

Food-web evolution in multivariate niche spaces

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Goal

To develop a model of food-web evolution based on multivariate trophic traits and to compare the structural properties of emerged food webs with those of real food webs.

Background and motivation

Recently, the evolutionary emergence of food-web structures has become a focus of mounting attention. One of the first studies addressing this issue is Drossel et al. (2001) who considered species that are characterized by a finite number of features determining their roles as predators and prey. Ito and Ikegami (2006) and Ito et al. (2009) considered one-dimensional niche spaces and applied a reaction-diffusion model to explore food-web evolution. Rossberg et al. (2006, 2008) investigated multivariate foraging and vulnerability traits, and assumed that predation of one species upon another depends on the distance between the former's foraging traits and the latter's vulnerability traits. Brännström et al. (preprint) studied food-web evolution by focusing on adaptations in body size, assuming that larger species can predate on smaller ones. Once in an evolutionarily steady state, the structural properties of model food webs – including the distributions of trophic links and of species abundances – can be compared with empirical data.

Several traits determine the foraging efficiency and vulnerability of a species. These include habitat preferences, body size, foraging behavior, and defensive mechanisms. Therefore, it is natural to consider species defined by their position in a multivariate niche space. Brännström et al. (preprint) focused on body size as the only adaptive trait: all interactions between species were assumed to depend on that trait. Ito's model examined evolution of a single foraging trait and a single vulnerability trait. Drossel et al. (2001) and Rossberg et al. (2006) considered multiple traits, but assumed that trait values were binary, taking no values other than 0 or 1. These studies assume that population dynamics are governed by deterministic differential equations, which ignores potentially important effects of demographic stochasticity. To date, only Rikvold and Sevim (2007) and Powell and Boland (2009) appear to have studied the effects of demographic stochasticity in evolutionary food-web models, but neither considered the gradual evolution of continuous traits.

Furthermore, Rossberg et al. (2006, 2008) assumed that the evolving community reached a steady state before a further speciation occurs, which cannot represent the simultaneous evolution of species. In addition, some ecologically important phenomena, such as succession and invasion of alien species, do not occur in a community residing in a steady state. Also Yoshida (2008) assumed deterministic population dynamics and the evolution of body size as the only adaptive trait, and then explored the relationships between the duration of food-web evolution and the number of extinctions that are caused by the introduction of alien species.

To further understand the dynamics of emerging structural properties of evolving food webs requires a model that includes multivariate continuous traits, demographic stochasticity, and non-equilibrium dynamics. The aim of this project is to implement such a model from an individual-based perspective.

Research questions

I will try to advance understanding of how ecological, evolutionary, and environmental factors alter the dynamics and outcomes of food-web evolution. To this end, I will create an individual-based model that assumes asynchronous birth and death events based on interactions between individuals in continuous time, where each individual is characterized by two vectors of continuous foraging and vulnerability traits.

I will focus on the following questions:

- What are the effects of niche-space dimensionality, demographic stochasticity, trophic interactions, interference competition, functional responses, and of the cost of extreme traits values on the structure and diversity of emerged food webs?
- Which choices of the aforementioned factors result in food webs whose structural properties agree with empirical data on real food webs?

In the longer term, I will consider the following extension:

- How does the introduction of patch structure affect food-web evolution in meta-communities?

Methods and work plan

Model description

Following previous studies of food-web evolution, I assume that the trophic traits consist of foraging traits and vulnerability traits, each taken from a continuous multivariate niche space. Each individual is assumed to be haploid with nearly-faithful asexual reproduction. All individuals are thus considered to reproduce clonally and to produce mutated offspring with a small probability m . I assume that a mutation alters a trait value by $t' = t + \xi_m$, where t' , t , and ξ_m are, respectively, the value of offspring's trait, that of its parent, and a random deviate following a normal distribution with mean 0 and variance σ_m^2 . No intrinsic difference between trophic classes – such as plants, animals, carnivores, and herbivores – is assumed (Rossberg 2008; Yoshida 2008). Instead, following Ito and Ikegami (2006), I will assume an external resource with a fixed vulnerability trait v_0 . Initially, the population consists only of individuals adapted to forage on this resource.

