

Food-web formation with recursive evolutionary branching

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Received 5 July 2004; received in revised form 20 April 2005; accepted 2 May 2005

Available online 5 July 2005

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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Keywords: Food-web; Evolutionary dynamics; Predator–prey model; Evolutionary branching; Reaction–diffusion model

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 $x = \{x_0, \dots, x_k\}$, 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

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

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):

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

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

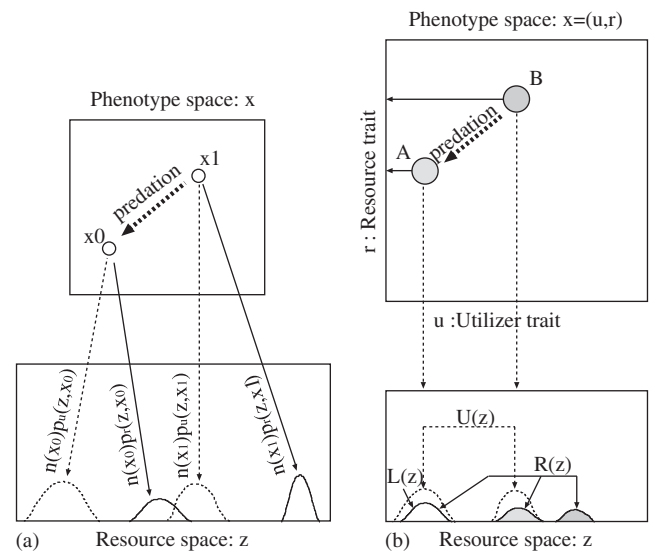


Fig. 1. Definition of predator–prey interactions. (a) Predator–prey relationship between two phenotypes x_0 and x_1 . Curves with a solid line in the resource space indicate resource distributions provided by the phenotypes, while curves with a broken line indicate their utilization distributions. Phenotype 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.

density existing at z , i.e. the total resource distribution. $L(z)$ is an inward resource distribution from outside the system, defined by a Gaussian function:

$$L(z) = L_0 \cdot \frac{1}{\sqrt{2\pi}\sigma_L} \exp\left[-\frac{(z - \mu_L)^2}{2\sigma_L^2}\right],$$

where L_0 , μ_L and σ_L denote the total amount, the position and the width of the resource, respectively. Since this study is concerned with the total biological community, the resource $L(z)$ is treated as sunlight.

This functional response $g(x, x')$ can be expressed differently, with the distribution of the total interaction amount $F(z)$

$$g(x, x') = \int F(z) \cdot \frac{p_u(z, x)}{U(z)} \cdot \frac{n(x')p_r(z, x')}{R(z)} dz, \quad (3)$$

where

$$F(z) = \Omega \frac{U(z)R(z)}{1 + (R(z)/M)}, \quad (4)$$

where $U(z) = \int n(x) \cdot p_u(z, x) dx$ is the total utilization density at z , i.e. the total utilization distribution. Since this formula clearly shows the core of the functional response, Holling type-II (Holling, 1958): $R(z)/1 + (R(z)/M)$, other types of functional response are easily implemented by using them for the definition of $F(z)$.

Substitution of formula (3) into formula (1) yields

$$\begin{aligned} \frac{dn(x)}{dt} &= \lambda \int \frac{F(z)n(x)p_u(z, x) \int n(x')p_r(z, x') dx'}{U(z)R(z)} dz \\ &\quad - \int \frac{F(z)n(x)p_r(z, x) \int n(x')p_u(z, x') dx'}{U(z)R(z)} dz \\ &\quad - d \cdot n(x) \\ &= \lambda \int F(z) \frac{n(x)p_u(z, x)}{U(z)} dz \\ &\quad - \int F(z) \frac{n(x)p_r(z, x)}{R(z)} dz - d \cdot n(x) \\ &= A(x) \cdot n(x), \end{aligned} \quad (5)$$

where

$$A(x) = \int \left[\lambda \cdot \frac{F(z)p_u(z, x)}{U(z)} - \frac{F(z)p_r(z, x)}{R(z)} \right] dz - d. \quad (6)$$

To describe evolutionary dynamics, a mutation process was introduced into this model as a diffusion process (Kimura, 1983), assuming that most of the extant phenotypes have a large number of individuals, and that the magnitude of each mutation is small,

$$\frac{\partial n(x)}{\partial t} = A(x) \cdot n(x) + \nabla(D \cdot \nabla n(x)), \quad (7)$$

where D denotes the diffusion coefficient vector. When explicit forms of the phenotype space x , the resource space z , resource pattern $p_r(z, x)$ and the utilization pattern $p_u(z, x)$ are given, the corresponding evolutionary dynamics can be studied by means of this equation.

