The interaction of coevolution, linkage rules and sampling in determining the structure of mutualistic networks

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This study examines the effect of different coevolutionary scenarios and linkage rules on the topologies of mutualistic networks. We simulated character evolution on different combinations of phylogenies representing neutral evolution and different modes of coevolution. Using the simulated traits, we built interaction networks by employing different linkage rules to determine the frequency of interaction between mutualists. We then simulated the effects of species abundance and sampling on the interaction network created by trait overlap alone and calculated network-level metrics to describe the topologies of the networks. Using this simulation based approach we addressed the following questions: 1) does coevolution leave a distinct mark on network topology that is detectable even when species abundance and sampling are considered? For example are tightly coevolved networks more modular than communities not influenced by coevolution? 2) Do different linkage rules (i.e. complimentary trait matching, barrier trait rules or neutral interactions) influence network topology? 3) how does including species abundance and sampling affect network structure?

**Simulation method**

**Step 1**: Phylogenies were 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 cospeciation (i.e. “tight” coevolution): the phylogeny and trait evolution of mutualisms are identical. This scenario represents the most extreme case of coevolution where mutualists cospeciate and coevolve. One phylogeny and trait evolution through Brownian motion is simulated and used for both mutualists.

b) Coevolution without cospeciation (i.e. “diffuse” coevolution): 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 were simulated independently. The traits of one of the partners are simulated using Brownian motion. The traits for the other partner were simulated by sampling from the traits of its partners and than using those traits as multiple optima in an Orstein-Uhlenbeck process.

c) Cospeciation without coevolution (i.e. geographic structuring): 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**: Next 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**: We used the interactions determined by the linkage rules to create four 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 were 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.

c) Good sampling: Unless sampling is perfect, we never see the true ecological and fundamental networks. We simulate the observation process by sampling from the ecological matrix a fixed number of times with the probability of seeing an interaction is based on its weight in the ecological network. To simulate “good” sampling we sampled the ecological matrix 1000 times (i.e. we see 1000 interactions).

d) Poor sampling: To simulate “poor” sampling we sampled the ecological matrix only 100 times.

**Step 4**: 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.