**A genetic basis to nestedness in ecological networks**

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Target Journal: PLoS Biology, Journal of Theoretical Biology, Heredity, Evolution

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.

Introduction

Genetic variation within foundation species is known to have profound effects at the community and ecosystem scales,

It is really important to note that stability or other community properties may arise from the structure of the network, which has not been suggested to be a function of genetic diversity in prior research.

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.

Networks are important.

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.

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).

In this study, first, we use an established mass-action community simulation method to develop to simulate genotype-species interaction networks, and, second, we test this framework using several empirical community datasets. We hypothesize that the community compositional effects of foundation species genotype will contribute to interaction network structure. A genetic basis to ecological networks has important implications for understanding how evolutionary forces act to structure interactions among species in ecosystems.

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.

*Selection 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 genotype with respect to local environmental variation were surveyed for arthropods in August of 2009 using timed sampling of similarly sized branches. Genotype averages 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*

Acknowledgements

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.

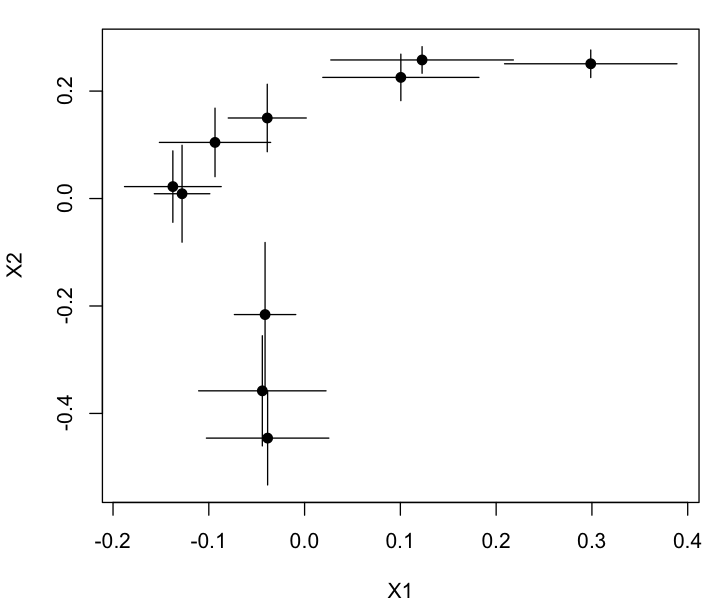
Figure 4. Scatterplots showing the relationship between selection intensity and the removal to first extinction metric (see methods) for (A) high and (B) low evenness communities for three tree individual removal scenarios: red = random, green = preference for higher connectedness and blue = preference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