Since the purpose of this study was to describe food-web evolution with minimal complexity, an assumption of a one-dimensional resource space z , and a two-dimensional phenotype space $x = (u, r)$ was made, where u only affects the utilization pattern, while r only affects the resource pattern. In this paper, r is called the ‘resource trait’ and u is the ‘utilizer trait’. Although certain limitations might exist on possible combinations between u and r caused by pleiotropy or physiological constraints, no assumption was made about this limitation in order to simplify the model. Moreover, for simplicity the utilization and resource patterns were defined with a delta function, assuming appropriate scaling among z , u and r ,

$$p_u(z, x) = \delta(z - u), \quad (8)$$

$$p_r(z, x) = \delta(z - r), \quad (9)$$

where $\int_{-\infty}^{\infty} \delta(z) dz = 1$. In other words, phenotypes with a trait $u = u_0$ prey on phenotypes whose r is equal to u_0 (Fig. 1(b)). Thus, phenotypes whose u is equal to their r are cannibalistic. In practice, the dynamics of the phenotype distribution $n(x)$ was calculated based on Eq. (7) by discretizing the explicit Euler method. At each time step, the phenotypes whose density become lower than a significantly small density $\varepsilon (= 1.0 \times 10^{-9})$ were removed, which is assumed to be the density of one individual. It was also assumed that the phenotype space has absorbing boundaries. The next section describes the observed evolutionary branching and the resulting food-web dynamics.

3. Simulation results

3.1. Formation of trophic species

The initial phenotype distribution is a single phenotypic cluster, utilizing the inward resource $L(z)$. Since $L(z)$ was treated as sunlight, this cluster corresponds to a producer (Fig. 2(a)). Within the wide range of parameter values (trophic efficiency: $0.05 < \lambda < 0.95$, interaction strength: $1.0 < \Omega < 50$, maximum predation amount: $1.0 < M < 100.0$, mutation rates: $1.0 \times 10^{-12} < D_u < 1.0 \times 10^{-4}$, $1.0 \times 10^{-12} < D_r < 1.0 \times 10^{-4}$, the position and the width of the inward resource: $0 < \mu_L < 1.0$, $0.02 < \sigma_L < 0.4$), the dynamics of the phenotype distribution is composed of directional evolution and evolutionary branching of isolated phenotypic clusters, beginning from the single cluster (Fig. 2). These clusters can be treated as ‘trophic species’ that are functional groups of taxa, consisting of species sharing the same predators and prey in the food-web. We call these phenotypic clusters ‘trophic species.’ The concept of trophic species has sometimes been criticized, but it is widely accepted,

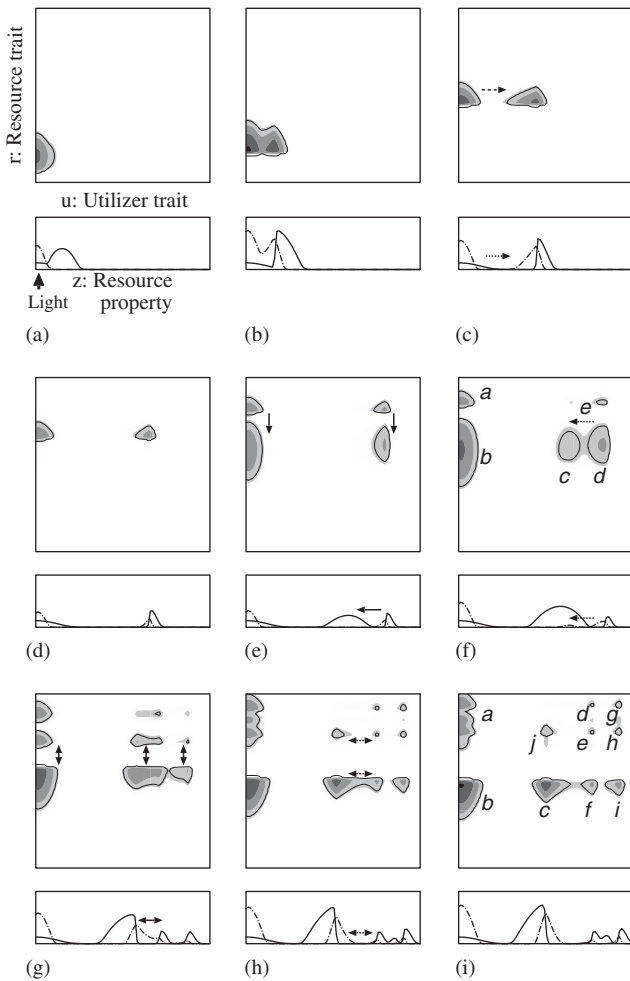


Fig. 2. Recursive evolutionary branching from a single cluster. Time elapses from (a) to (i). In the phenotype space (the larger boxes), the darker colors indicate higher biomass densities. Contours with solid lines correspond to the threshold density for counting trophic species. In the resource space (the smaller boxes), curves with solid lines indicate the total resource distributions ($R(z)$) provided by the extant phenotypes and the inward resource, while curves with broken lines indicate their utilization distributions ($U(z)$). The arrow indicates the type of branching: solid arrows for type- r , broken arrows for type- u and double-head arrows for type- c . Model parameters: $M = 10.0, \Omega = 13.0, D_u = 1.2 \times 10^{-7}, D_r = 0.6 \times 10^{-7}, \lambda = 0.1, d = 1.0, K = 1.0 \times 10^4, \varepsilon = 1.0 \times 10^{-9}, \varepsilon_c = 5.0 \times 10^{-2}, L_0 = 15/\Omega, \mu_L = 0, \sigma_L = 0.08, \Delta t = 5.0 \times 10^{-4}$.

and structural food-web studies can reduce biases in the data by its use (Williams and Martinez, 2000).

