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Evolutionary Dynamics of a Food Web with Recursive Branching and Extinction

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Abstract

A dynamic systems approach to evolutionary branching and its development in an artificial food web is presented. Predator-prey interaction among trophic species with two traits generates a variety of evolutionary branching patterns, depending on interaction strengths and mutation rates. Studying branching patterns in a phenotypic space reveals three branching patterns: prey-bifurcation, predator-bifurcation, and net-bifurcation. In particular, a complex food web network emerges through net-bifurcation. A relationship between biomass and the number of species is analysed by changing the interaction strength. We report that the branching and extinction rates of trophic species reaches a maximum when the number of species, but not the entire biomass, reaches a maximum.

Introduction

The origin and evolution of species have been tested by many mathematical models. Recent advances in models for sympatric speciation (Dieckmann & Doebeli 1999; Higashi, Takimoto, & Yamamura 1999; Doebeli & Dieckmann 2000; Kaneko & Yomo 2000) have shown that various intra- and inter-species interactions split a single founding population into two different populations, called "evolutionary branching". Doebli and Dieckmann have demonstrated that various ecological interactions (resource competition, mutualism and host-parasite relationships) can cause branching with the evolution of assortative mating. Highashi's sexual selection model has shown evolutionary branching only through evolutionary divergence of sexual preferences, while Kaneko and Yomo have shown that dynamic clustering caused by the internal degrees of freedom in each reproductive unit drives the branching.

The main concern of these models is evolutionary branching at each trophic level. Here we are more concerned with higher-order branchings, which generate populations at new trophic levels. In particular, we investigate how the complexity of the ecosystem may be built up from a bottom trophic species (e.g. plants) only by predator-prey interaction.

Mathematical studies on the evolution of a food web have been mainly based on the replicator or Lotka-Volterra models. Yasutomi and Tokita (Tokita & Yasutomi 2002) have studied the evolution of replicator dynamics by adding new columns and rows to the original interaction matrix. Jain and Krishna (Jain & Krishna 2002) have shown the role of innovation and of keystone species in large extinctions using an evolutionary replicator model. The other approach can be found in Lindgren and Mats Nordal's (Lindgren & Nordahl 1993) study on the evolution of a food web, using the model of the iterated prisoner's dilemma game. In this model, a basic strategy (Tit for Tat) is used and new strategies are constantly introduced through genetic algorithms. They analysed what kind of food web emerges.

These previous approaches for evolutionary dynamics of a food web invite new species from outside. Namely, these models cannot deal with the mechanism of creating new species from the intrinsic ecological dynamics that maintain the food web. In this paper, we investigate how patterns of autonomous development and collapse of a food web with recursive branching and extinction may be classified and we show how ecological diversity and evolution are interrelated.

Modelling phenotype space and dynamics

In nature, individuals use inorganic resources and other individuals as foods. Individuals are also used by other individuals as resources. Quantifying those characteristics of individuals as a resource by a simple measure, we represent individuals as a resource distribution on the measured space. Suppose that a single variable z for the measure and each individual is characterized by two traits, which are measured by the factor z and interpreted as a resource trait (prey) and a utilizer trait (predator). Formally, they are labelled as $\mathbf{r}$ and $\mathbf{u}$, respectively. With these labels, we define a phenotypic space (Fig.1). A phenotype distribution function $p(u, r)$ is defined on this space. A resource distribution $R(z)$ and a resource utilization distribution $U(z)$ are computed as

