Coevolution and the structure of mutualistic networks

Lauren Ponisio

**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 & Jordano 2007). 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 (Bascompte & Stouffer 2009, Santamaria & Rodriguez-Girones 2007) and the contribution of coevolution and neutral processes to the evolution of these traits (Vazquez 2009). Using a simulation-based approach, I will examine the effect of different evolutionary scenarios and trait linkage rules on the topologies of mutualistic networks.

**Background:**

In a network analysis mutualistic communities, such as plants and pollinators, are modeled as bipartite or two-party network where the partners are nodes 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) (Bascompte et al. 2003), weak asymmetric links (specialist plants are visited by generalist pollinators, and vice versa) (Vazquez and Aizen, 2004) and modularity (the network can be separated into sub-units or “modules” in which species interact more inside than outside their respective sub-units) (Olesen et al. 2007). Particularly, Olesen et al. (2007) 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 how coevolution process shapes species’ interactions and diversification. The first coevolutionary 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 recently even obligate mutualisms have been shown to deviate from its predictions (e.g. fig-fig wasp: Machado et al. 2005, Cruaud et al. 2012; oil producing orchids and Euglossine bees: Ramirez 2012; yuccas and yucca moths Althoff et al. 2012).

The second evolutionary scenario suggests trait convergence is the result of natural selection honing the 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) and oil production by orchids (Ramirez 2012).

Recently, models of network coevolution have explored the effect of evolution and coevolution on the topology of networks (Guimarães et al. 2011, Nuismer et al. 2012). Whether the structures observed in mutualistic networks could also be produced by neutral processes, however, has been less explored (Vazquez 2009). Interacting mutualistic species will experience the same biogeographic and climatic events that may cause allopatric divergence in both mutualistic lineages as an interaction spreads across the landscape (Smith et al., 2008), leading to congruence between mutualist phylogenies without evidence of coevolution driving co-speciation (Althoff et al. 2012). Additionally, neutral trait evolution (e.g. drift through trait space, also know as Brownian motion) causes the traits of closely related species to be more similar than distantly related species (e.g. Bloomberg 2001, Revell 2008, Losos 2008). These phylogenetic constraints on species’ traits will cause closely related species to interact with similar species independent of coevolution.

In both coevolutionary and neutral evolution scenarios, whether two mutualists can interact is due to their traits, either morphological (e.g. pollinator body size and plant flower size) or behavioral (e.g. pollinator and plant phenology). Several “linkage-rules” have been proposed to describe how the traits of a species determine who it can interaction with including complementary traits, exploitative barriers and neutral interactions (Santamaria & Rodriguez-Girones 2007). With complementary trait linkage rules, the mechanism underlying an interaction is the similarity between the resource a one species has to offer and the reward the other is seeking, while with exploitative barrier linkage rules an interaction is determined by whether a species can overcome the exploitation barrier imposed by its potential partner (Santamaria & Rodriguez-Girones 2007). Neutral linkage rules allow all partners to interact independent of their traits. Simulated networks resulting from simple combinations of complementarity and exploitative barrier linkage rules have been shown to approximate the structure of observed mutualistic networks (Santamaria & Rodriguez-Girones 2007).

Using a simulation-based approach, I will contrast different coevolutionary and neutral community assembly scenarios and linkage rules. I will simulate character evolution on phylogenies representing different modes of coevolution and neutral evolutionary scenarios. Using 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 traits, exploitative barriers or neutral interactions) influence network topology? Understanding the different interaction patterns produced by communities assembled through neutral process and coevolution has implications for understanding the properties of these communities, for example how they respond to species extinction (Memmot et al. 2004).

**Methods:**

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 using the R package TreeSim (Stadler 2012). Trait evolution was simulated with the R package ape (Paradis et al. 2004). 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 (Farenholz 1913). Few if any mutualistic interactions evolve through this strict mechanism, but because it is so extreme it represents a useful comparison because communities assembled under this scenario will exhibit the strongest signal of coevolution if one exists. To simulate this scenario, a single phylogeny for both mutualist partners with traits evolving through Brownian motion is constructed.

