**No genotype is an island: Genetic variation creates nested, robust ecological networks**

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**Abstract**

* Studies of ecological networks have demonstrated the importance of indirect effects of interactions in communities to contribute to community dynamics but have not incorporated genetics even though genetic variance has been shown to have important community and ecosystem level effects.
* Here, we conduct a series of simulation experiments and analysis of an empirical genotype-species interaction network to develop a framework for a genetic basis of interaction network structure and test its possible effect on community level responses to selection on co-evolved traits.
* We found three major results:
  1. Nestedness of genotype-species networks increased as the effect of genetic variation increased,
  2. The impact of selection on a co-evolved trait was higher in low diversity (i.e. even) communities.
  3. An empirical genotype-species network exhibited significant nestedness when controlling for both genotype and species marginal totals.
* These findings demonstrate that the community level impact of genetic variance can alter the structure of species interaction networks, which leading to more stable communities. This work points to a previously overlooked consequence of genetically based, intra-specific diversity and provides a mechanism for evolution to act on ecological network structure. This study presents a major step toward incorporating a genetics based, evolutionary perspective into ecological network theory.

**Keywords:** foundation species, ecological networks, species interactions,nestedness, community dynamics

**Introduction**

Evolutionary dynamics in the context of complex ecological communities is important to explore. Species interactions have been shown repeatedly to drive the evolution of biological diversity creating persistent evolutionary dynamics (Thompson 1999; Thompson 2013). Genetic variation itself has been shown to influence a suite of community and ecosystem level patterns (cite the battery of whitham, Johnson, agrawal and crutsinger papers). Beyond purely ecological consequences of genetic variation, genetic correlation among individuals of different species has important implications for evolutionary dynamics. Kin selection, group selection and co-evolutionary theory all provide examples of how genetic correlations can be both manifested and selected on at levels higher than the individual and beyond the population.

Species interactions are known to have profound effects in ecosystems. For over half a century, ecologists have been studying the structure of interaction networks and how this can change the dynamics of ecological communities (MacArthur 1955, May 1972, Ulanowicz 1981, Patten and Higashi 1991, Bascompte et al. 2003). The structure of ecological networks is now known to affect nutrient cycling (Borrett et al. ????), Although all of these studies employ an evolutionary perspective to explain common patterns in network structure, none have explicitly incorporated a genetic perspective or intra-specific variation into models or empirical studies of ecological networks. One possible exception to this is recent studies of evolution of pseudo-ecological software or artificial life networks (see Fortuna et al. 2013).

In line with long standing concepts of variability in the importance of species in ecosystems (e.g. foundation species), work with trophic and mutualistic ecological networks have all shown strong asymmetry in the effects of species within these networks. The field of ecological networks has demonstrated some ecological mechanisms for how indirect effects can influence community dynamics; however, none of these studies have included genetic variation, and thus, are limited in establishing how evolutionary mechanisms that are playing a role in structuring ecological networks. Network centrality (Borrett ????). Asymmetric, co-evolved networks (Bascompte et al. 2003).

Although the consequences of this variation are known to impact biological diversity across multiple spatial scales, the effect this variation has on the structure of ecological interaction networks has not been explored (Fig. 1). Thus, focusing initially on foundation species has been an important step forward, but has obviously been ignoring the insights that could be made by incorporating evolutionary genetics and a community level interaction network perspective. In this study, we first use an established mass-action community genetics simulation to study the effect of intra-specific variation on interaction network structure. We hypothesize that genetically based variation in a clonal foundation species. Second, we examine the robustness of these communities to the loss of genetic diversity, where we hypothesize that co-evolved traits will reduce network robustness. Last, we examine the structure of an empirical network where plant genetics is known. This study of the influence of genetic diversity on ecological network structure and dynamics has important implications for understanding how genetic variability influences community stability and how evolutionary forces act to structure ecological interaction networks.

**Methods**

*Simulations*

We used the community genetics simulation method previously developed in Shuster et al. 2006. Briefly, this method starts by creating a population of individuals assigned a genotypic value (i.e. genotypes). Each genotype is comprised of multiple individuals (i.e. clones), which are mapped to phenotypic values as a single numeric value for each individual. This population represents the foundation species. Next, a set of species representing the rest of the community is assigned an average genotypic value that is then also mapped to a numerical phenotypic value using an additive, bi-allelic genetic system. At each step of genotype-phenotype mapping variance is introduced through random draws from a uniform distribution, which simulates the introduction of phenotypic variance arising from non-genetically based “environmental” variation. It is important to note here that interactions among species beyond the foundation species’ effect on the community is not explicitly accounted for in this process but introduced as a contribution to non-genetic, environmental variation. Finally, the foundation species phenotypic values for each individual are used to determine the equilibrium population value for each species (Ronce and Kirkpatrick 2001).