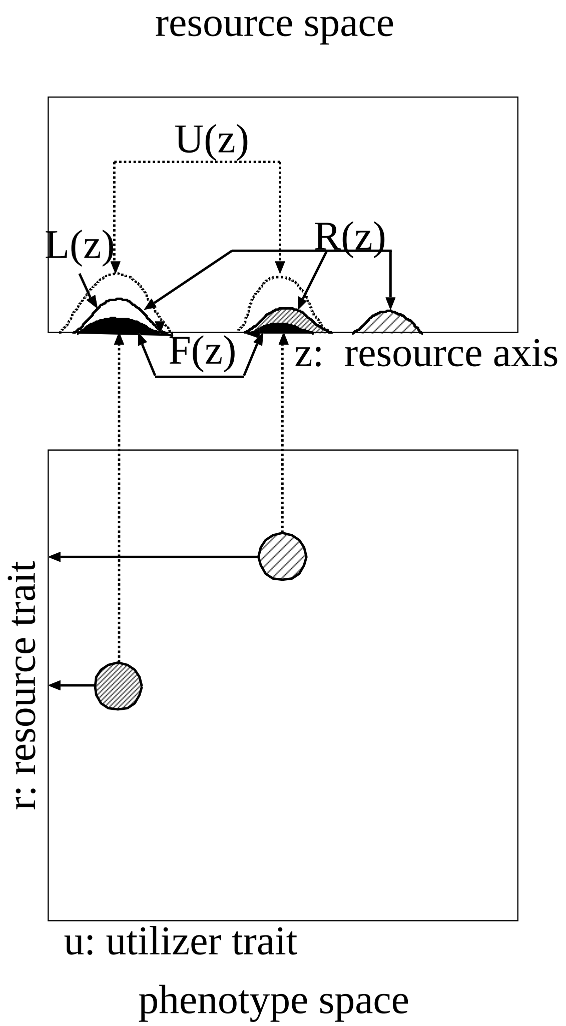

Figure 1: A phenotype space (u, r) and a resource space. Light grey and dark grey circles denote phenotypic clusters in the phenotype space (below rectangle) with axes of utilizer trait u and resource trait r. In this case, the dark phenotype uses the light source (L(z)) and is eaten by the light grey phenotype. On the resource space (above), we express the situation in terms of the distributions of $U(z)$ and $R(z)$.

follows:

$$R(z) = \int_u p(u, z)du + L(z), \tag{1}$$

$$U(z) = \int_r p(z, r)dr, \tag{2}$$

where $L(z)$ is a constant inward resource distribution given from without. Species at the lowest trophic level in the focussed range of the food web use this resource. Thus, the type of the inward resource (organic/inorganic, plants/animals) depends on what range of food web we consider. Because we are concerned with the total biological community here, the inward resource L(z) corresponds to sunlight. We define L(z) as the Gaussian distribution function:

$$L(z) = L_0 \cdot \frac{1}{\sqrt{2\pi\sigma_L}} \exp[\frac{-(z-\mu_L)^2}{2{\sigma_L}^2}], \tag{3}$$

where L_0 is the total resource amount. μ_L and σ_L denote the position and the width of the resource, respectively.

An assumption here is that phenotypes whose r are equal to u of phenotypes will be eaten by those phenotypes. In other words, the phenotypes that have the trait u utilize the phenotypes whose r is equal to u. We now define a "resource flow" at each point in the resource space (Fig. 1) as follows:

$$F(z) = \Omega \cdot \frac{U(z)R(z)}{1 + \frac{R(z)}{M}} \tag{4}$$

where Ω determines the strength of predator-prey interaction, and M gives a maximum predation constant per individual when there are infinite amounts of food. This formula is a type II function response, which is known to be a characteristic response of actual predator populations to prey density.

It should be noted that, when $R(z)$ is relatively much smaller than $U(z)$, the resource flow is proportional to the cross term $U(z) \cdot R(z)$. However, when $R(z)$ becomes larger, F(z) becomes proportional to $M \cdot U(z)$, because the maximum predation amount per individual is saturated to M. To keep the amount of the maximum resource flow into the system constant irrespective of changes to the interaction strength Ω, we assume that the amount of the inward resource L_0 is given by L_a/Ω, where L_a is a constant positive value.

Each individual of phenotype (u, r) acquires a $1/U(u)$ rate of resource flow, assuming that it is equally distributed. Similarly, each phenotype (u, r) is used by the others at the rate $1/R(r)$. Concerning this point, we compute the gain $(g(u))$ and loss $(l(r))$ per individual of each phenotype as,

$$g(u) = F(u)/U(u) \tag{5}$$

$$l(r) = F(r)/R(r) \tag{6}$$

We finally obtain the following equation for the time of evolution of the density function $p(u, r)$ as,

$$\begin{aligned} \frac{\partial p(u,r)}{\partial t} &= p(u,r) \cdot (c \cdot g(u) - l(r) - d) \cdot (1 - \frac{p(u,r)}{K}) \\ &\quad + D_u \cdot \frac{\partial^2 p(u,r)}{\partial u^2} + D_r \cdot \frac{\partial^2 p(u,r)}{\partial r^2} \end{aligned} \tag{7}$$

where c denotes the efficiency of resource use, which in practice is estimated at 0.1 in empirical studies (Pauly &

Christensen 1995). and K denotes the physical carrying-capacity of the habitat. The natural death rate is given by the parameter d. The last two terms correspond to the mutation flow in the phenotype space. The mutations generate new phenotypes in parents' neighbours in the phenotype space. In practice, we run the above equation by discretizing the explicit Euler method. To avoid unnecessary numerical underflow, we remove the phenotype whose population density is below a given threshold ε that is significantly small. We also assume that the phenotype space has absorbing boundaries to avoid numerical divergences.

