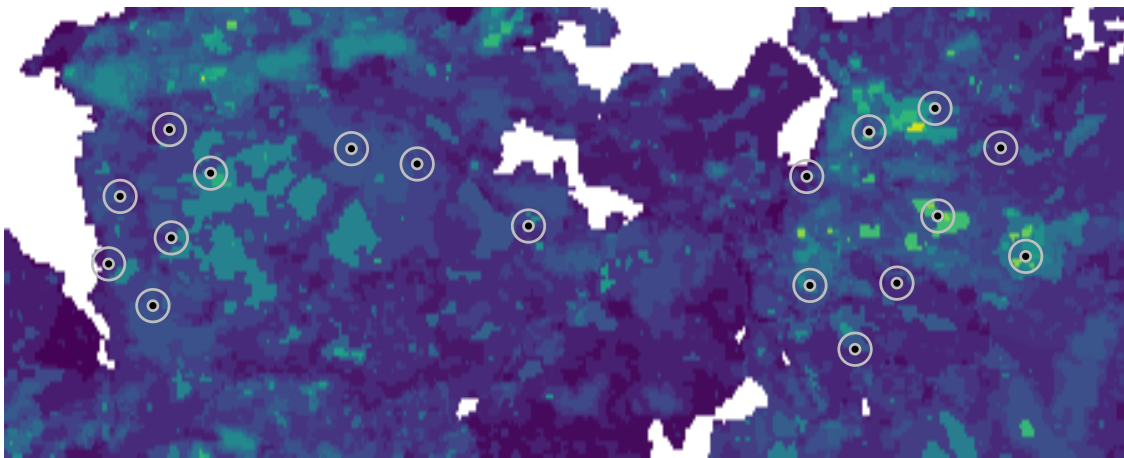# Workflow and detailed analyses for: "Interaction flexibility and pyrodiversity interact to increase pollinator population resistance"

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1 Overview

I examine the whether pyrodiversity enhances the resistance of plant-pollinator communities and pollinator populations using a variety of methods including 1) calculating metrics for describing network topology 2) interaction turnover, 3) network role variability and 4) extinction simulations. I am committed to reproducible science and all analytical code will be maintained on github, along with this write up.

The entire analysis is executable from the main.sh file. All of the packages needed to run the analyses are listed in the packages.sh file. All R scripts were run in v3.5.3. Navigate to the analysis folder within the github repo (Yosemite) then the main.sh file can be selected and run in terminal. This will somewhat helpfully print the results of each analysis and re-create any accompanying figures.

I will walk through each the main script for each analysis individually. I also outline all of the decision points for each of the analysis.

2 Data Prep

In analysis/data the dataPrep.R script creates all the data structures needed for the analyses. It references the raw data, however, so all needed files are in the github repro and this file cannot be run.

2.1 Decision points

1. Drop all non bees. Rational: non-bees not identified to species with the same rigor as bees. Also, life histories are less well understood, and bees are the more dominant pollinator in this system.

2.2 Pyrodiversity

To estimate pyrodiversity, I developed a metric in collaboration with Kate Wilkin to quantify the diversity of the fire histories in relation to fire frequency, age, extent and severity experienced in an area. This metrics was published in our previous publication (Ponisio *et al.*, 2016b). We obtained fire history data of our study area, dating back to 1984, from Yosemite National Park and the United States Forest Service (van Wagtendonk *et al.*, 2012; Miller, 2012; Yosemite National Park, 2012). Each fire digitization contains rasterized values of burn severity (Miller & Thode, 2007). Fire season, another component of fire history, was not directly considered. There was, however, little variability in fire season within any one fire, and most fires occurred in different months. Thus, season is indirectly included in the identity of each fire.

To estimate pyrodiversity, we evaluated the uniqueness of the fire history of each raster cell $(30 \text{ m})^2$ resolution. We first created categories of fire severity within a fire (Miller, 2012). For each raster cell, we then used the sequence of fires and the severity of each of those fires to define unique fire histories. We identified 135 unique fire histories in the basin. To calculate the pyrodiversity score, raster cells received different categories if they differed in any aspect of fire history; for example, if they were burned by the same fire but at different severities, or if they were burned by different fires, even if at the same severity. Pyrodiversity was then calculated as the Simpson's diversity of fire history categories (the compliment of the sum of the squared proportion of each fire history category) around a monitoring plot within 150 m.

Pragmatically, to calculate pyrodiversity, I combined the cell values of rater layers into a single character string. I then converted those strings to categories such that each unique fire history experience by a cell would be a unique category.

