

# Evolutionary dynamics of food-webs and the Ideal Free Distribution

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## Abstract

Evolutionary dynamics of food-webs were numerically analyzed, using a multi-phenotype predator-prey model. In the model, a two-dimensional phenotype space was defined by two traits that determine strategies as prey and as predator, respectively. Evolutionary dynamics of food-webs was numerically calculated as time evolutions of phenotype distributions. Numerical simulation showed autonomous development of complex trophic structures through recursive evolutionary branching. Successful development and maintenance of large food-webs were associated with the Ideal Free Distribution among predators and prey within them.

## Introduction

The present biological communities are ultimately derived from a universal ancestor by repeated speciation through a long evolutionary history of life, is a widespread idea among evolutionary biologists (Di-Giulio, 2001). The history seems to have been influenced by both external and internal factors. Ecological interaction among organisms (e.g. predator-prey interaction, resource competition), that is one of the internal factors, induces their coevolution. It is notable that their evolutionary changes can also change the ways of interactions among them, which change their ways of evolution further. Such feedback process of coevolutionary dynamics may have induced autonomous diversification and development of biological communities.

Reducing complexity not in community structure but in ways of interaction and reproduction, Ito and Ikegami (2003, 2006); Ito et al. (unpublished) constructed a model that describes evolutionary dynamics of a community as a continuous time dynamical system in a two-dimensional phenotypic space. These studies numerically showed that predator-prey interaction among the phenotypes induces coevolutionary formation of a food-web with recursive evolutionary branching of asexual lineages from a single ancestor lineage.

The present study analyzes long term evolutionary dynamics of food-webs, focusing on how the dynamics is related to Ideal Free Distribution.

## Model

Here we use the same predator-prey model with Ito et al. (unpublished). We suppose a two-dimensional phenotype space  $x = (u, r)$ , in which biomass density distribution  $n(x)$  is represented. Traits  $u$  and  $r$  are real numbers that determine strategies of phenotype  $x$  as a predator and as a prey, respectively. We write the biomass change of  $i$ th phenotype as,

$$\frac{dn(x)}{dt} = \lambda \int n(x') \cdot g(x', x) dx' - \int n(x') \cdot g(x, x') - d \cdot n(x), \quad (1)$$

where  $g(x', x)$  denotes the predation rate by phenotype  $x$  on  $x'$ , i.e. functional response, and a constant  $\lambda$  denotes the biomass production per unit predation amount, i.e. trophic efficiency, and a constant  $d$  denotes the rate of biomass loss by energy consumption and natural death.

We define the prey strategy of phenotype  $x$  as a resource distribution in a one-dimensional “resource space”,  $z$ , provided by unit biomass of the phenotype, which we call a “resource pattern”:  $p_r(z, r)$ . The  $z$  can be e.g. body size, hardness, toxicity, or abilities to hide or escape. On the other hand, we define the predator strategy of phenotype  $x$  as its energy investment distribution in the resource space provided by a unit biomass of the phenotype, which we call a utilization distribution:  $M \cdot p_u(z, u)$ . A constant  $M$  is the total amount of utilization and  $p_u(z, u)$  determines its allocation to each resource, i.e. utilization pattern. Here  $\int p_r(z, r)dz = \int p_u(z, u)dz = 1$  is assumed.

The sum of utilization patterns of extant phenotypes gives the total utilization distribution,

$$U(z) = \int n(x) \cdot M \cdot p_u(z, u)dx \quad (2)$$

while the total resource distribution,  $R(z)$ , is given by the sum of resource patterns of extant phenotypes,

$$R(z) = \int n(x) \cdot p_r(z, r)dx \quad (3)$$

The basal resource can be treated as the sunlight.

