The temporal assembly of plant-pollinator networks following restoration

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Abstract

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. The assembling communities are paired with un-restored field margins (controls) and mature (non-assembling) hedgerows. We determine whether there are change points in the assembly of the communities where the network undergoes significant reorganization. We are also ask how are the individual species changing their interaction patterns? What does this mean for the topology/resilience of the network? We also attempted to adapt a financial model to mutualistic networks. Our biggest difficulty with this approach was to translate the price term to mutualistic systems. We explored a range of approaches, such as number of visits a species performs. However, it seems that financial systems cannot be easily translated to mutualistic systems. In addition, we used a Changing Point Detection Algorithm to assess weather the different communities went through a critical reorganization on their interaction patterns. We were able to identify some changing points in the communities, and also to explore some general patterns commonly used to describe ecological networks. For example, on the network level, networks become increasingly modular and less nested, whereas on the species level, species become more specialized, as resources become more reliable.

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

Introduction

- The structure of networks is related to ability of communities to maintain function in the face of species extinction.

- A key restoration aim is to facilitate assembly of robust networks; thus it is critical to study how restoration influences the assembly of plant-pollinator interactions.

- In general, however, few mechanisms of network assembly have been developed and analyzed.

- The mostly widely explored mechanism of network assembly, preferential attachment (Barabási & Albert, 1999), predicts that a new species (or node more generally) is more likely to interact with species that are already well-connected ("the rich-get-richer" principle, Barabási & Albert, 1999).

- To date, only two field studies have examined how networks assemble over time, often using space for time gradients.

- Olesen *et al.* (2008) was investigated day-to-day, temporal assembly of a plant-pollinator network within a season, taking advantage of the extreme seasonality of pollinator communities in Greenland. Olesen *et al.* (2008) found that within a season, the network assembly was similar to preferential attachment. New species tended to interact with already well-connected species, likely because these species are either more abundant or more temporally persistent.

- Studying primary succession along a glacier foreland, Albrecht *et al.* (2010) found a similar pattern where nestedness, a pattern of interactions where a generalist core interacts with both specialist and generalist species, increased as the community aged.

- Even non-successional temporal dynamics suggest a stable core of generalists persist despite high turnover of peripheral species (Fang & Huang, 2012; Díaz-Castelazo *et al.*, 2010; Alarcón *et al.*, 2008).

- In contrast to the ordered network build-up described by preferential attachment, assembly may be punctuated by significant reorganizations of interactions. 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 (Peel & Clauset, 2014).

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=XX) and established hedgerows (greater than 10 years since planting, N=XX). 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. The mean distance between

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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 mono-culture.

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 (Table XX). 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 XX and XX 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.

Change point analysis

We employed a change point detection method (Peel & Clauset, 2014) to identify funda-mental 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). 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). ADD NEWMAN PAPER. 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 fir 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.

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.

To further elucidate the nature of the change points, we examine the characteristics of the species that contributed the reorganization of interactions. To do so, we first generate dendrograms using the GHRG model before and after each change point. We then determined which species belonged to the "core" and "peripheral" network communities at each site. The "core" network communities contain the majority of species and are more basil than the more derived, less specious "peripheral" network communities. We next use a Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson & Walsh, 2013) to determine whether the species compositions of the species that belonged to the core and peripheral communities differed. We also test whether core or peripheral species had more variability in their species compositions (i.e., multivariate dispersion, Anderson *et al.*, 2011, 2006).

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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 topologies — modularity (e.g., Olesen *et al.*, 2007) and nestedness (e.g., Bascompte *et al.*, 2006, 2003). Modular community 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, 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.

Network robustness

Lastly, we test the changes in interaction patterns associated with network assembly affect the robustness of the network to species loss. 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 effect plant populations in the

hedgerows. However, plants ceasing to bloom, for example in response to drought, will likely effect 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.

Results

Discussion

Acknowledgments

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