Coevolution and the structure of mutualistic networks

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**Abstract:**

Both ecologically and evolutionarily, mutualisms represent one of the most influential of all biological interactions, with fundamental consequences for the evolution and maintenance of biological diversity (Thompson 2005, Bascompte). Pair-wise interactions between mutualists are embedded in larger networks of interacting species, and understanding how natural selection operating at the level of a population scales up to shape the interactions of the entire community has implications for understanding how these communities come together and fall apart. There are different hypotheses for the role of traits in governing the assembly of mutualistic communities () and the contribution of coevolution and neutral processes to the evolution of these traits (Vazquez). Using a simulation-based approach, I will examine the effect of different evolutionary scenarios and trait linkage rules on the topologies of mutualistic networks. I will simulate character evolution on phylogenies representing different modes of coevolution and contrast them with neutral evolutionary scenarios. Using the simulated traits I will build interaction networks by employing different linkage rules to determine the frequency of interaction between mutualists, and calculate metrics to describe the topologies of the networks. I will address the following questions: 1) does coevolution leave a distinct mark on network topology distinguishable from neutral evolution? For example are tightly coevolved networks more modular than communities not influenced by coevolution? 2) do different modes of coevolution (tight coevolution coupled with co-speciation vs. coevolution without co-speciation) give rise to unique network structures, and 3) do different linkage rules (complimentary trait matching, barrier traits or neutral interactions) influence network topology?

**Background:**

In a network analysis, plant-animal communities are modeled as nodes in a bipartite or two-party network, linked by their interactions. Network-based metrics have helped uncover a number of predictable patterns in mutualistic communities that have been attributed to coevolution including nestedness of interactions (where specialists interact with a subset of the species that generalists interact with) ([*7*](#_ENREF_7)), weak asymmetric links (specialist plants are visited by generalist pollinators, and vice versa) ([*8*](#_ENREF_8)) and modularity (the network can be separated into sub-units or “modules” in which species interact more inside than outside their respective sub-units) ([*9*](#_ENREF_9)). Particularly, Olesen et al. (9) suggested modules should be regarded as coevolutionary units, in which reciprocal selection within a module leads to trait convergence in unrelated species.

Coevolution is a key process producing and maintaining complex networks of interacting species (Ehrlich & Raven 1964; Thompson 2005) and there are different hypotheses regarding the coevolutionary process. The first co-evolutionary hypothesis suggests there is high species-level interaction specificity leading to strict-sense coevolution and tight co-speciation and the perfect congruence of interacting lineages (Farenholz 1913). In this scenario, speciation of one interacting species (e.g. the plant) drives speciation of the other (e.g. pollinators, seed dispersers). This hypothesis has been extensively criticized (e.g. Page et al. 1996) and even obligate mutualisms have been shown to deviate from its predictions (fig-fig wasp, yucca-yucca moth, oil producing orchids andEuglossine bees).

The second evolutionary scenario suggests trait convergence is the result of natural selection honing the complementarities of traits involved in mutualistic interactions (e.g. corolla tubes of plants and the length of pollinator tongues/proboscises). Mutualisms accumulate phylogenetically related and unrelated species over time as species converge through natural selection on similar traits, leading to trait convergence without co-speciation. This pattern of trait convergence is often observed in mutualisms, such as patterns of fruit design in unrelated plant species (Jordano 1995), color patterns in cleaning fishes (Cote 2000), oil production by orchids (Stantiago).

Recently, models of network coevolution have explored the effect of evolution and coevolution on the topology of networks (Paulo, Nusimer). There has been little exploration, however, of whether the structures observed in mutualistic networks could also be produced by neutral processes (Vazquez). Interacting mutualistic species will experience the same biogeographic and climatic events that may cause allopatric divergence in both lineages as a mutualistic interaction spreads across the landscape (Smith et al., 2008). Additionally, trait evolution is limited by phylogenetic constraints (e.g.) and thus patterns of co-speciation and trait convergence and arise by purely neutral processes.

**Simulation plan:**

**Step 1**: **Simulate tree topology and character evolution**. Phylogenies will be simulated with a birth-death process with a set tree age, number of species and extinction and diversification rate. We used four combinations of mutualistic partner phylogenies and trait evolution:

a) Coevolution and co-speciation: the phylogeny and trait evolution of mutualisms are identical. This scenario represents the most extreme case of coevolution where mutualists co-speciate and coevolve. One phylogeny and trait evolution through Brownian motion is simulated and used for both mutualists.

b) Coevolution without co-speciation: the trait evolution of one mutualists tracks the evolution of the other but speciation occurs independently within each of the trees. To represent this scenario the phylogenies of the mutualists will be simulated independently. The traits of one of the partners are simulated using Brownian motion. The traits for the other partner will be simulated by sampling from the traits of its partners and than using those traits as multiple optima in an Orstein-Uhlenbeck process.

c) Co-speciation without coevolution: the tree topologies of the mutualists are similar, but the traits are not co-evolving. This represents a case where an environmental factor is driving speciation leading to geographic structuring. We simulate a single tree for both mutualists and evolve traits independently on the trees by Brownian motion.

d) Neutral evolution: The phylogenies and traits of the mutualists evolve independently.

**Step 2**: **Define interactions between species using linkage rules**. We used the traits simulated in the previous step to define the interactions among mutualistic partners using different linkage rules:

a) Complimentary traits: The probability of interaction is defined by the amount of trait overlap in the range of acceptable traits of each of the species. The traits simulated in the previous step represent a range instead of a single trait value.

b) Barrier trait: If the trait of the higher trophic level mutualistic partner is greater than the trait of its partner, the species interact with probability = 1.

c) Neutral trait: all species can interact with probability = 1.

**Step 3**: **Create Fundamental and Ecological interaction matrices**. We used the interactions determined by the linkage rules to create two realizations of each interaction network:

a) Fundamental: the interaction network where the probability of two species interacting is based on linkage rules alone.

b) Ecological: a realization of the fundamental network where the abundance of species is considered. The abundances of species will be drawn from a log-normal distribution with mean and standard deviation equal to one. The probability of interaction is determined by the abundances of the species in question and their trait overlap from the fundamental network.

**Step 4: Evaluate interaction structure**. We calculated network-level metrics of each of the interaction networks produced in step 3. We focused on network nestedness and modularity, metrics often associated with coevolution. We used weighted NODF to evaluate network nestedness () and a weighted measure of edge-betweeness to divide the network into modules and calculate a modularity score ().

