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Food-web formation with recursive evolutionary branching

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Abstract

A reaction–diffusion model describing the evolutionary dynamics of a food-web was constructed. In this model, predator–prey relationships among organisms were determined by their position in a two-dimensional phenotype space defined by two traits: as prey and as predator. The mutation process is expressed with a diffusion process of biomass in the phenotype space. Numerical simulation of this model showed co-evolutionary dynamics of isolated phenotypic clusters, including various types of evolutionary branching, which were classified into branching as prey, branching as predators, and co-evolutionary branching of both prey and predators. A complex food-web develops with recursive evolutionary branching from a single phenotypic cluster. Biodiversity peaks at the medium strength of the predator–prey interaction, where the food-web is maintained at medium biomass by a balanced frequency between evolutionary branching and extinction.

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1. Introduction

The origin and evolution of species have been studied by various empirical and theoretical approaches. Recent advances in theories of speciation (Geritz et al., 1998; Dieckmann and Doebeli, 1999; Higashi et al., 1999; Doebeli and Dieckmann, 2000; Kaneko and Yomo, 2000) have shown that various intra- and inter-species interactions split a single founding population into two different populations, a process called 'evolutionary branching' (Geritz et al., 1998). Doebeli and Dieckmann (2000) have demonstrated that various ecological interactions (resource competition, mutualism and predator–prey relationships) can cause evolutionary branching, even in sexual populations, accompanied by evolution of assortative mating. Highashi's sexual selection model has shown that selection only on mating traits can give rise to evolutionary branching. The main concern of these models is evolutionary branching at each trophic level. This study considers higher-order branching, which generates populations at new trophic levels, focuses on predator–prey interactions, and investigates how the complexity of a food-web is built up through evolutionary dynamics.

Previous theoretical studies on food-web evolution have been mainly based on replicator or Lotka–Volterra models. Drossel et al. (2001) have shown the development of a food-web structure from bottom trophic species by generalizing the Lotka–Volterra model. Using an evolutionary replicator model, Jain and Krishna (2002) have shown the role of innovation and of keystone species in large extinctions. An other approach can be found in the study by Lindgren and Nordahl (1993) on the evolution of a food-web, using a model of the iterated prisoner's dilemma game. However, these previous approaches to evolutionary dynamics of a food-web invite new species from outside, as these cannot deal with the mechanism of creating new species from the intrinsic ecological dynamics that maintains the food-web.

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The approach used in this study, building a food-web from scratch with recursive evolutionary branching, has a critical role in bridging the gap between previous speciation models and food-web models. In this paper, a predator–prey model is constructed in the form of a reaction–diffusion model with minimal complexity, and the evolutionary dynamics within it is analysed by numerical simulation. The observed evolutionary branches were classified, and how the patterns of autonomous development and collapse of the food-web depends on the model parameters was investigated. Finally, the issue of how ecological diversity and evolution are interrelated is discussed.

2. Modeling

Assume a large k-dimensional phenotype space $x = \{x_0, ..., x_k\}$, large enough to represent all kinds of creatures in it. For simplicity, it is assumed that all phenotypes reproduce their offspring asexually, and that the population dynamics of each phenotype's biomass $n(x)$ is determined by a predator–prey interaction among them

$$\frac{\mathrm{d}n(x)}{\mathrm{d}t} = \lambda \int n(x) \cdot g(x, x')\,\mathrm{d}x' - \int n(x') \cdot g(x', x)\,\mathrm{d}x' - d \cdot n(x), \qquad (1)$$

where $g(x, x')$ is the predation amount by a unit biomass of phenotype x on phenotype x' per unit time, i.e. a functional response. λ denotes biomass production per unit resource gain, i.e. trophic efficiency, which is fixed at 0.1, which is a medium value among empirical studies (Humphreys, 1979). This formula is a continuous expression of a general description of food-web dynamics by Drossel and McKane (2003).

