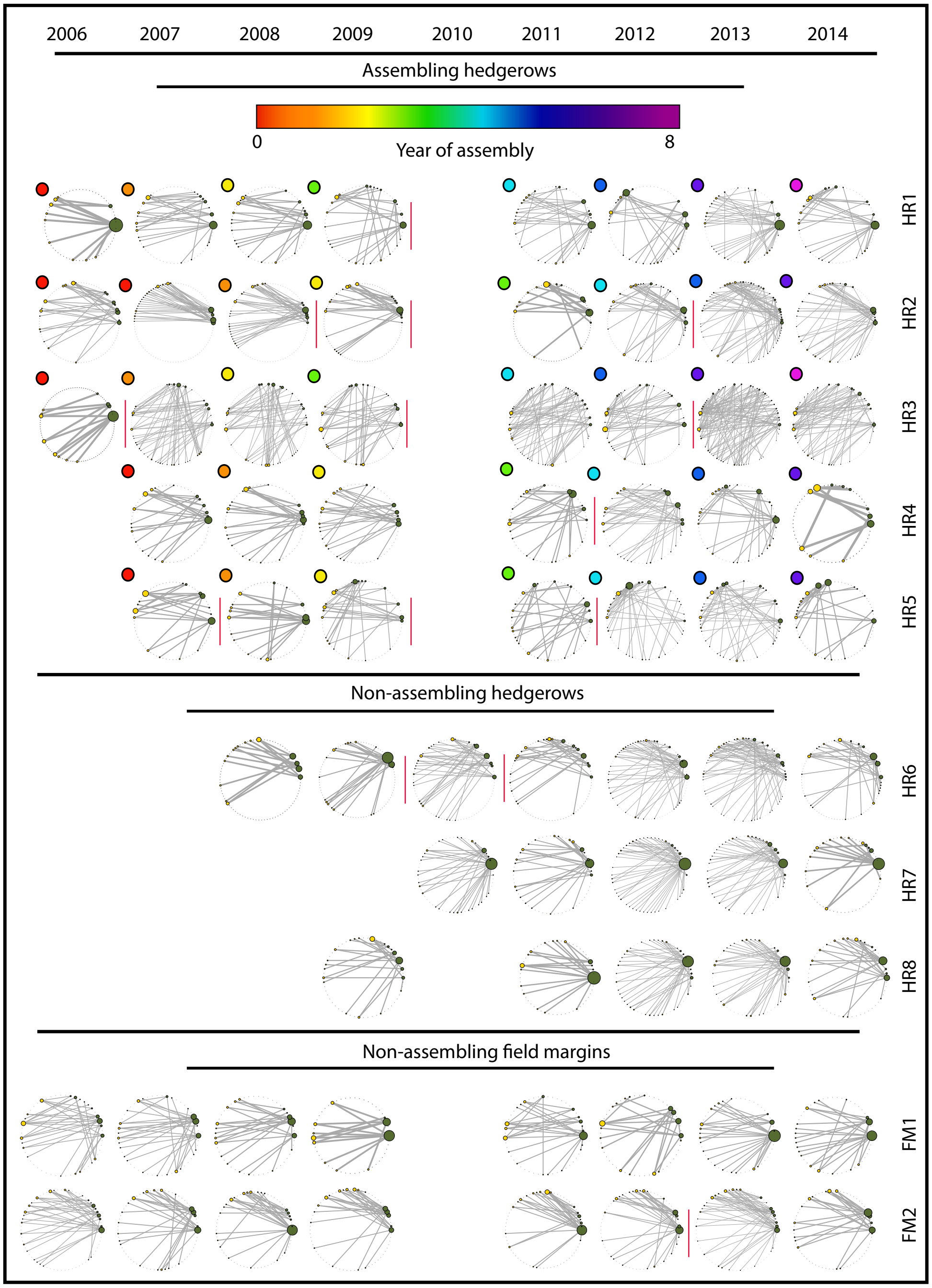

Figure 1: The network structure and changing points (vertical red lines) in assembling hedgerows and a representative sample of non-assembling hedgerows and weedy field margins. In each network, plants and pollinators are represented by green and yellow circles, respectively, weighted by their degree. Each species has has a consistent position in the network across years. In the assembling hedgerows, colored circles in the corner of each network represent the years post restoration.