These calculations were done for the the previous publication so the .Rdata files are in the github repo, but not the code, specifically.

3 Network metrics

Within the analysis/networkLevel folder, the metrics.R script runs calculates the network topology metrics. The step to this analysis are 1) randomize the interactions within communities, 2) calculate network metrics, 3) calculate z-scores for network metrics, 4) use linear mixed models to estimate the relationship between pyrodiversity and network metrics.

The analysis begins be calculating null models by constraining of a connectance as developed by Deigo Vazquez. The algorithm was described as follows: "The algorithm randomized the total number of individual interactions observed in the original interaction matrix, F. To this end, the algorithm first created a binary matrix, assigning interspecific interactions according to species-specific probabilities, requiring that each species had at least one interaction. As in Vazquez et al. (2005b), the species-specific probabilities were proportional to species' relative abundances (probabilities are in fact approximately proportional and not equal to relative abundances because of the requirement that each species receives at least one interaction; this requirement causes probabilities to deviate from relative abundances, especially for rare species). Once the number of filled cells in the original matrix was reached, the remaining interactions were distributed among the filled cells, so that connectance in the original and randomized matrices was the same." (Vázquez *et al.*, 2007, , page 1122-1123)

I then used the bipartite package to calculate metrics related to functional redundancy and complementarity. Mainly, partner.diversity.LL" (plant Shannon's partner diversity), "partner.diversity.HL" (pollinator Shannon's partner diversity), "functional.complementarity.LL" (plant complementarity, based on (Devoto *et al.*, 2012)), "functional.complementarity.HL" (pollinator complementarity, based on (Devoto *et al.*, 2012)), and "links.per.species" (average for plants and for pollinators). Any metric calculated by bipartite can be used however.

For each network metrics, I then examined the effect of pyrodiversity and drought using linear mixed models. The equation for the models was:

$$y_{i,j} = \alpha_j + \beta 1 * pyrodiv_j * drought_i + \epsilon_{i,j}$$
$$\epsilon_{i,j} = N(0, \sigma_\epsilon) \tag{1}$$
$$\alpha_j = N(0, \sigma_\alpha)$$

Where $y_{i,j}$ is the network metric from the ith sample round of the jth site, and drought is an indicator variable that is 1 in the extreme drought year and 0 otherwise. $pyrodiv_j$ is the pyrodiversity of the jth site. α_i is the random intercept for site.

The figures are produced by running the *plotting/networkLevel_mods.R* script.

3.1 Decision points

1. which metrics best represent redundancy and complementarity? There are a plethora of metrics to chose from. I decided on the most direct metrics developed primarily by (Devoto *et al.*, 2012) for complementarity, and following Kaiser-Bunbury *et al.* (2017), the partner diversity (i.e., generalization) for redundancy and H2 for reciprocal specialization. I considered nestedness as a metric of redundancy, but none of the networks were significantly nested.

4 Community resistance

In the *analysis/networkLevel* folder, the robustness.R script runs the extinction simulations (robustness is the term for resistance to species loss in the network world). Plants are removed sequentially based on their abundance before the increase in drought intensity (from lowest to highest). The pollinator species without

any plant partners left go secondarily "extinct". I modified the second.extinct function from bipartite and then slope.bipartite to calculate the area under the co-extinction curve (Memmott *et al.*, 2004).

To generate the potential network, made a vector of all the plant species a pollinator was ever observed visiting. I then filled each network, adding a 1 in a cell if the pollinator was ever observed visiting the corresponding plant.

The figures are produced by running the *plotting/robustness.R* script.

4.1 Decision points

1. What order to drop plant species to simulation a drought-like event? Sensible options: from least to most degree or abundance calculated from network data or veg survey data. Veg survey data is based on the number of flowers vs. individuals, which is a bit misleading in terms of drought susceptibility. Dropping species by degree (sum of unique bee interaction partners at each site) and abundance (sum of total interactions) were qualitatively similar in terms on the results of the linear mixed models. Rational: drop species by abundance because that is the most like a drought perturbation (more likely to loose the least abundant first).

5 Population resistance

In the *analysis/variability* folder, the steps to calculating population resistance are as follows: 1) calculate the null communities (again using vaznull) in order to standardize partner "β-diversity" (nulls.R), 2) calculate partner turnover (partner.R), 3) calculate role variability (pca.R), then 4) the change in abundance of each pollinator species at each site (deltaAbund.R) and then the linear mixed models. To test whether the variability metrics were indeed an accurate representation of variability, I generated communities with no to high variability and examined the values of the variability scores (*test$_f$lex$_m$ets.R*). The variability metrics for partners and roles were small when the interaction matrices generated had little interaction turnover, and high with high interaction turnover, as intended.