In the area occupied by each trophic species, phenotypes with a few prey and many predators become extinct, while phenotypes with many prey and few predators rapidly increase, generating new phenotypes in their neighbors. This process continuously changes the position, size and shape of the occupied areas of the trophic species in the phenotype space, which corresponds to evolutionary dynamics. In general, these trophic species evolve their u -trait for more gain (predation), and evolve their r -trait for less loss (being

preyed on). There is an evolutionary arms race within and between them, which maintains their phenotypic cohesiveness.

To count these trophic species, a threshold biomass density $\varepsilon (> 1.0 \times 10^{-9})$ was defined to identify each connected cluster in the phenotype space. The number of trophic species at each time step did not change significantly, unless the threshold was set too low or high.

3.2. Evolutionary branching

Various patterns of evolutionary branching arise, depending on interaction relationships within and between trophic species, which are given by their formation in the phenotype space. In the early stage of development, the network of a food-web immediately evolves from a simple graph (Fig. 3(a)) to a complex structure (Fig. 3(b)). To know this whole process, the evolutionary tree is depicted in three-dimensional space (Fig. 4). These branching patterns are classified into three types in terms of biological functions, by referring to Fig. 2 (a–i).

- *Type-u*: Branching as predator, in the direction of the u -trait to utilize new resources. Fig. 2 (a) → (d) shows a typical example of this branching pattern. The initial trophic species provides itself as a resource in

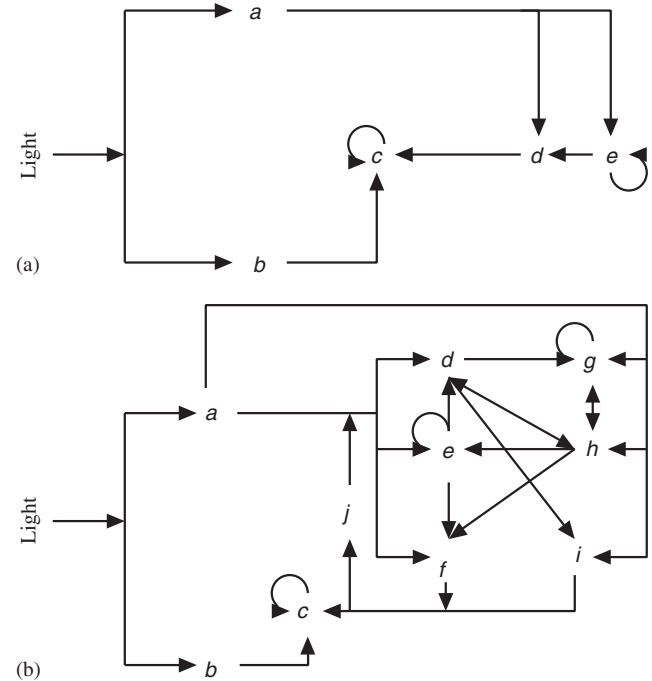


Fig. 3. Extracted food-web topology from Fig. 2(a) and (b) correspond to (f) and (i) in Fig. 2, respectively. Each letter denotes the trophic species in Fig. 2. Arrows indicate the resource flows among the trophic species.

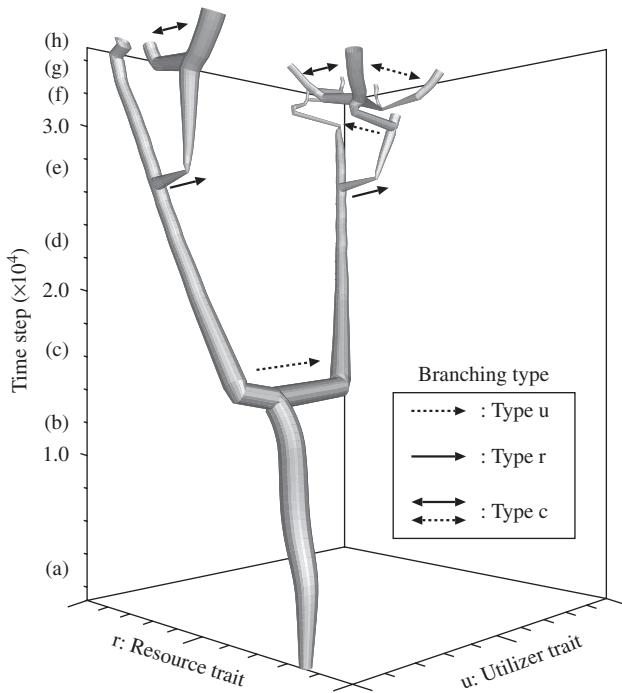


Fig. 4. Phylogenetic tree extracted from the dynamics in Fig. 2. Each pipe indicates a historical trace for each trophic species, where the pipe width expresses the biomass of the species. An appropriate time slice of this phylogenetic tree gives each phenotype distribution in Fig. 2. Branching type is denoted by line and arrow styles.