With the  $U(z)$  and  $R(z)$ , we define the functional response using a general form known as the Beddington-DeAngelis type (Beddington, 1975; DeAngelis et al., 1975),

$$g(x', x) = M\Omega \int p_u(z, u)\phi(z)n(x')p_r(z, r')dz, \quad (4)$$

where

$$\phi(z) = \frac{1}{\beta + \beta' \cdot U(z) + R(z)}, \quad (5)$$

Substituting this into Eq. (1) yields,

$$\frac{1}{n(x)} \cdot \frac{dn(x)}{dt} = \lambda M\Omega \int p_u(z, u)\phi(z)R(z)dz - \Omega \int p_r(z, r)\phi(z)U(z)dz - d. \quad (6)$$

Since no biomass inflow into the system is assumed, the system cannot sustain its total biomass. Here we introduce a basal resource  $I(z)$ , which is added to the total resource distribution,

$$R(z) = \int n(x) \cdot p_r(z, r)dx + I(z) \quad (7)$$

This equation gives population dynamics under asexual reproduction.

We introduce sexual reproduction into Eq. (6), as additional biomass flows among phenotypes,

$$\frac{dn(x)}{dt} = (\lambda \cdot G(x) - L(x) - d) \cdot n(x) + B(x) - b(x), \quad (8)$$

where  $b(x)$  is the rate of reproduction of phenotype  $x$  (i.e. biomass outflow from  $x$ ), given by  $b(x) = \zeta \cdot \lambda G(x)n(x)$ , where  $\zeta$  is a constant ( $\leq 1$ ). The  $B(x)$  is the rate of offspring production with phenotype  $x$  by all phenotypes (biomass inflow into  $x$ ). Following Dieckmann and Doebeli (1999),

we assume that mating probability between phenotypes  $x$  and  $x'$  is a decreasing function with their phenotypic distance,  $\exp(-(x - x')^2/2\sigma_m^2)$ . We also assume that mating between phenotypes  $x$  and  $x'$  produces phenotype  $(x + x')/2$  only, that is simplification of (Drossel and McKane, 2000). With these assumptions the  $B(x)$  is derived as,

$$B(x) = \int \frac{b(y) \int \exp(-(y - y')^2/2\sigma_m^2) b(y') \delta(x - (y + y')/2) dy'}{\int \exp(-(y - y')^2/2\sigma_m^2) b(y') dy'} dy, \quad (9)$$

where  $\int B(x) dx = \int b(x) dx$  is fulfilled.

Then Eq. (8) with Eq. (9) describes population dynamics under sexual reproduction. Note that this formulation only expresses one possibility of the effect of hybridization that counteracts disruptive selection.

In order to describe evolutionary dynamics, mutation process is introduced into Eq. (8) as diffusion of biomass from extant phenotypes to their neighbour phenotypes.

$$\frac{\partial n(x)}{\partial t} = (\lambda \cdot G(x) - L(x) - d) \cdot n(x) + B(x) - b(x) + \nabla(D \cdot \nabla B(x)), \quad (10)$$

where  $D = (D_u, D_r)$  denotes a diffusion coefficient vector corresponding to the mutation rates.

## Calculation method

For simplicity, the utilization and resource patterns were defined with a delta function  $p_u(z, x) = M \cdot \delta(z - u)$ ,  $p_r(z, x) = \delta(z - r)$ . In this case, phenotypes with trait  $u = z_0$  prey on phenotypes whose  $r$  is equal to  $z_0$ . In this paper,  $r$  and  $u$  are called a ‘‘resource trait’’ and a ‘‘utilizer trait’’, respectively.

Time evolutions of phenotype distributions were calculated with the Explicit Euler Method, on the discretized phenotype space. Absorbing boundaries were assumed for the phenotype space. Considering that densities of phenotypes cannot be lower than that of one individual in real populations, phenotypes with their densities lower than a given threshold,  $\epsilon$ , were removed instantly at each time step. For fast calculation, we assumed that the mating between phenotypes only occurs when both distances in traits  $r$  and  $u$  between them are less than a given threshold,  $\epsilon_m$ . This study treated each phenotype density peak as one cluster.

