

The Evolution of Ecological Interactions in Complex Ecosystems

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7 May 2012

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Introduction

The dynamics of species interactions are fundamental to the evolution of biodiversity. Thompson (1999) wrote that, “the history of evolution and biodiversity is fundamentally a history of the evolution of species interactions.” And Darwin in “Origins” described communities as “tangled” banks (Darwin 1859). Primarily developed as coevolutionary theory, extensive research has shown empirically that species interactions contribute to the generation of diversity in ecosystems (Ehrlich & Raven, 1964).

Recently, the advances in the field of community genetics have begun to put complex communities into an evolutionary framework. Historically, investigations and the theory of the evolution of species interactions have focused on one or a few species; however, the complexity of communities arising from both species richness and indirect effects suggest that a purely reductionistic approach is likely to yield limited insight into species rich communities (Antonivics, 1992). And over the past 20 years multiple studies have shown that genetic variation within a single species can have community and ecosystem consequences (Crutsinger et al., 2006; Fritz & Price, 1988; Johnson & Agrawal, 2005; Strauss et al., 2005; Whitham & et al., 2006; Wimp et al., 2004). In addition, evolutionary theory has expanded to incorporate greater complexity beyond simple two-way interactions (Shuster et al., 2006; Wade, 2007).

Network theory originated over 300 years ago with the work of Leonard Euler to address problems of relationships among discrete entities, and now the application of network theory to studies of ecological interactions are providing a useful framework for addressing both theoretical and analytical challenges in community genetics. Starting at least as early as Robert MacArthur’s work on community stabil-

ity, network theoretic methods have been applied to community ecology (MacArthur, 1955). Following in these footsteps, many theoretical and empirical advances have been made employing a network approach, including work on ecological complexity (May, 1972), food-webs (Cohen, 1979), plant-animal interactions (Bascompte et al., 2003; Thebault & Fontaine, 2010). Recently, researchers have started to apply network theoretic methods to evolutionary questions (Guimaraes et al., 2011; Ohtsuki et al., 2006).

The goals of this dissertation are to:

1. Explore how real communities evolve as networks of ecologically connected species,
2. Integrate community genetics and network dynamics theory, and
3. Develop useful theoretical and computational methods for evolutionary network research.

1 Review: Ecological and evolutionary interaction network exploration (Lau et al. 2010)

Abstract

Ecological communities play an integral role in determining ecosystem functions. However, community-level patterns and processes are complex because they are typically comprised of many interacting components. Therefore, pair-wise reductionist investigations of interactions among species are unlikely to reveal the dynamics of the whole community. Here, we present results from a study of the interactions among

members of a lichen community associated with different genotypes of a foundation tree species, *Populus angustifolia*. Three key findings emerge. First, null-model based analysis of species co-occurrence patterns suggest that interactions are likely contributing to lichen community structure. Second, the pattern of co-occurrences and pair-wise correlations of lichen species suggest that interactions among lichens are primarily facilitative. Third, the significance and magnitude of co-occurrence patterns vary among genotypes of *P. angustifolia* suggesting that the strength of facilitative interactions among lichens is tree genotype dependent. In combination, direct and indirect plant genetic effects on the interactions of lichens appear to play an important role in defining the lichen community. We believe that a community genetics approach focused on foundation species will allow researchers to better understand the selection pressures that shape communities and that many unexpected outcomes will emerge. From this perspective we discuss future research directions that employ greater analytical power to further quantify the complex network of species interactions within communities.

2 Genetically based phenotypic variation in foundation species influences lichen species co-occurrence patterns.

Introduction

- Species interactions are an important component of biological diversity, contributing to the dynamics of communities and ecosystems.
- Only recently have ecologists begun to put communities into an evolutionary

context, and in particular the evolution of species interactions have typically been studied in small groups of species (i.e. pairs and triplets).

- As interactions are difficult to quantify directly, we will use a co-occurrence pattern based approach to infer potential shifts in the underlying structure of interactions.
- Using lichen communities as a model system, we will ask how genetic variation in a foundation species influences the co-occurrence patterns in multi-species community.

Hypotheses

- Lichen co-occurrence patterns will depend on the genetics of the foundation tree species (*Populus angustifolia* and *Pinus edulis*).
- Variation in heritable traits of the foundation species produce these co-occurrence patterns.

Methods

- Lichen co-occurrence patterns will be quantified in two ecosystems to provide greater generality of the findings:
- *Populus angustifolia* riparian forest, Utah
 - Surveys will be done in two common gardens with replicated genotypes and in an adjacent wild stand of *Po. angustifolia*.
 - Epiphytic lichen will be observed on the trunk of each tree.