the resource space in Fig. 2(a). A part of the trophic species starts to exploit this resource, which brings about type-*u* branching (Fig. 2(b) → (c)). This predation forces the original ‘prey’ species to evolve its *r*-trait to avoid predation, and the newly generated ‘predator’ species also evolves its *u*-trait to pursue the prey species, which results in an evolutionary arms race (Fig. 2(c) → (d)). Since in this case the predator species is cannibalistic, it also shifts its *r*-trait simultaneously. Whenever a simulation was started from a single trophic species, the primary branching was always of this type.

- *Type-r*: Branching as prey, in the direction of the *r*-trait to escape from predation. Predation on the middle of a resource distribution provided by certain trophic species induces type-*r* branching of the resource. Trophic species evolving in the direction of the *r*-trait under predation pressures are also likely to generate new trophic species through this type of branching, in the direction opposite to the arms race. Fig. 2(d) → (e) shows simultaneous type-*r* branching due to predation pressure by the ‘predator’ species located on the right-hand side in Fig. 2(d).
- *Type-c*: Simultaneous branching of both prey (*r*-direction) and predator (*u*-direction) through co-evolutionary dynamics of the predator–prey system. A clear example can be found in Fig. 2 (f → i). The

trophic species labeled ‘*c*’ exploits the middle of the wide resource distribution provided by the species labeled ‘*b*’ and ‘*d*’ (Fig. 2(f)), which leads to type-*r* branching of species ‘*b*’ and ‘*d*’, and type-*u* branching of species ‘*c*’ almost simultaneously (Fig. 2(h)). In this case, cannibalism of species ‘*c*’ also brings about additional type-*r* branching (Fig. 2(g)). Due to this branching, the structure of the entire food-web becomes complicated. The complexity of the network is well observed by abstracting the food-web structure (Fig. 3). The topology associated with Fig. 2(f) is depicted in Fig. 3(a). This evolves into the complex network (Fig. 3(b) that corresponds to Fig. 2(i)), in which the maximum length of the food chain reaches four.

Note that a new resource derived from type-*r* branching induces type-*u* branching, and that the new predation pressure from the type-*u* branching induces another type-*r* branching. Thus, these branchings can arise recursively from a single trophic species, generating a complex food-web. Since each trophic species in this dynamics can act as both prey and predator at the same time in the food-web, the generic mechanism of the whole evolutionary dynamics seems intricate.

3.3. Dynamics of the number of trophic species and the total biomass

The whole co-evolutionary dynamics of interacting trophic species comprises the evolutionary dynamics of the food-web. To grasp the features of the macro-dynamics, the long-term dynamics of the number of trophic species and the total biomass (i.e. $\int n(x) dx$) were calculated.

The model presents a problem if any producers escape predation during the long-term simulation, as a type-II functional response allows unlimited growth of the producer until the simulation crashes. However, such unlimited growth should not occur in real biological communities because of competitive interference or a shortage of essential nutrients, etc. To avoid this unrealistic phenomenon, a competition term was introduced into the model

$$\frac{dn(x)}{dt} = A(x) \cdot n(x) \cdot \left(1 - \frac{\int \alpha(x', x)n(x') dx'}{K(x)} \right) + \nabla(D \cdot \nabla n(x)), \quad (10)$$

where $K(x)$ is the carrying capacity of phenotype x , and $\alpha(x', x)$ gives the amount of negative effect on phenotype x by the unit biomass of phenotype x' . One possible competition function is

$$\alpha(x', x) = \exp\left(-\frac{(x' - x)^2}{2\sigma_c}\right)$$

that assumes competition among phenotypes similar to each other. Under this competition function, qualitatively similar food-web evolution arises, including the three types of evolutionary branching. However, Dieckmann and Doebeli (1999) showed that this competition function alone can bring about evolutionary branching, which makes the mechanism of evolutionary branching in the model redundant and unclear. Therefore, to keep the model simple, it was assumed that competition occurs only within the same phenotype, $\alpha(x', x) = \delta(x' - x)$, which does not induce evolutionary branching by itself. In addition, for simplicity, the carrying capacity $K(x)$ was assumed to be constant.

The critical control parameters for the macrodynamics are the interaction strength Ω and the maximum amount of predation M . Since Ω and M are qualitatively similar to each other in their effects, this study focuses on the interaction strength Ω .