### b) *Coevolution without co-speciation*: the trait evolution of one mutualist tracks the evolution of the other (trait convergence) but speciation of the mutualistic partners occurs independently. To represent this scenario the phylogenies of the mutualists will be simulated independently, and the traits of one of the partners are simulated using Brownian motion. The traits for the other partner are simulated by sampling from the traits of its partners and than using those traits as multiple optima in an Ornstein-Uhlenbeck process (Gillespie 2006).

c) *Co-speciation without coevolution*: the tree topologies of the mutualists are similar, but the traits of the partners are not co-evolving. This represents a case where an environmental factor is driving speciation leading to geographic structuring. A single tree simulated for both mutualists, but traits evolve independently on the trees through 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) *Exploitative* *barriers*: If the trait of the higher trophic level mutualistic partner is greater than the trait of its partner, the species interact with probability equal to 1.

c) *Neutral interactions*: all species can interact with probability equal to 1.

**Step 3**: use the interactions determined by the linkage rules to create two realizations of each interaction network:

a) *Evolutionary*: the interaction network where the probability of two species interacting is based on linkage rules alone. This matrix would most clearly represent the strength of the interactions between mutualists over evolutionary time-scales.

b) *Ecological*: a realization of the evolutionary 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 network structure. I will calculate network-level metrics of each of the interaction networks produced in step 3. I will focus on network nestedness and modularity, metrics often associated with coevolution. I will use weighted NODF to evaluate network nestedness (Almeida-Neto et al. 2008) implemented in the R package vegan (Oksanen et al. 2013) and a weighted measure of edge-betweeness to divide the network into modules and calculate a modularity score (Newman and Girvan 2004) implemented in the R package igraph (Csardi et al. 2006).

Most mutualistic networks deviate from a 1:1 partner ratio. This deviation is strong for plant–pollinator and ant–nectar networks, with almost four times more animal than plant species, but more modest for plant–seed disperser and ant- myrmecophyte networks (Bluthgen et al., 2007; Guimaraes et al., 2007a).

References:

J. Bascompte, P. Jordano, Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. (2007).

J. Thompson, *The geographic mosaic of coevolution*. (University of Chicago Press, Chicago, 2005).

Bascompte J, Stouffer DB (2009) The assembly and disassembly of ecological networks. Philosophical Transactions of the Royal Society B: Biological Sciences 364:1781-1787

J. Bascompte, P. Jordano, C. Melian, J. Olesen, The nested assembly of plant-animal mutualistic networks. *Proc Natl Acad Sci USA* 100, 9383 (2003).

D. Vázquez, M. Aizen, Asymmetric specialization: a pervasive feature of plant-pollinator interactions. *Ecology* 85, 1251 (2004).

J. M. Olesen, J. Bascompte, Y. L. Dupont, P. Jordano, The modularity of pollination networks. *Proceedings of the National Academy of Sciences* 104, 19891 (2007).

Almeida-Neto, M., Gumarães, P., Gumarães, P.R., Loyola, R.D. & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117, 1227–1239.

Jari Oksanen, F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens and Helene Wagner (2013). vegan: Community Ecology Package. R package version 2.0-6. <http://CRAN.R-project.org/package=vegan>

Paradis E., Claude J. & Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20: 289-290.

Tanja Stadler (2012). TreeSim: Simulating trees under the birth-death model. R package version 1.7. <http://CRAN.R-project.org/package=TreeSim>

Csardi G, Nepusz T: The igraph software package for complex network research, InterJournal, Complex Systems 1695. 2006. <http://igraph.sf.net>

M Newman and M Girvan: Finding and evaluating community structure in networks, *Physical Review E* 69, 026113 (2004)

Gillespie, D. T. (1996) Exact numerical simulation of the Ornstein-Uhlenbeck process and its inte- gral. *Physical Review E*, 54, 2084–2091.

Althoff et al. Geographic isolation trumps coevolution as a driver of yucca and yucca moth diversification. Molecular Phylogenetics and Evolution (2012) vol. 62 (3) pp. 898-906

Revell, L.J., Harmon, L.J. & Collar, D.C. (2008). Phylogenetic signal, evolutionary process, and rate. Systematic Biology, 57, 591– 601.

Losos, J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecol. Lett., 11, 995– 1007.

Blomberg, S.P., Ives, A.R. & Garland, T. (2001). Detecting phylogenetic signal in comparative data. Am. Zool., 41, 1395.

