Predictive phylogenetic and trait associations in space, but not in time, in a tropical flowering community.

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Abstract:

Keywords:

Introduction

Explaining the co-occurrence of related species in diverse assemblages is a persistent challenge in community ecology (Colwell, Fine, Brown). The balance between differences in species mean fitness and niche overlap lead to observed patterns of presence within local assemblages (Chesson, Adler, Kraft). In tropical plant assemblages, the observed co-occurrence of many congeneric species suggests that niche-based (Swenson, Cavender-Bares), non-equilibrium (Jetz), and neutral processes (Hubble) contribute to the formation of local assemblages. Co-occurring species can partition resources in time or space, thereby reducing niche overlap and increasing local alpha diversity. The complex interplay between evolutionary history, morphological adaptations and biotic interactions makes it difficult to document the presence of non-random associations among species, and even more difficult to disentangle the relative predictors of local co-occurrence.

To further complicate the challenge of identifying the mechanisms underlying species interactions, the quantitative basis for disentangling abundance, interaction and environment is unclear. Species occur at different frequencies, leading to uneven patterns of distribution solely by chance. Even within suitable habitat, these frequencies are modulated by temporal and spatial heterogeneity due to incomplete detection. Identifying the signature of current versus past niche partitioning remains murky, with extensive debate on the structure (kraft), strength (morlan), and even direction (mayfield) of evolutionary history on species interactions. Statistical analysis of these mechanisms fall largely into randomization or model-based approaches. Randomization approaches seek to identify a neutral model of species co-occurrence as a baseline, and then compare a given test statistic to that underlying model to determine whether the observed configuration species is different from expectations (webb, Cavender-bares review). The challenges of the approach are well documented (), but lack of hypothesis testing(), struggles with non-model formulation(), no estimate of uncertainty(), and a reliance on arbitrary significance levels () are all limiting. In contrast, model-based approaches provide explicit hypothesis, clear structure, and can be used to estimate new data while capturing both process and observation uncertainty (ives). In particular, phylogenetic models of covariance in species occurrence have been used to identify non-random associations within assemblages (helmus and ives), among geographic areas(pearce), and within interacting guilds (rafferty and ives). The drawbacks are a complicated model fitting process, the need for substantially large datasets, and difficulty in model selection among competing hypothesis.

In flowering plants, the timing of flowering can lead to strong interactions among species vying for pollination resources. Competition among closely related species should lead to low co-flowering, thereby reducing heterospecific pollen transfer and potentially negative impacts of hybridization. Alternatively, co-flowering among related species could lead to pollinator facilitation, in which the local abundance of resources attracts many pollinators, leading to increased fitness for all species.

Here we analyze a multi-year dataset of co-flowering and pollinator overlap among related Gesneriaceae species in a diverse cloud-forest assemblage. Combining data on floral morphology, evolutionary relatedness, and observed pollinator visitation, we test: 1) Whether closely related plants tend to be visited by similar pollinators, 2) Whether closely-related plants tend to flower at similar locations and times, 3) Whether phylogeny, trait and biotic interactions can be used to predict flowering timing in a diverse assemblage. The first two goals are linked, both often analyzed separately. A phylogenetic signature of interactions would only appear in the pattern of co-flowering if closely related plants tend to be visited by similar pollinators. Therefore, to establish a phylogenetic hypothesis for community structure, there needs to be both non-random associations among plants in their pollinator visitation patterns, and a non-random association in their co-flowering timing. Given the variable nature of flowering timing, the final goal of predicting new data is key in generalizing our findings. Using an extensive dataset from Northern Ecuador, we withhold a portion of the data to use as validation for out candidate models of flowering associations. We then compare the ability of phylogenetic, trait and pollinator interactions to fit both the observed data, and the withheld data to assess non-random patterns of co-flowering.

Methods

* Data Collection
  + Transects
  + Cameras
  + Traits
  + Phylogeny
* Pollinator overlap and relatedness
  + Pagels Lambda
  + Niche Overlap
* Models of co-flowering

To identify non-random patterns of association among co-flowering species, we follow the general philosophy of phylogenetic generalized linear mixed models presented in (Ives & Helmus, 2011; Rafferty & Ives, 2013). Our quantitative approach, 1) estimates co-flowering occurrence based on models of phylogeny, trait, and interaction co-variance, 2) estimates both the strength and uncertainty of co-flowering, 3) generates testable predictions for model comparison.

* + Baseline model

The simplest model is each flowering observation for a plant species (i), recorded on transect (j), during month (k) is a species-specific intercept ( for all sites, months and years. This is a model of species prevalence and does not take into account any ecological difference among sites, or months within each site.

Rather than modeling the intensity of flowering timing, we prefer to simplify the problem by using a Bernoulli to estimate a probability of flowering at a given time and transect. To eliminate the effect of a small number of plants leading to a positive observation, we first filter the data to eliminate flowering observations with fewer than X% of the total flowering observations from the year. The result can be thought as “peak flowering”, but we use the term flowering for clarity.

Models of flowering covariance

The goal of this analysis is to determine whether the remaining variation in flowering shows covariance with respect to phylogenetic, trait, or biotic distances among species. To model this interdependence, we add an additional error term (e), which is a multivariate normal draw for each species, site, and month combination, following Ives (2011).

The covariance among species is a function of the distance among plant species (D), the strength of covariation ( and the decay in covariance ( with distance. The strength of covariation can range between 1 and 0. As approaches 0, the equation reduces to the matrix identity, resulting in no covariance among species. The distance matrix D is a square matrix containing the similarity among species in phylogenetic, trait, or biotic interactions. For phylogeny, we use the cophenetic matrix to measure the relatedness among individuals. For traits, we use the Euclidean distance among species in corolla morphology (see trait data). For interactions, we use the mean similarity in partner choice (see inferring species interactions).

* + - We have intentionally left out elevation and julian day as a predictor of co-flowering. The models of covariance outlined below describe the correlation in intensity of flowering among sampling periods. If we use elevation or julian day, for example as a proxy of environmental conditions, the phylogenetic and trait co-variance will be captured by the variation in response to date or location. In practice, it is not possible to differentiate the phylogenetic effect of the timing of flowering, versus the phylogenetic effect on co-occurrence leading to different flowering times. Both parameterizations represent changes among sampling periods.
  + Models of Covariance for phylogenetic and trait distance
    - Attraction
    - Repulsion
  + Model evaluation
* Results
* Figure 1
  + Conceptual: Co-flowering competition and facilitation with raw data, flowchart to show how data comes together
* Figure 2
  + Pollinator niche overlap matrix
* Figure 3
  + Discrepancy in covariance models and observed data
* Figure 4
  + Discrepancy in covariance models and predicted data

Discussion

Analysis of species communities tend to focus on species occupancy as the primary window into mechanisms of co-occurrence. Fewer studies have evaluated the importance of species interactions as mediating patterns of co-occurrence at local and regional levels. In temperate systems, the strong environmental filter on the timing of flowering may limit phenological variability, even if it minimizes reproductive fitness due to decreased pollination services. Unlike temperate systems, tropical phenology is presumed to be less constrained by annual environment variation. While there are considerable environmental fluctuations during the year, the more stable climate may reveal interactions among co-occurring species.