For this study, we generated a set of 10 replicate communities for 8 scenarios of selection intensity for a total of 80 communities. Each of these communities was generated using the same initial phenotypes for both the “foundation species” individuals (n = 100 with 10 individuals for each of 10 genotypes) and the “associated species” (n = 25) (see Online Supplementary Materials, Appendix X). For the main set of analyses, a carrying capacity (K) of 100 individuals was used for to remove the effect of differences in total abundances among species.

*Genotype-species networks*

Genotypic averages of species abundances were then used to generate a bipartite network of genotype-species interactions. As the network nestedness matrix rely on presence-absence data, each network was reduced to a minimal set of connections. A cut-off of 5 observations for a given species on an individual tree was used as a threshold to “prune” the network to the minimal connections. This threshold value was chosen because it is the point at which a binomial test of significance had enough power to produce a significant test.

*Network Nestedness*

Nestedness was then calculated for each of these networks using the nestedness temperature metric (Rodríguez-Gironés and Santamaria 2006). This method uses a packing algorithm first described in Atmar and Patterson (1993) that compares a presence-absence representation of the observed matrix to a “low temperature” or non-nested re-arrangement of the matrix. The greater the difference is between the observed and the re-arranged matrix, the higher the nestedness temperature value.

*Robustness Experiments*

To examine the robustness of these networks, we conducted a series of foundation species removal experiments. Trees were removed according to three different algorithms: 1) random removal, 2) connectedness removal and 3) phenotypic similarity. The random removal algorithm used a uniform probability distribution to select individuals. The connectedness removal algorithm assigned individuals with more interactions with species higher probability for removal. The phenotypic removal algorithm assigned removal probabilities by the phenotypic similarity among individuals. These algorithms were applied to the communities for species with equal carrying capacities as described and to a second set of communities in which the carrying capacities for the dependent species were selected from a Poisson distribution intended to simulate the highly skewed, un-even distribution of species total abundances most often observed in natural communities.

*Empirical cottonwood genotype canopy arthropod network analysis*

An empirical network of canopy arthropod species on known genotypes of *Populus angustifolia* James (narrowleaf cottonwood) was taken from Keith et al. 2014. Trees planted in a common garden in 1991 (Martinsen et al. 2001) that randomized replicate genotypes (based on RFLP genotypic) with respect to local environmental variation were surveyed for arthropods in August of 2009 using timed sampling of similarly sized branches. Genotype averages for species abundances were used to construct a genotype-species network. A nestedness significance test was performed on this network using 1000 permutations of the original data and a 50 iteration burn-in. A fixed row and column permutation algorithm that maintained marginal totals was used to control for differences in total abundance of both genotypes and arthropod species.

*Software*

All simulations and analyses were conducted in R version 3.0.2 (R Development Core Team 2014). Simulations were conducted using the *ComGenR* package (Lau 2014). Non-metric multidimensional scaling (NMDS) ordination, co-occurrence analyses and the nestedness test were conducted using *vegan* (Okasanen et al. 2013). Network plots were constructed using *bipartite* (Dormann et al. 2008). All simulation scripts are hosted at https://github.com/MKLau/cg\_simulations.

**Results**

*Genetic variation altered species co-occurrence patterns to produce nestedness*

Composition and co-occurrence patterns of the simulated communities were affected by tree genetics (Fig. 2).

The nestedness of simulated networks increased with the intensity of selection (Fig. 3).

*Genetically based nestedness increases network robustness*

Communities with carrying capacities drawn from a Poisson distribution were on average 19% less even (Pielou’s Evenness) than communities with a fixed carrying capacity for all species (*t* = 154.55, *P* <<< 0.001).

Networks with low evenness were more susceptible to removals overall, but this susceptibility was driven by the species abundances and not the effect of genotype. When species abundances were even, the effect of selection on a genetically based phenotype had a strong impact on the robustness of the community to fluctuations in the foundation species (Fig. 4).

*Empirical genotype-species network exhibits Nestedness*

The cottonwood canopy arthropod genotype-species network showed significant nestedness. The nestedness was statistically different from the null expectation (Fig. 5; nested temperature = 19.542, *P* = 0.017).