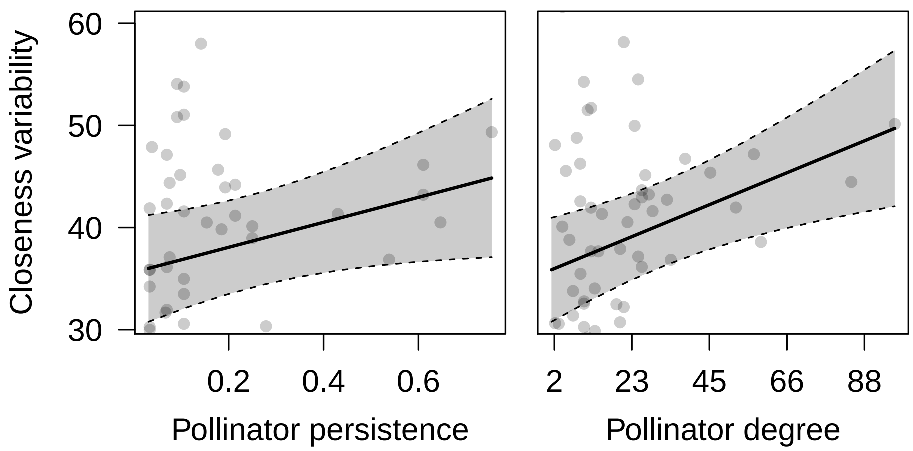

Figure 2: The coefficient of variation of network position, as represented by closeness, plotted against pollinator persistence and degree. Points represents means for each species across sites. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

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. (ADD STATS IF KEEPING RESULT).

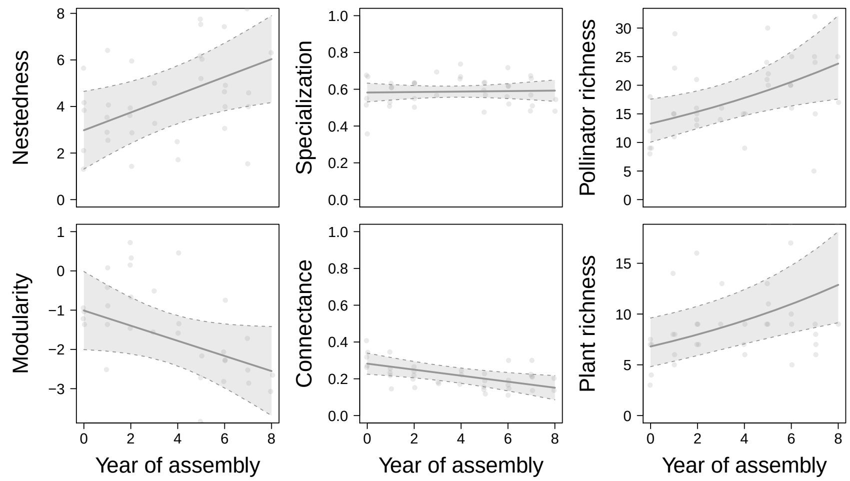

Figure 3: The change in nestedness, modularity, specialization and connectance as the networks assemble. The left panels represent z-scores. Scores greater than ~ 2 or less than ~ -2 are significantly more or less structured than randomly assembled networks. Points are the value for each site at each year of assembly. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

Temporal changes in interaction patterns

Network structure

Network nestedness significantly increased with assembly (estimate of the slope of nestedness through time $\pm$ standard error of the estimate, 1.834 ± 0.6142, p-value=0.022, Fig. 3). Modularity decreased (Fig. 3), though the slope was not significantly different from zero (estimate of the slope of modularity through time $\pm$ standard error of the estimate, -0.524 ± 0.295, p-value=0.124). Specialization remained relatively constant (estimate of the slope of specialization through time $\pm$ standard error of the estimate, 0.003 ± 0.015, p-value=0.827).

Network robustness

Assembly did not effect the robustness of the networks to species extinction when species where removed incrementally by degree (estimate of the slope of robustness through time $\pm$ standard error of the estimate, $6 * 10^{-5} \pm 4 * 10^{-3}$, p-value=0.987) or abundance (0.001 ± 0.003, p-value=0.65, Fig. 4).

In contrast, the robustness of networks to perturbation, as measured by the algebraic connectivity of the network, increased as the network assembled (estimate of the slope of robustness through time $\pm$ standard error of the estimate, 0.6814 ± 0.272, p-value=0.042, Fig. 4).