In the relatively weaker strength regions, the system does not frequently give rise to type- r and type- u branchings and seldom shows type- c branching, which results in a low branching frequency. During this slow development of the food-web, excess growth of certain trophic species leads to massive extinction before the food-web attains a certain complexity, resetting the dynamics. Then the evolutionary development starts again from the bottom trophic species. A typical phenotype distribution in this mode is depicted in Fig. 6(a), where only a few trophic species coexist because the low frequency of branching cannot complement frequent extinction. This scenario of repeated development and collapse changes from periodic (Fig. 5(a)) to chaotic (Fig. 5(b)) with an increase of the interaction strength Ω .

Conversely, at the larger interaction strength, a lattice-like formation composed of many trophic species (Fig. 6(b)) is likely to develop with frequent type- u , type- r and type- c branching. The generated complex network effectively suppresses the excess growth of each trophic species. In the phenotype space, the organized formation of trophic species continues to expand outwards. Subnetworks on the periphery of the formation continuously become extinct, while new networks are created in the middle of the formation. Since the frequency of the collapse and the creation of the network are balanced in this mode, the total biomass and the numbers of trophic species are maintained dynamically. This is well demonstrated in Fig. 5(c). It is notable that the system in this mode has a much larger number of species than the case of the smaller interaction strength, despite the total biomass being relatively much smaller. However, mass extinction is aperiodically induced, accompanied by growing oscillation of the total biomass (Fig. 5(c)).

At a much larger interaction strength (Fig. 5(d)), the amplitude of the biomass changes is small and

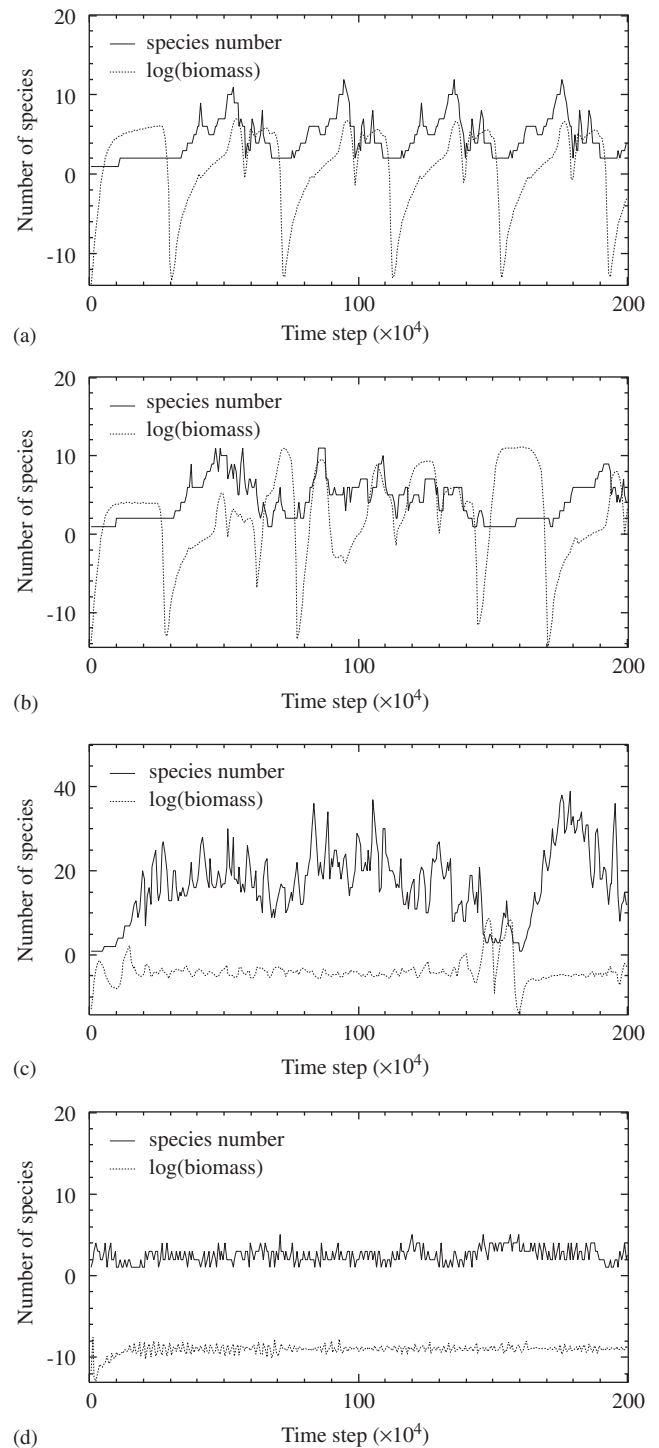


Fig. 5. Long-term dynamics of the number of trophic species and the total biomass at different interaction strengths Ω : (a) $\Omega = 10$, (b) $\Omega = 11$, (c) $\Omega = 20$, (d) $\Omega = 100$. Other parameters used have the same values as in Fig. 2, except for $L_0 = 22/\Omega$.

branching arises frequently. However, rapid energy consumption through strong interaction keeps the total biomass at a considerably small level. Consequently, the food-web cannot sustain a large number of species because of the shortage of biomass.