Practically, when the number of predators is much larger than that of prey, the consumption rate may be proportional to the number of prey irrespective of the number of predators. In order to compensate for this fact, we can also use a modified version for the resource flow as,

$$\tilde{F}(z) = \Omega \cdot \frac{U(z)R(z)}{U(z) + \frac{R(z)}{M}} \tag{8}$$

With this formulation, $\tilde{F}(z)$ approaches to $MU(z)$ for $R(z)/U(z) \to \infty$ and to $R(z)$ for $R(z)/U(z) \to 0$. We mainly report below the simulation results of the first model. However, we also argue for a difference between the first and second model by comparing the main result with preliminary results of the second model. Instead of parameter value c (i.e. an efficiency of resource utility), we chose other parameters arbitrarily. However, the basic scenario presented below (three type of branching patterns, etc.) is not sensitive to the parameter values.

Simulation Results

An initial food web is prepared with a single phenotype utilizing an inward resource ($L(z)$), that corresponds to, for example, plants (Fig.2 (a)). Within the wide range of parameter values, several isolated phenotype clusters are generated.

These clusters correspond to "trophic species" which are functional groups of taxa consisting of species sharing the same predators and prey in a food web. Here, we call these phenotypic clusters "trophic species." To count these species, we define a base line level for the density function $\epsilon(> \varepsilon)$ to identify each connected cluster in the phenotype space. The number of species does not change significantly unless we take base line values that are too low or too high. Below, we report the details of this branching phenomenon and analyse it with regard to the interaction strengths and biomass.

Branching pattern

We observe evolutionary branching of trophic species in a wide range of parameter values. These bifurcation patterns are classified into three types in terms of biological functions, by referring to Figure 2 (a–i).

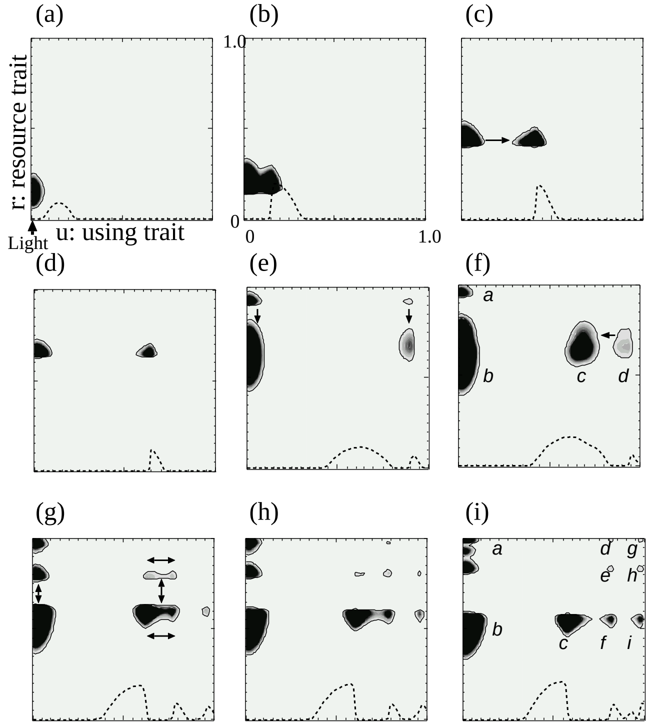

Figure 2: Evolutionary branching of trophic species is simulated. Darker colours indicate higher densities of the phenotype. Contours with solid lines correspond to the base line abundance truncated by ϵ. Dashed lines on the u axis indicate the organic resource distributions (R(z)-L(z)). Model parameters: $M = 10.0, \Omega = 13.0, D_u = 1.2 \cdot 10^{-7}, D_r = 0.6 \cdot 10^{-7}, c = 0.1, d = 1.0, K = 1.0 \cdot 10^4, \varepsilon = 1.0 \cdot 10^{-9}, \epsilon = 5.0 \cdot 10^{-2}, L_0 = 15/\Omega, \mu_L = 0, \sigma_L = 0.08, \Delta t = 5.0 \cdot 10^{-4}$

- Type u: predator-branching

  In Figure 2(a) → (d), the initial trophic species branches to produce new trophic species. The r-trait of the initial trophic species, expressed as a distribution function (with a broken line) on the u-axis, provides another potential resource to the initial trophic species. Thus, a part of the trophic species evolves to exploit the new resource by branching its u-trait.

  This predation forces "prey" species to evolve an r-trait to avoid being predated and "predator" species also evolve a u-trait to pursue the "prey" species, which gives rise to a evolutionary "arms race" (Fig. 2 (c) → (d)). Whenever we start from a single trophic species, the primary branching is always this type.