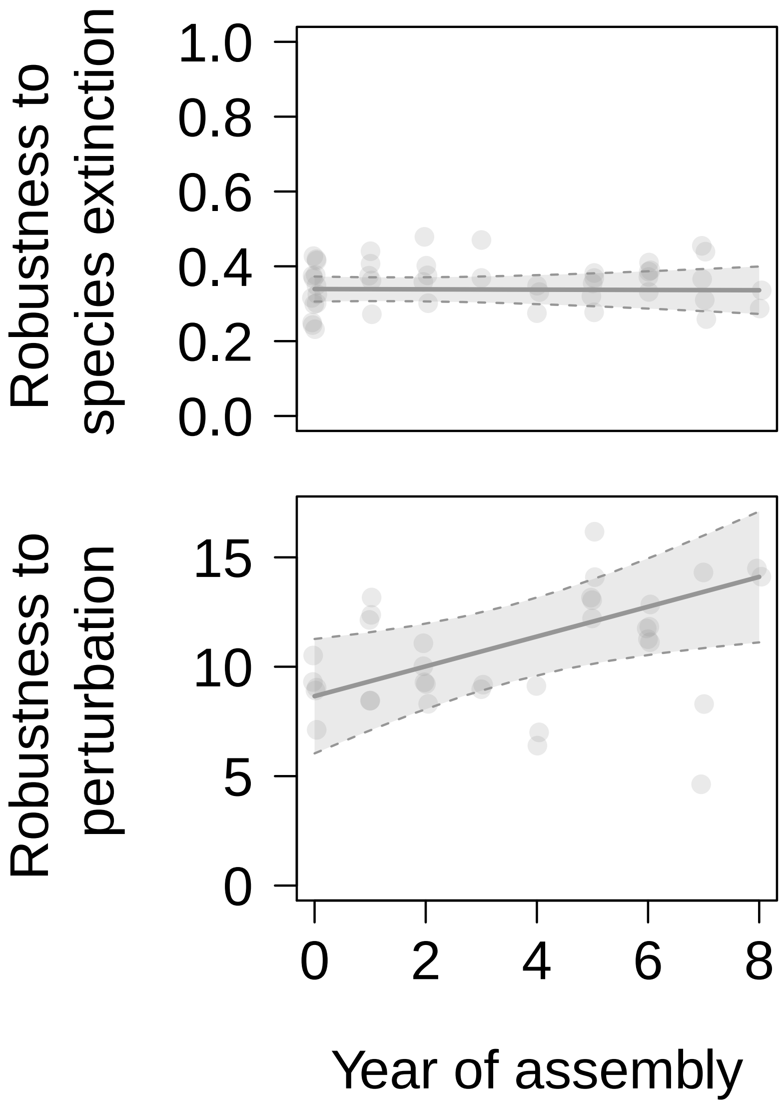

Figure 4: The robustness of networks to species extinction and perturbation. The robustness to species extinction is measured by incrementally removing species by degree, through removing species by abundance did not yield qualitatively different results. Points are the value for each site at each year of assembly. The solid line indicates the mean slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

Discussion

We show that the temporal assembly of plant pollinator communities following restoration do not occur through preferential attachment. Instead, the community seems to undergo through a critical internal reorganization with major changes in species composition and interaction patterns.

Changing points through time = more in the assembling communities than in the control ones, as would be expected given the species turnover.

Preferential attachment is the most widely accepted theory explaining community assembly in mutualistic networks. Communities assembling through preferential attachment are formed by a core of generalist species, to which new species arriving to the community interact with. Thus, communities assembling through preferential attachment exhibit an increase both in nestedness and in the overall level of species specialization, since specialist species are being added to the community. However, our changing point analysis results show that there is a critical reorganization in the interaction patterns as communities assembly, which contradicts the preferential attachment theory. Even though we encountered an increase in nestedness through time, specialization did not increase. Furthermore, this increase in nestedness could be explained by the increase in species richness. blablabla mechanistic models.

Other interesting result is that even though nestedness increased through time, modularity and connectance did not. Fortuna *et al.* (2010) suggest that at low connectance levels, mutualistic networks would present high nestedness and high modularity, while at high connectance levels networks would present low nestedness and low modularity. However, our results show the contrary: early communities presented low nestedness, smaller richness, and higher levels of modularity and connectance, while more mature communities presented higher nestedness, higher richness, and smaller modularity and connectance. SO blabla... XX Temporal overlap.

Evidence indicates that there is a positive relationship between abundance and diet breadth, with the more generalist species having higher abundances. Because of the high generalism, species more abundant also present higher degrees. Thus, we expected that more generalist species would be part of the network core. Surprisingly, the five most common species were also the ones that exhibited the most changes in interaction patterns. These species (names!) were always present in the periphery of the network. One hypotheses is that their high generalism allows them to explore the resources more broadly, allowing them to change their position in the network. XX mention the closeness variability and the species persistence.

High nestedness has been related to an increase in the robustness of communities to species extinctions because the core of generalist species would act as a buffer against species loss (REF). Similarly, communities with greater modularity would be more robust in general, because modules would act as a buffer against perturbation spreading and the pervasive effects of species loss. We expected that as communities assemble and species richness increase, communities would become increasingly robust to species loss. however, we found that robustness to species loss did not change through time. This is interestingly from the conservation biology point of view, because even early assembling communities seem to be as robust as more mature communities, despite the richness insurance hypothesis. However, communities are not only subjected to species loss, but also to other types of perturbations that can cascade through the network. Gaiarsa et al. (submitted) suggest using algebraic connectivity to explore how vulnerable ecoogical communities might be to cascading effects. Our results indicate that more mature communities are more robust to cascading effects than early on assemblages, and that this result is related to species richness. This migth be related to XX....

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