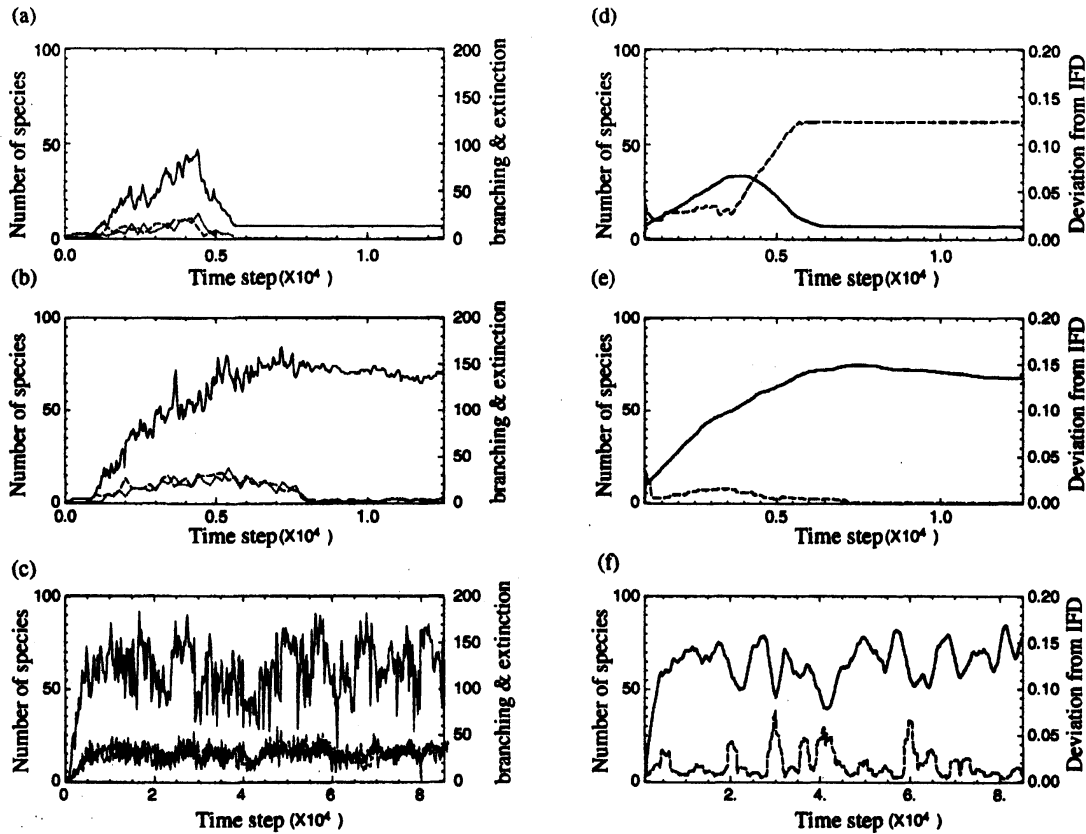


Figure 1: Long term dynamics of food-webs. The number of species (solid line) and the rates of branching (broken line) and extinction (dotted line) in different three long-term evolutionary dynamics, (a): collapse, (b): static maintenance, (c): dynamic maintenance, are plotted. (d), (e) and (f) are moving-averaged dynamics of the number of species (solid line) and the deviation from IFD (broken line) of (a), (b) and (c), respectively. Deviation from IFD was calculated as  $\int (U(z) + R(z)) \cdot \{\log(U(z)/R(z)) - \log(M \cdot \hat{A})\}^2 dz / \int (U(z) + R(z)) dz$ . Model parameters:  $\lambda = 0.15, d = 1.0, \beta = 0.0, \varepsilon = 1.0 \times 10^{-5}, \sigma_m = 2.8 \times 10^{-2}, \zeta = 1.0, \Delta t = 1.0 \times 10^{-2}, L(z) = 4000/M \cdot \exp[-(z - \mu_L)^2 / (2\sigma_L^2)], \mu_L = 0.0, \sigma_L = 0.08, \varepsilon_m = 1.25 \times 10^{-2}, u = [0, 2], r = [0, 2], \Omega = 20, D_u = 3.6 \times 10^{-4}, D_r = 2.0 \times 10^{-3}, M = 9.0$  for (a),  $M = 10.5$  for (b) and  $M = 9.7$  for (c)