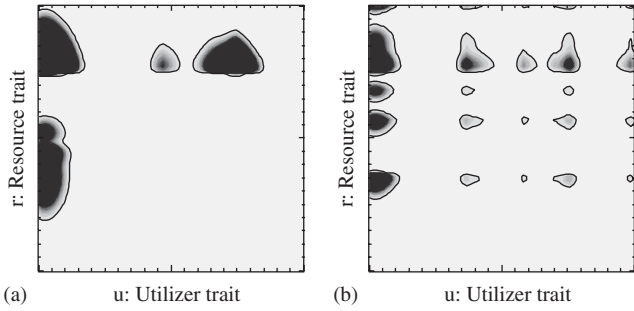


Fig. 6. Typical phenotype distributions at different interaction strengths Ω . (a) and (b) are the typical phenotype distributions in Fig. 5(a) and (c), respectively.

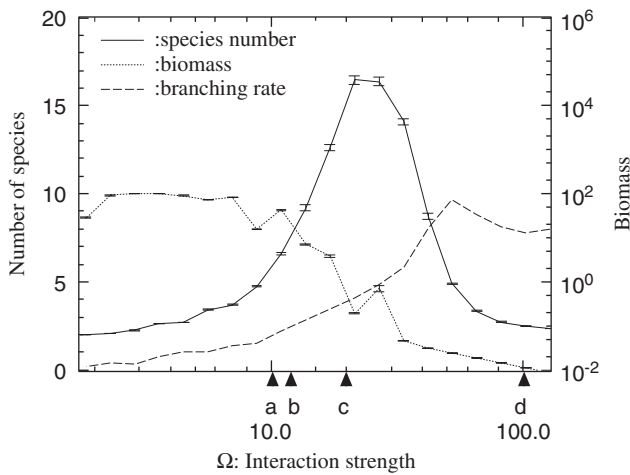


Fig. 7. The effect of interaction strength on time-averages of the number of trophic species and the total biomass. Time-average of the number of trophic species, the total biomass and the frequency of evolutionary branching per 1000 time step, through a long time (6×10^5 steps), are plotted. Each parameter value has 20 replications of calculation and the error bar indicates s.e.. Each letter on the horizontal axis indicates the interaction strength corresponding to each simulation in Fig. 5. Model parameters: $L_0 = 22/\Omega$, and the others have the same values as in Fig. 2.

3.4. Parameter dependencies on time-averaged properties

This study investigated the effects of parameter changes on long-term averages of the number of species, the total biomass, and the frequency of evolutionary branching per species.

(1) *Interaction strength* (Ω (Fig. 7)): Time-averaged properties of the system at different interaction strengths were plotted. The branching rate increases with the interaction strength, while the total biomass decreases. The number of trophic species reaches its maximum when the branching rate and the total biomass are both at a medium magnitude.

(2) *Mutation rates* (Fig. 8): Time-averaged properties of the system at different mutation rates were plotted. When the mutation rates of the two traits (D_u, D_r) are small and close to each other, the system tends to have a

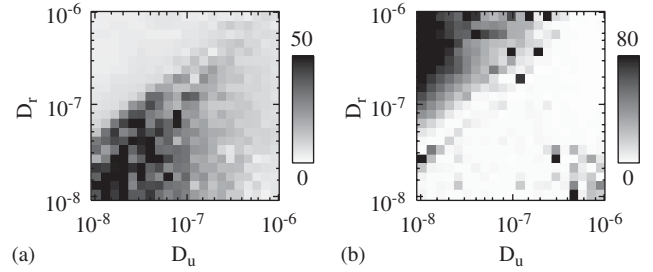


Fig. 8. The effect of mutation rates on time-averages of the number of trophic species (a) and of the total biomass (b). Horizontal and vertical axes are mutation rates of the utilizer trait u , and of resource trait r , respectively. Model parameters: $\Omega = 13.0, L_0 = 20/\Omega$, and the others have the same values as in Fig. 2.

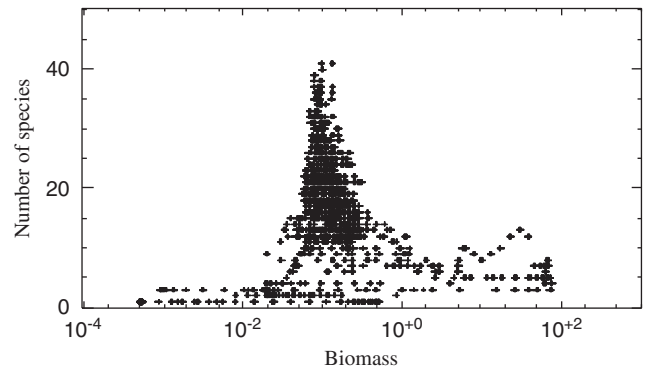


Fig. 9. A relationship between the total biomass and the number of trophic species. This is a scatter plot of the time series data used for Fig. 5(c).

large number of trophic species. In the area where D_r is less than D_u , the system holds more species and less biomass than in the opposite area ($D_r > D_u$), in which a predator with slow evolution cannot suppress the excess increase in prey numbers.