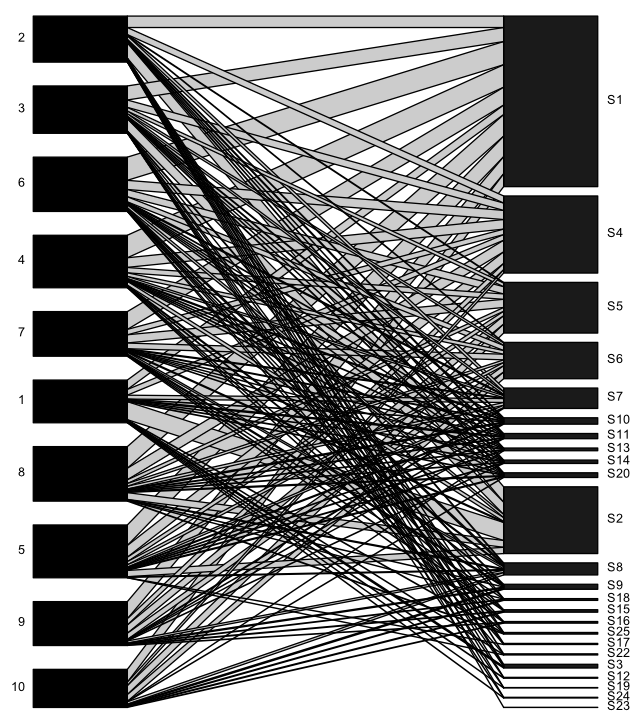
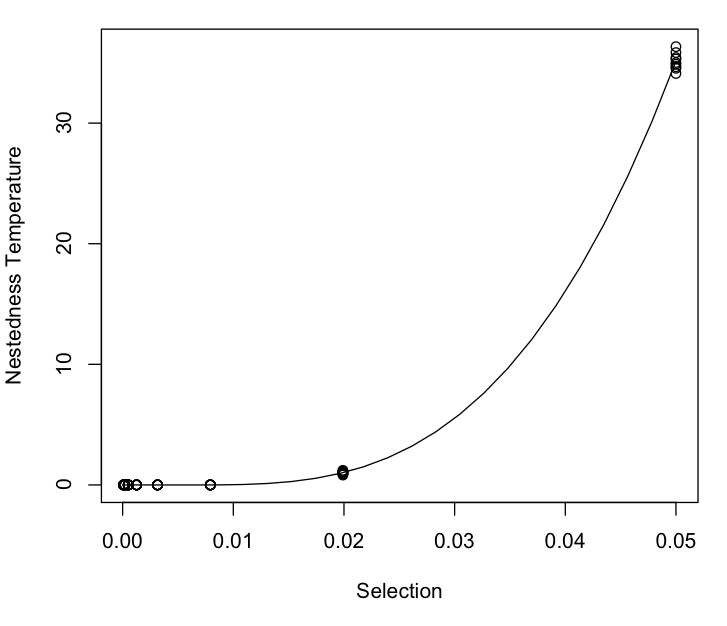
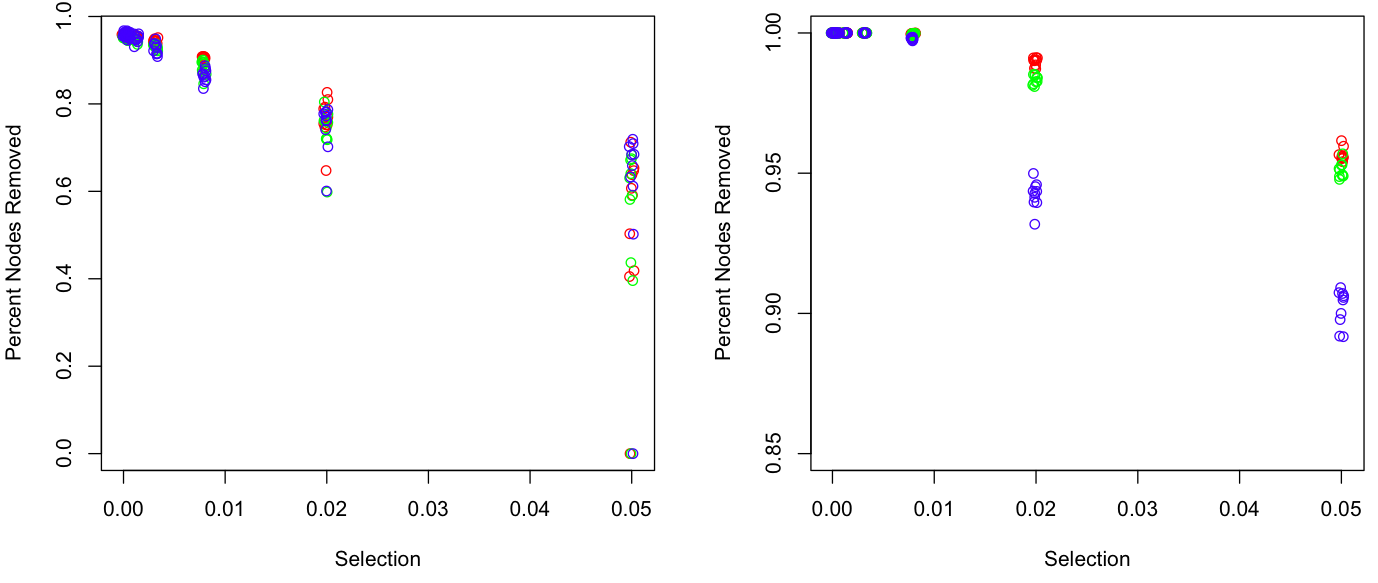


Figure 4.



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Figure 5.