Functional response $g(x, x')$ can be understood as an integration of the interrelationship between the strategy of phenotype x as predator, and the strategy of phenotype x' as prey. Although these strategies are implicit in most of the previous models (Kondoh, 2003; Drossel et al., 2001; Jain and Krishna, 2002), these are important footholds for ecological reasoning of evolutionary dynamics. For example, why and how directional change or diversification occurs are thought to be strongly related to feeding strategies or escape behavior from predation (Schluter, 2000). Thus, in this study, prey and predator strategies are explicitly defined separately and their functional response is defined.

Prey strategies can be translated into resource properties, such as body size, hardness, toxicity, and the ability to hide and escape. We suppose a space z, with resource properties as its axes and call it the 'resource space'. In this resource space, each phenotype x is represented as a resource distribution $n(x) \cdot p_r(z, x)$, where $p_r(z, x)$ gives a resource density at location z (i.e. with property z) provided by a unit biomass of phenotype x (Fig. 1(a)). This function corresponds to the prey strategy and is called the 'resource pattern.' The resource pattern can have a certain breadth because resource properties of the same phenotype can be different among individuals, depending on their age, diet, environment, etc.

Conversely, predator strategies were translated into utilization distributions on the resource space. The utilization distribution of phenotype x was defined by $n(x) \cdot p_u(z, x)$, where $p_u(z, x)$ gives the density of 'energy investment' provided by a unit biomass of phenotype x, for a resource with property z (Fig. 1(a)). This utilization pattern $p_u(z, x)$ corresponds to the predator strategy. Energy investment can be due to a searching effort, physiological features like detoxification, or for special structures such as a sonar sensor or strong jaws.

The functional response of phenotype x was then defined as a predator to phenotype x' as prey, based on the overlap between $p_u(z, x)$ and $p_r(z, x')$, in the form of a type-II functional response (Holling, 1958):

$$g(x, x') = \int \Omega \cdot \frac{p_u(z, x) \cdot p_r(z, x') \cdot n(x')}{1 + (R(z)/M)}\,\mathrm{d}z, \qquad (2)$$

where Ω is the interaction strength, M is the maximum predation amount by unit biomass of phenotype x, and $R(z) = \int n(x) \cdot p_r(z, x)\,\mathrm{d}x + L(z)$ is the total resource

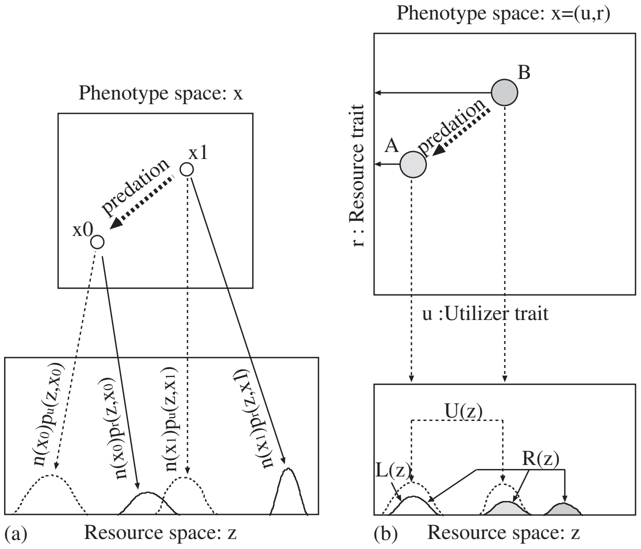

Fig. 1. Definition of predator–prey interactions. (a) Predator–prey relationship between two phenotypes x_0 and x_1. Curves with a solid line in the resource space indicate resource distributions provided by the phenotypes, while curves with a broken line indicate their utilization distributions. Phenotype x_1 preys on phenotype x_0 in this case. (b) Predator–prey relationship among phenotypic clusters under the specific definitions of the phenotype space $x = (u, r)$, the resource space z, $p_r(z, x) = \delta(z - r)$ and $p_u(z, x) = \delta(z - u)$. In this case, cluster A utilizes the inward resource $L(z)$ and is preyed on by cluster B. $R(z)$ denotes the total resource distribution, while $U(z)$ denotes the total utilization distribution.

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