3.5. Relationship between biomass and species diversity

A large biomass does not necessarily imply a large number of species. The model showed a strong tendency where the medium magnitude of the total biomass gave the maximum number of trophic species. Fig. 9 shows a scatter graph of time-series data for Fig. 5(c), which has a sharp peak at around 0.1. This convex form is commonly observed in temporal dynamics over a wide range of parameter values. Moreover, when the number of species and the total biomass are time-averaged through dynamics at each parameter set, a scatter graph of the time-averaged data at different parameter sets (e.g. in mutation rates, the interaction strength and the maximum predation amount) also tends to form convex shapes (not shown).

We argue that the dependency can be explained as follows: when the amount of biomass is low, the system simply cannot sustain a large number of species. On the other hand, the system may have a large biomass only when producer species are prospering in the absence of predators. In this case, the number of trophic species is kept small. Only the medium range of biomass corresponds to balanced suppression among prey and predators, which maintains a rich and complex food-web network with many trophic species.

4. Discussion

4.1. Evolutionary dynamics of species

Numerical simulations using the model showed the formation of isolated phenotypic clusters and their co-evolutionary dynamics, including various types of evolutionary branching, which were classified into type-*u*, type-*r* and type-*c* branching. Type-*u* and type-*r* branchings induce each other, generating a recursive branching sequence. Co-evolutionary branching of predator and prey, that is, type-*c* branching, can be understood as a part of the sequence of type-*u* and type-*r*, with no time lag. These evolutionary branchings also arise in the case in which resource pattern and utilization have a certain width (e.g. Gaussian function). Analytical conditions for this evolutionary branching will be obtained based on the Adaptive Dynamics theory (Geritz et al., 1998; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2000).

As for previous theoretical studies for evolutionary branching or ecological speciation, type-*u* branching is essentially similar to the evolutionary branching through resource competition described by Doebeli (1996) and Dieckmann and Doebeli (1999), showing that even sexual populations can bring about evolutionary branching, with the existence of assortative mating or accompanied by evolution of assortative mating. Type-*r* and type-*c* branching have also been demonstrated in both asexual and sexual populations by Doebeli and Dieckmann (2000).

All of the three types of branching described above have already been previously successfully described in theoretical studies. However, none of the previous models described recursive emergence of higher trophic levels, which is essential for the emergence of complex food-webs in nature. This limitation in previous models probably stems from the pre-assignment of the basic structure of trophic relationships. These relationships should be much more flexible in real communities, in a long time-scale of evolutionary dynamics. Our model realized this feature, assuming that any phenotype has the potential to prey on or be preyed on by any phenotype through evolutionary changes.

4.2. Evolutionary dynamics of food-webs

The dynamic properties of food-webs have been investigated in many theoretical studies (reviewed by Drossel and McKane (2003)). Some of these have focused on long-term dynamics, in which not only migration and extinction of species but also speciation, becomes an important factor. In isolated islands or continents, a large fraction of new species have been generated through their intrinsic evolutionary dynamics (Schluter, 2000). Speciation processes in previous food-web models (Drossel et al., 2001; Jain and Krishna, 2002; Tokita and Yasutomi, 2003; Yoshida, 2003) are expressed by artificial introduction of new species, irrespective of the ecological condition of the community, which might be taken as allopatric speciation that is thought to be triggered by external factors such as geographic changes.

However, recent advances in empirical and theoretical studies (Dieckmann et al., 2004) have provided a new view that sympatric and parapatric speciation are likely to have occurred through various ecological interactions, contrary to the previous view arguing the dominance of allopatric speciation. If ecological interaction has an important role in speciation, when and how speciation arises depend on the food-web that provides an interaction relationship among species, which might be further changed by that speciation. The present model has enabled investigation of such interrelationships between different scales of dynamics in a food-web. Two different time-scales were distinguished in the present simulations. The longer time-scale corresponds to an evolutionary food-web scale, which is detected by intermittent large extinctions. The shorter time-scale corresponds to a within-food-web developmental time-scale, where new trophic species are synthesized on the local portions of the food-web structure. It is commonly observed that the system autonomously breaks down its own food-web structure to synthesize a new food-web. It might be said that the instability that generates evolutionary branching of local species results in large-scale instability that resets the entire food-web.

4.3. Necessary extensions of the model

This paper proposes a minimal mechanism for food-web evolution. The model describes a wide range of population dynamics and evolutionary dynamics, from phenotypic to food-web level, despite using relatively simple formulas. The observed food-web development through recursive evolutionary branching does not seem naive, but appears to be a robust phenomenon. Thus, appropriate modifications and extensions of the model will offer a useful tool for elucidation of the inter-relationship between different scales of evolutionary

phenomena which have been studied separately in previous studies. The necessary extensions to the model are briefly summarized below.