Dissimilarity estimates can be affected by the total number of species/interactions sampled at a site (e.g., Chase *et al.*, 2011). So I used null models to estimate the deviation of the observed β-diversity from that which would be expected under a random community assembly process, with constrained connectance and approximately constrained marginals. I then calculated the fraction of randomly assembled communities with dissimilarity values less than (and half of those equal to) that of the observed community. I used this fraction as a "corrected dissimilarity score" for our observed data. Corrected dissimilarity values near one indicate that the observed communities exhibit more species turnover between sites than expected under a random assembly process while values near 0.5 indicate that the observed communities exhibit levels of turnover more in line with the null expectation.

The general equation for the models was:

$$
\begin{aligned}
y_{i,j} &= \alpha_i + \beta_1 * pyrodiv_j * partnerVar_i + \beta_2 * pyrodiv_j * roleVar_i + \\
&\quad \beta_3 * meanRole_i + beta_4 * deltaFlowers_j + \epsilon_{i,j} \\
\epsilon_{i,j} &= N(0, \sigma_\epsilon) \\
\alpha_j &= N(0, \sigma_\alpha)
\end{aligned}
\tag{2}
$$

Where $y_{i,j}$ is the log ratio abundance from the ith species at the jth site. $pyrodiv_j$ is the pyrodiversity of the jth site, $partnerVar_i$ is the partner variability of the ith species, $roleVar_i$ is the network role variability of the ith species, $meanRole_i$ is the average network role (mean PCA1 score) of the ith species, and $deltaFlowers_j$ is the change in floral richness of the jth between the years 2013 (drought) and 2014 (extreme drought). α_i is the random intercept for pollinator species.

5.1 Decision points

5.1.1 Partner turnover

1. Null models: Constrain alpha diversity and not the number of individuals in the null models for calculating the expected β-diversity. Rational: Little difference in the results when different null models are used (Ponisio *et al.*, 2016a)

2. Turnover calculation: weight interactions by their "abundance" vs. binary interactions and use Chao as a dissimilarity estimate. Rational: turnover in the number of interactions is ecological meaningful and a part of interaction flexibility. Chao (Chao *et al.*, 2005) is density invariant, replication invariance, and monotonic.

3. Turnover calculation: calculate the corrected interaction turnover by using the Chase et al. (calculating the fraction of randomly assembled communities with dissimilarity values less than and half of those equal to that of the observed community). Rational: calculating the corrected turnover using z-scores (the alternative) was not qualitatively different (Ponisio *et al.*, 2016a).

4. Species-specific turnover calculation: the CV of the turnover across all sampling periods (both through time at a site and across sites) in 2013. Rational: 2013 is our baseline, pre-extreme drought data point. Interaction flexibility can be both within a season (at the same site through time and different plant come into and out of bloom) and across sites (re-shuffle the plant community composition). Other options, 1) cv corrected by samples size, an unbiased estimates when sample sizes are low. Ruled out because sample size is not particularly small. The pvalue for the interaction between partner variability and pyrodiversity becomes marginal (0.06), but this does not substantially change the results (unless you are very militant about pvalues). 2) sd. Ruled out because does not control for mean.

5.1.2 Role turnover

1. Role quantification: chose "rarefied degree", "weighted.betweenness", "weighted.closeness", "niche.overlap", "species.strength", "d" as representatives of a species network role. Rational: These metrics cover a range different aspects of a species' role, though there is some overlap. Choose different similar metrics did not change results qualitatively.

2. Role variability calculation: CV of pca1 scores for each species across samples in 2013. Rational: CV measures the variability while controlling for the mean of values. SD and corrected CV rules out for same reasons as with partner variability. pca1 is the primary axis for differentiating roles. Interaction flexibility can be both within a season (at the same site through time and different plant come into and out of bloom) and across sites (re-shuffle the plant community composition).

5.1.3 Linear mixed models

1. drop two species with really extreme values of role flexibility. Rational: from examining their interactions, they seem to have occupied basically the exact same role in every network they were observed in (though interestingly different species). The model diagnostic look a lot better without including them. In addition, the model results are mostly consistent. Removing them makes the coefficient for pyrodiversity less negative, as expected by removing an extreme value that is shaping the slope.

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