## Results

Simulated food-webs typically show repeated collapse and development of their structures. Some food-webs never recover (Fig. 1 (a)), while some are maintained for long periods of time without losing the diversity (Fig. 1 (b) and (c)). We have roughly two distinct dynamic phases in the system. One is “static-maintenance” phase, in which both population dynamics and evolutionary dynamics are stabilized (Fig. 1 (b)). The other is “dynamic maintenance” phase in which frequencies of evolutionary branching and extinction are roughly balanced. This keeps the magnitudes of collapse and development relatively small (Fig. 1 (c)). In the static-maintenance phase and during development in the dynamic maintenance phase, almost all species have both prey and predators. That is, any species as a node in the food-web has both biomass inflow and outflow from/to other nodes. In other words, the food-web forms a closed structure. Moreover, when  $\beta = 0$  (i.e. the ratio dependent response) is assumed, the distribution of  $U(z)/R(z)$  tends to be flat in the resource space, during static main-

tenance. This corresponds to the Ideal Free Distribution (IFD) (reviewed by Kacelnik et al. (1992)), because assuming flat  $U(z)/R(z)$  and  $\beta = 0$  in Eq. (6) results in an identical gain  $G(x)$  for all possible strategies of predation. Under these assumptions, the equilibrium ratio in Eq. (6) is given by  $U(z)/R(z) = M(\lambda\Omega - d/M)/(\Omega + d)$ . Since  $U(z)/M$  is the biomass of predators preying on resource  $z$ ,  $\hat{A} = (\lambda\Omega - d/M)/(\Omega + d)$  gives the biomass ratio of interacting predator and prey. We call the ratio, “ $\hat{A}$ -ratio”, and its state, “ $\hat{A}$ -equilibrium”.

Indeed, as the system falls into a static-maintenance phase, the ratio  $U(z)/R(z)$  converges to  $M \cdot \hat{A}$  at all locations of extant resources, and the deviation from IFD ( $\hat{A}$ -ratio) converges to zero (Fig. 1 (e)). In the case of the dynamic-maintenance, the system tends to have a larger number of species when the deviation is smaller (Fig. 1 (f)), which implies that convergence to IFD corresponds to successful development and maintenance of a food-web structure.

## Discussion

There are several models focusing on such longer time scales of dynamics, considering evolutionary adaptation of species (Kondoh, 2003), or expressing speciation by introducing new species similar to their parent species (Caldarelli et al., 1998; Drossel et al., 2004; Yoshida, 2003). Describing phenotype-level dynamics of a community, Ito and Ikegami (2003, 2006); Ito et al. (unpublished) demonstrated food-web formation with recursive evolutionary branchings of asexual phenotypic clusters. The observed relationship between food-web dynamics and IFD can be explained as follows (Ito et al., unpublished). In any situation,  $u$  evolves towards higher density of resource, while  $r$  evolves to escape from predation. As a result,  $U(z)$  evolves so that  $U(z)$  becomes similar to  $R(z)$  (i.e. toward IFD), while  $R(z)$  evolves so that  $R(z)$  becomes dissimilar to  $U(z)$ . Thus if evolutionary speed of  $u$  is slow relative to  $r$ , there is a large difference between  $R(z)$  and  $U(z)$ . In this case phenotypes under very low selection pressures exist, which easily exclude other phenotypes, destroying the food-web structure. Then complex food-web cannot develop. On the other hand, if evolutionary speed of  $u$  is fast relative to  $r$ , the deviation from IFD is kept small, in which emergence of too strong competitors are suppressed. In this case complex food-webs may develop. And if  $u$  is sufficiently fast to suppress evolution of  $r$ , static food-web structures emerge, otherwise the dynamics is continued with endless arms race between  $u$  and  $r$ .

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