First, to represent a resource by a single dimension might be an extreme simplification, lacking some important aspects of real evolutionary dynamics, although there is strong empirical support for one-dimensional representation of food-webs (Williams and Martinez, 2000). For example, in the model, when two pairs of predator–prey systems approach each other in the resource space, they always collide. On the other hand, they might not collide if there is enough distance between the pairs in the direction of another niche-axis. Thus, it might be necessary to extend the present model to take into account multidimensionality of phenotype and resource space.

Second, a trophic species cannot be divided further into its components, i.e. species, under assumption of asexual reproduction in this study. Whether a trophic species consists of one or more species might affect the evolutionary branching process, because the former corresponds to speciation, while the latter may be taken as character displacement among species in the same guild. Introduction of sexual reproduction is essential to investigate this difference that might lead food-webs to different evolutionary outcomes.

Third, functional response and trophic efficiency have no variation among phenotypes in the model, contrary to the large variation in nature, depending on their diet, feeding strategy and body size, etc. In addition, developmental and physiological constraints might restrict certain evolutionary change of populations through skewing relationships between the phenotype and resource spaces. The robustness of our scenario for food-web evolution against these variations should be verified.

4.4. Comparison with empirical studies

Evolutionary branchings of the trophic species in the present model were categorized into three types: type-*u*, type-*r* and type-*c*. Type-*u* is evolutionary branching as a predator (consumer) through niche-shift for new resources. Clear evidence for this phenomenon come from many taxa, including apple maggot fly (Feder et al., 1997) and Darwin's finches (Grant, 1999). On the other hand, empirical support for type-*r* branching (branching as prey) come from passion-vine butterflies (McMillan et al., 1997) and house mice (Chown and Smith, 1993), supporting the importance of predation pressure in their speciation process. Co-evolutionary branching of predator and prey, type-*c* branching, is supported by diversifying co-evolution between bill morphology of crossbills and cone morphology of black spruce (Parchman and Benkman, 2002).

As for the dynamics of food-webs, the results might imply that a weak interaction strength tends to destabilize the whole food-web and results in a relatively small diversity. In contrast, there are empirical studies reporting that a weak interaction has a stabilizing effect and maintains high diversity, by dumping the population dynamics of the food-webs (McCann, 2000; Neutel et al., 2002). This paradox might occur since this study was concerned with dynamic stability through evolution of trophic species including branching and extinction, while these empirical studies do not consider evolutionary dynamics, but only population dynamics. Since evolutionary changes can arise within dozens of generations this can influence the population dynamics (Yoshida et al., 2003), and evolutionary properties should be considered in future investigations of the stability of food-webs.

Another important result shown in this study about food-web dynamics is that the number of trophic species peaks at the medium amount of the total biomass. There are many empirical studies investigating the relationships between biomass or productivity and species diversity (Currie and Paquin, 1987; Leibold, 1999; Waide et al., 1999; Dodson et al., 2000; Gaston, 2000). Some of these have shown a hump-shaped relationship, that is, diversity peaks at intermediate productivity (Leibold, 1999; Dodson et al., 2000), while others have shown that diversity increases monotonically with productivity (Currie and Paquin, 1987; Waide et al., 1999; Gaston, 2000). Chase and Leibold (2002) have shown evidence that these discrepancies can be settled by considering the spatial scale of the sampling area; a unimodal relationship is observed in a local area (α diversity), while a linear relationship is observed in the regional area ($\alpha + \beta$ diversity). Since α diversity corresponds to species richness in equal habitats and β diversity corresponds to habitat diversity among patches, the diversity observed in the model corresponds to α diversity. Thus, the results of this study, that diversity peaks at an intermediate biomass, are consistent with their explanation. It is notable that this empirical research focused on a restricted range of trophic levels in food-webs, while this study investigated the relationship at the level of the whole food-web structure. This concordance beyond scale difference in food-web structure might imply universal restriction on the relationship between biomass and diversity.

Regarding the evolutionary development of the total food-web, there are very few ecological examples in the paleontological record (Crame, 1990) to support this scenario. However, at a local scale of food-web development, strong support comes from the recent radiation of cichlid fish (Schliewen et al., 1994), which are thought to have diverged through a sympatric speciation process from a single ancestor species into

several trophic levels, constructing a food-web structure within themselves (Schluter, 2000).

Acknowledgements

We thank Masakazu Shimada for valuable discussions, Ulf Dieckmann for helpful comments, and two anonymous reviewers for their valuable comments. This work was partially supported by a Grant-in aid (No. 09640454 and No. 15-11941) from the Ministry of Education, Science, Sports and Culture and from the 21st Century COE (Center of Excellence) program (Research Center for Integrated Science) of the Ministry of Education, Culture, Sports, Science, and Technology, Japan. H.I. was supported by a Research Fellowship of the Japan Society for the Promotion of Science for Young Scientists.

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