- Occurrences will be recorded for all species in 1cm² cells of a 10cm² quadrat on each tree.
 - Tree traits, such as bark roughness and size, will be recorded for each surveyed tree.
 - All lichen species have been confirmed by an expert lichenologist (R.R. Naesborg).
- *Pinus edulis* arid woodland, Arizona
 - Rock lichen will be surveyed on rocks directly beneath the canopies of *Pi. edulis* in a common environment.
 - Lichen species occurrences will be quantified in cells of each quadrat.
 - Previous work in this system has shown that susceptibility to an herbivorous moth, which has both community and ecosystem consequences, is genetically based.
 - Tree trait data will be recorded for each tree, including canopy architecture variables relating to herbivore damage and under-story plant cover.

Anticipated Results

- Previous studies in both systems have shown that lichen community composition tracks genetically based trait variation.
- Lichen species often interact both through competition (e.g. space) and photobiont stealing and often exhibit co-occurrence patterns, depending on the environmental context.

- Thus, co-occurrence patterns will vary significantly depending on the underlying genetic gradient of the foundation species.

3 Intra-specific variation in a foundation tree species influences herbivore interaction network structure.

Introduction

- Plant-herbivore interactions are key components of ecosystems and have been a useful model system for studying the evolution of species interactions.
- The modeling of plant-herbivore interactions as bipartite networks has helped to advance the theory of community level dynamics in these systems.
- Here, we will investigate how genetic variation in an foundation tree species influences the structure of plant-herbivore interaction networks.

Hypotheses

- Plant genetics contributes to phenotypic variation in traits controlling plant-herbivore interactions that will influence the structure of interaction networks.

Methods

- Observations of canopy arthropod species will be conducted at two scales of genetic variability in a common garden setting:
 1. Trees forming a gradient of species hybridization (*Po. angustifolia* x *Po. fremontii*).
 2. Trees of known genotype (*Po. angustifolia*).
- In addition, surveys of canopy arthropods will also be conducted at the scale of both individual leaves and branches on *Populus angustifolia*.
- Network structure will be explored at three scales:
 1. The hybridizing stand scale using trees along the hybrid gradient.
 2. The single species stand scale using replicated trees of know genotype.
 3. The scale of single trees using intra-tree replicates at both the finer scales of branches and leaves.

Anticipated Results

- Extensive work in this system has shown that community composition of canopy arthropods is strongly influenced by genetic variation across the hybridizing complex and within species.
- In addition, previous work has shown that arthropod trophic interactions vary among genotypes.
- We therefore can expect:
 - * Both hybridization and intra-species genetic variation to contribute to the structure of bipartite plant-herbivore networks, and

- * Co-occurrence patterns of canopy arthropods to vary among genotypes.

4 The evolution of ecological networks in foundation species driven ecosystems: A simulation based approach

Introduction

- The theory of the evolution of ecological interactions is based on overly simplified systems of one or a few species.
- Network theory has enabled the investigation of complex (i.e. multi-species) communities from a mathematically rooted framework.
- An important concept in community genetics is that communities are primarily structured by one or a few species that drive the ecology and evolution of many other species.
- From a network perspective, we can say that ecological and evolutionary networks should tend to be centralized.
- Empirical investigations of the functional consequences of network structure is that centralized networks tend to be highly resistance to random species loss; however, targeted loss of the central species tends to produce global instabilities.
- In this study, we will develop and use a network dynamics model to investigate the influence of ecological network centralization on the evolution

of both local and global network structure.

Hypotheses

- Network centralization will tend to stabilize ecological networks
- The evolution of species in the network will tend to track the evolution of the most central species

Methods

- Design network dynamics simulator
 - * Individual based model
 - * Traits of individuals from species specifications
 - * Interactions are determined by traits
- Simulations will be parameterized for three scenarios:
 - * High centralization
 - * Moderate centralization
 - * Low centralization
- Simulations will be carried out on the Cottonwood server, Amazon cloud or other server for computationally intensive tasks.

Anticipated Results

- Previous analytical and simulation based studies have shown strong connections between ecological network structure and stability.

- Also, recent work has shown that ecological network structure has direct consequences for the propagation of evolutionary dynamics in simulations of species removals.
- Thus, we can expect that network structure, i.e. centralization or “foundation-ness”, will determine the evolutionary dynamics of the community.

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