Structure and Stability of Evolving Food Webs

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Goal

To study how food webs are expected to change their structure, composition of interactions, and stability properties in the course of evolution.

Background and motivation

The relationship between the diversity and stability of ecological systems has long been an issue for research and debate. Using theoretical evidence from food web models as well as verbal arguments several studies suggest that large complex communities will be more stable than small and simple ones, whereas other studies show the opposite (McKann 2000). Some models corroborating both views have been proposed (e.g. Wilmers et al. 2002) and recently it has been proposed that the presence of weak links in food webs is important for the stability of ecological systems (Janssen and Kokkoris 2003; McKann 2000).

Models of evolving food webs have also been used in order to understand patterns of speciation and extinction in the fossil record (e.g. Yoshida 2003). Some of these studies show fluctuating species diversity with periods of increasing diversity followed by extinction avalanches (Calderelli et al 1998), while others have resulted in more stable number of species over time (Drossel et al. 2001)

Evolution in food webs has been simulated as small random changes in the interaction coefficients themselves (Ginzburg 1988) or in abstract traits that map onto interactions (e.g. Calderelli et al 1998; Drossel et al. 2001; Yoshida 2003). Competitive communities (i.e. communities excluding predation), have also been modeled using evolution along fitness gradients in trait space (Rummel and Roughgarden 1983).

Using the theoretical framework of adaptive dynamics, novel techniques have been developed to model community evolution under ecological interactions such as competition and predation (Doebeli and Dieckmann 2000). Applying these techniques in order to simulate food web evolution could yield new insights into long-term diversity patterns and into the issue of stability of ecological systems.

Research questions

In this project I will try to address questions such as the following:

- How do the interactions between species change in terms of their strength and distribution during the evolution of a food web? Do weak links evolutionarily appear as stabilizing factors?

- How will food web structure change in the evolving community? Will food chains be long or short? Will community stability increase or decrease? Will genetic similarity between species correspond to ecological and functional similarity?
- How do speciation and extinction events affect the structure of the evolving community and its stability properties?
- Does speciation rate change during evolution? Can we expect cascade extinctions? Will the food web evolve towards a fixed community (an ESS solution)?

Methods and work plan

To address these questions, adaptive dynamics theory is a suitable tool, since it is a general approach that ties evolution and ecology together and requires relatively few assumptions.

Each species will be characterized by *L* different traits. The traits of a species *i* will be modeled as vectors $\mathbf{u}_i = (u_{i1},....,u_{iL})$ with elements containing continuous values between 0 and 1, as a generalization of the model of Calderelli et al. (1998). The interaction coefficients α_{ij} between two species *i* and *j* will be functions of a 'score' defined as

$$S_{ij} = \mathbf{u}_i \mathbf{M} \mathbf{u}_j^T = \sum\nolimits_{pq} u_{ip} u_{jq} M_{pq}$$

where **M** is an asymmetric random matrix chosen in the beginning of the simulation.

Evolution and population dynamics will then be modeled using a fitness function, *G*, that depends on the traits of the species and their vector of population densities **x**. The fitness landscape of a mutant with traits $\mathbf{u}'$ in a resident population with traits $\mathbf{u}_1, \mathbf{u}_2, ..., \mathbf{u}_m$ will then be described by

$$G(\mathbf{u}', \mathbf{x}, \mathbf{u}_1, \mathbf{u}_2, ..., \mathbf{u}_m) = \lambda \sum\nolimits_j x_j \alpha(\mathbf{u}', \mathbf{u}_j) - \sum\nolimits_j x_j \alpha(\mathbf{u}_j, \mathbf{u}') .$$

The population growth will be proportional to the fitness function and the evolution will be governed by the canonical equation of adaptive dynamics derived for this fitness function.

The trajectory of the evolving community will be monitored and the resulting distribution of interaction strength will be measured. Community stability will be assessed using return time and statistics describing the variation in population dynamics. Other features characterizing the food web, such as connectance and proportion of basal species versus intermediate and top species will also be considered.

To start with, the interaction coefficients could be linear functions of the score, S_{ij}, as in Calderelli et al. (1998). A set of rules or restrictions taking into consideration energetic constraints will be applied to avoid unrealistic effects in the structure of the evolving food web. Further adjustments of the fitness function may be made in order to make the evolutionary process natural and smooth when species change the direction of their trophic links, for example when evolving from competitor to predator.

The model could then be extended to include more realistic functional responses, since these have been shown to be of crucial importance for the stability of communities (Drossel et al. 2004). Speciation events and possibly also extinctions could be included as parts of the evolutionary dynamics, in which the appearance of fitness minimas can give raise to evolutionary branching.

The analysis will be conducted both analytically (for simplified cases) and by employing computer simulations.

Relevance and link to ADN's research plan

The project uses an integrative approach in which a complete food web is subject both to short-term ecological dynamics as well as to long-term evolutionary change. Moreover, evolution will take place in many traits simultaneously, inducing adaptations of species belonging to different levels of the trophic structure. The modeling techniques used in this study are inspired by adaptive dynamics theory, developed by researchers connected to ADN. The present study will apply this framework to a partly new setting, exploring evolutionary dynamics in the multi-dimensional trait space of a complex food web.

Expected output and publications

The suggested project is expected to result in a jointly authored paper, which will be integrated in my PhD thesis.

References

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