The evolving community is updated asynchronously. For each update, the birth and death rates of all individuals are calculated. We denote the i th individual's birth event by e_{ib} and its death event by e_{id} . With $N(x, \sigma) = \exp(-\frac{1}{2}x^2 / \sigma^2)$, the rates of these events are given by

$$r_{ib} = ac_F \sum_j C_1(v_i) F_{i \rightarrow j} \quad \text{and}$$

$$r_{id} = c_F \sum_j C_1(v_j) F_{j \rightarrow i} + c_I \sum_j N(f_i - f_j, \sigma_I) + c_d C_2(v_i),$$

respectively, where f_k and v_k are the foraging and vulnerability traits of the k th individual, a represents assimilation efficiency, and d is the intrinsic death rate. The sec-

ond sum in the expression for the death rate above represents the effects of interference competition between predators. The difference $r_{ib} - r_{id}$ measures the per capita growth rate of individual i . $F_{i \rightarrow j}$ denotes the functional response, i.e., the predation intensity of species i on species j . I will investigate several forms of this functional response:

- (i) $F_{i \rightarrow j} = N(f_i - v_j, \sigma_F)$
(linear functional response),
- (ii) $F_{i \rightarrow j} = \alpha N(f_i - v_j, \sigma_F) / [\beta + \alpha \sum_k N(f_i - v_k, \sigma_F)]$
(Holling type-II functional response),
- (iii) $F_{i \rightarrow j} = N(f_i - v_j, \sigma_F) / [1 + \alpha \sum_k N(f_i - v_k, \sigma_F) + \beta \sum_k N(f_i - f_k, \sigma_C)]$
(Beddington functional response), and
- (iv) $F_{i \rightarrow j} = N(f_i - v_j, \sigma_F) / [\beta + \alpha \sum_k N(f_k - f_i, \sigma_C) N(f_k - v_j, \sigma_F)]$
(ratio-dependent functional response; Drossel et al. 2001).

The parameters σ_F and σ_C , respectively, represent the trophic niche width of each individual and the width of the effect of similarity in foraging traits on reduced predation intensity through interference competition.

We assume that extreme values of vulnerability traits are costly, so that trait evolution toward infinite values will not occur. After a suitable coordinate transformation, the functional form of this cost can be approximated to be radially symmetric with a minimum at the origin. The reduction in assimilation rate, and thus in birth rate, resulting from this cost is measured by $C_1(v_i)$. With $C(v) = c_c v^2$, we will consider three functional forms: (i) $C_1(v_i) = 1$ (no cost), (ii) $C_1(v_i) = 1 / [1 + C(v_i)]$, and (iii) $C_1(v_i) = \exp[-C(v_i)]$. The increase in death rate resulting from this cost is measured by $C_2(v_i)$. We will consider two functional forms: (i) $C_2(v_i) = 0$ (no cost) and (ii) $C_2(v_i) = C(v_i)$.

After calculating the birth and death rates for all n individuals in the evolving community, one event $e^* \in \{e_{1b}, \dots, e_{nb}, e_{1d}, \dots, e_{nd}\}$ is randomly chosen with probability $\Pr[e_{ix}^*] = r_{ix} / \sum_{jy} r_{jy}$. If a birth event occurs, one individual is added to the population, potentially with a mutation of its trait values relative to those of its parent. Otherwise, a death event occurs, and the target individual is removed.

To enhance computational efficiency, I will group individuals with the same trait values, and increment such a clone's abundance by 1 upon a birth event without mutation occurring in the clone, and decrement it by 1 upon a death event occurring in the clone. When a mutation occurs, a new clone with an initial abundance of 1 is added to the evolving community. Extinction of a clone occurs when its abundance falls to 0. Also, to increase computational efficiency when calculating interactions between clones, I will partition trophic niche space into cells, so that clones interact non-negligibly only with clones in neighboring cells.

For comparing the evolving food webs with empirical data, I will distinguish species based on cluster analysis, such as the k -means method or QT clustering (Heyer et al. 1999). On this basis, I will compare the species-abundance curve, species link distribution, and the maximum trophic level of evolving food webs with previous studies and empirical data, such as that of a Caribbean marine ecosystem (Bascompte et al.

2004). Recently, Kondoh (2008) showed that the distribution of intraguild predation modules in empirical food webs is not random. If time permits, I will try to check the distribution of these modules in the food webs generated by my model.

Work plan

To achieve my goals, I intend to complete the following steps:

- Implement the individual-based model of food-web evolution.
- Using R, convert the model's output into clustered food-web data.
- Compare the emerged food-web structure with that of previous studies. The model should produce results that are qualitatively similar to previous studies.
- By changing parameters and functional forms involved in the model, find settings that produce high species diversity.
- Compare model results with empirical food-web data, such as that from a Caribbean marine ecosystem (Bascompte et al 2004). This comparison is important because a high diversity of modeled food webs does not necessarily mean that they are similar to real food webs. Based on this comparison, model settings will be adjusted.

In future, I intend to extend this model to include migration between multiple patches.

Relevance and link to EEP's research plan

Clarifying the evolutionary dynamics of biodiversity is a main theme of the research project on *Evolving Biodiversity* of the Evolution and Ecology Program at IIASA. Since species in ecosystems strongly interact through prey-predator relationships, to understand the structure of ecosystems we need to understand how trophic networks are created and maintained by evolution. This project aims to develop a basic and extensible model for comparison with other food-web models and empirical data.

Expected output and publications

This work will be included as a part of my Ph.D. thesis, and I intend to publish it as a co-authored article in an international scientific journal.

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