**Discussion**

*Nestendess: An overlooked benefit of genetic diversity*

*Nestedness, genetic diversity and community dynamics*

*Reality Check*

How does this apply to real systems?

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**References**

**Figure Legends**

Figure 1. Although interspecific variation in interaction traits is known to lead to nested ecological networks (e.g. mutualistic networks), the contribution of intra-specific variation to network structure has not been explored. This figure shows a bipartite graph of a mutualistic network of plant species (left; green circles) and associated species (right; red circles) connected by light grey lines representing their interactions. The center set of green nodes shows a hypothetical scenario in which the top-most plant species is comprised of two genotypes that have distinct phenotypes that affect their interactions between species (dark grey lines).

Figure 2. Plots of the (A) densities of tree phenotypic values and (B) the NMDS ordination of the simulated communities for each tree genotype.

Figure 3. The scatterplot on the left shows the effect of selection intensity on nestedness temperature. The effect of selection on nestedness increases non-linearly because levels of selection intensity were scaled exponentially. An example simulated bipartite genotype-species network is shown on the right with tree genotype (left) and associated species (right) where connections are scaled by the average species abundance across genotype replicates and nodes are scaled by the number of connections. This network displays a high degree of nestedness with genotypes and species of lower connectedness being subsets of the community.

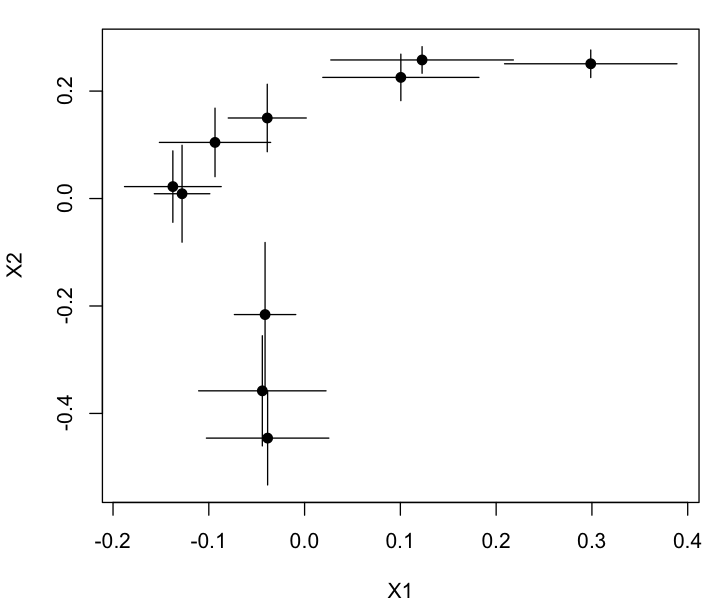
Figure 4. Scatterplots showing the relationship between selection intensity and the percent trees removed for the first extinction metric (see methods) for (A) high and (B) low evenness communities for three tree individual removal scenarios: red = random, green = preference for higher connectedness and blue = preference for phenotypic similarity.

Figure 5. Empirical bipartite genotype-individual network of canopy arthropod species associated with *Populus angustifolia* genotypes exhibiting significant nestedness.

Figure 1.

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Figure 2.



**B**

**A**

Figure 3.

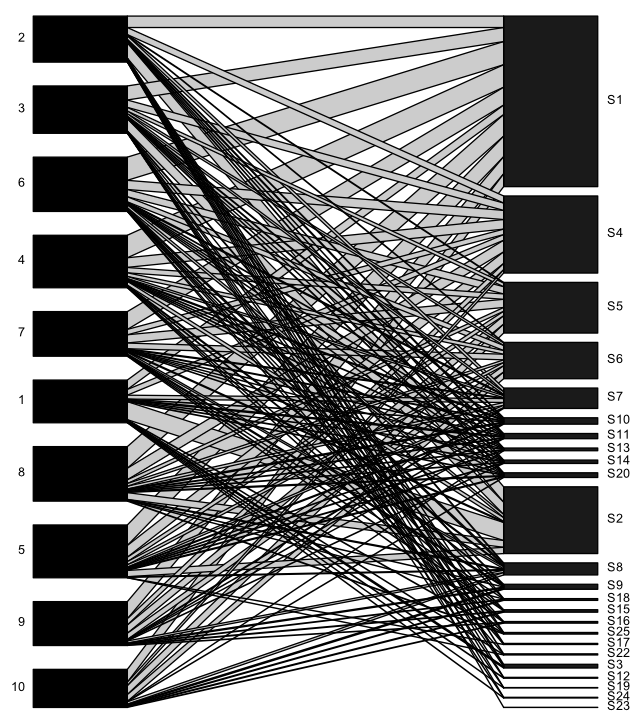
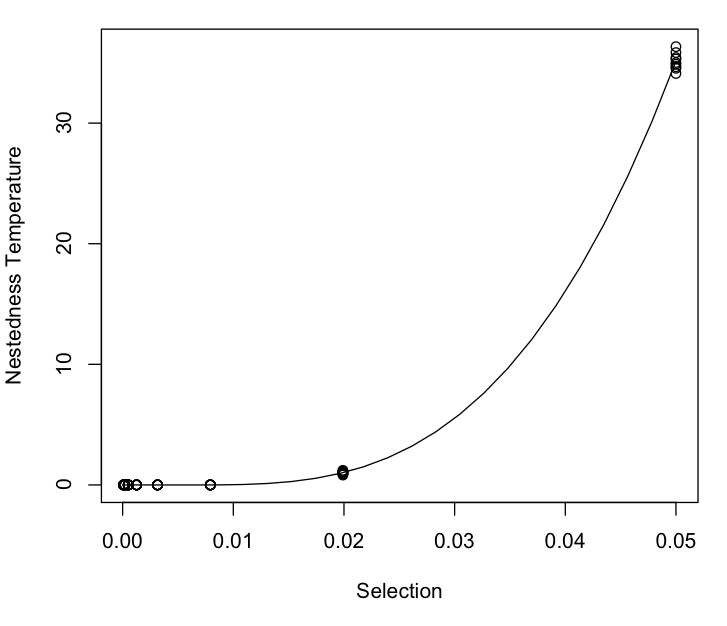
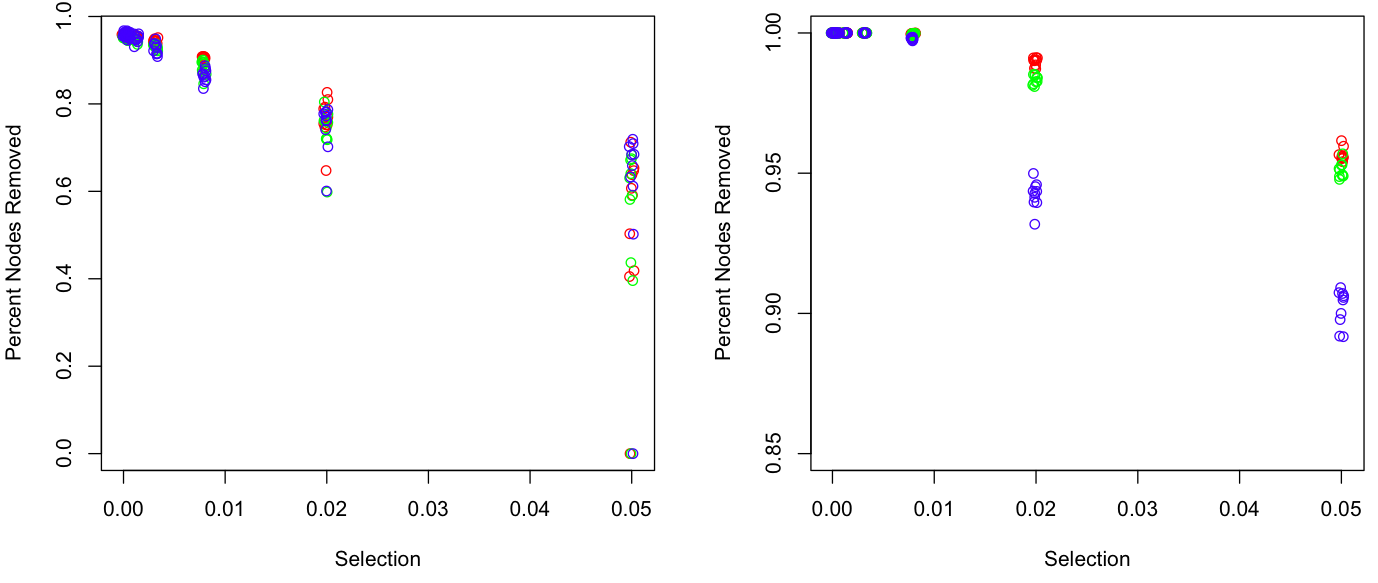


Figure 4.



**B**

**A**

Figure 5.