- Type r: prey-branching

  Instead of escaping from predators, a trophic species as prey sometimes branches its r-trait. In Figure 2(e),

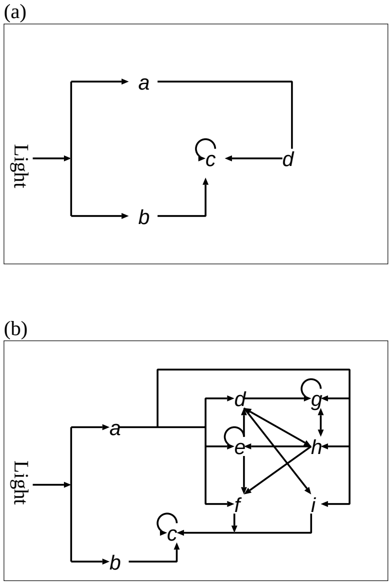

Figure 3: Extracted food-web topology from Fig. 2. (a) and (b) correspond to (g) and (i), respectively. Each letter denotes a trophic species. Arrows indicate the resource flows among the trophic species.

  the two phenotypes simultaneously branch their r-characteristics, developing four new phenotypes.

- Type n: net-branching

  Simultaneous branching of both r- and u-traits. A clear example can be found in Figure 2(g). Some other cases are found when two predators exploit a single prey from both sides or when two predator-prey systems collide with each other. By this branching, the structure of the entire food web diverges abruptly and becomes complicated. The complexity of the network is well observed by abstracting the relational network topology as in Figure 3. A topology associated with Figure 2(f) is depicted in Figure 3(a). This will evolve into the network-Figure 3(b)-of Figure 2(i).

Because each trophic species acts both as prey and predator for other trophic species at the same time, the generic mechanism of the evolutionary branching is complicated. The network evolves from a directed graph (Fig. 3 (a)) to a rhizome structure (Fig. 3 (b)). To see this whole process, the total branching tree is depicted in three-dimensional space (Fig. 4). Successive branchings occur along the time axis. A type-n branching only occurs at the later stages.

The degree of complexity a network can attain depends on, for example, the interaction strength. The evolution is not a homogeneous process, but accompanies various dynamics, We study these features below.

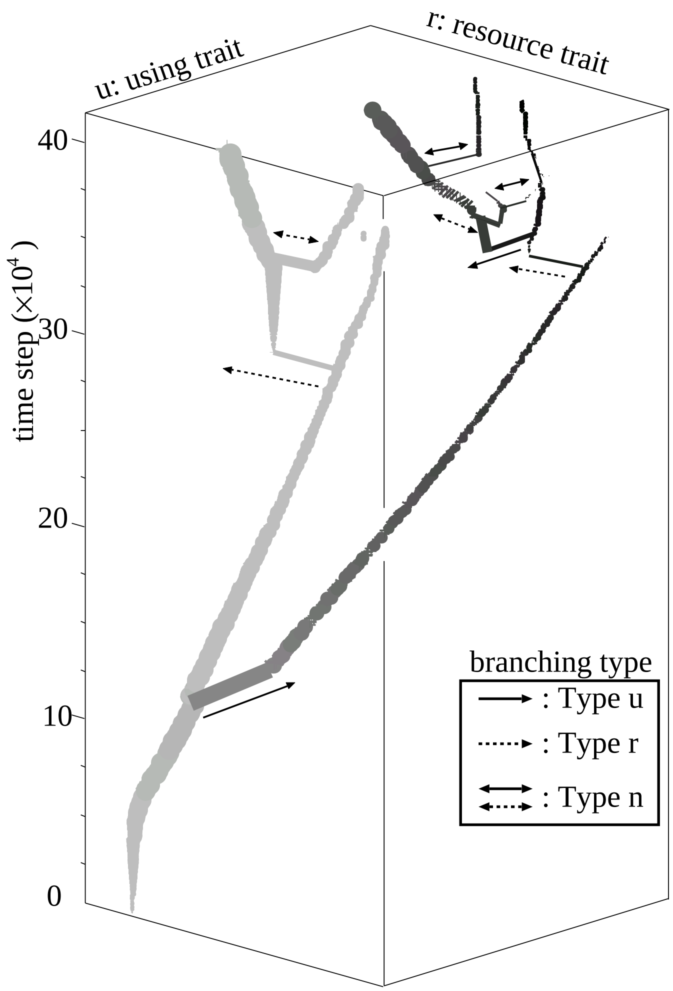

Figure 4: Phylogenetic tree extracted from the simulation with the same conditions as in Figure 2. Each line indicates an historical trace of each trophic species, where the line width expresses the population size of the trophic species at that time. The time slice of this phylogenetic tree gives a phenotype distribution on a phenotype space (u, r). Each branching type is denoted by a different line style.

Dynamics of evolutionary branching

This evolutionary branching is associated with various temporal dynamics related to the numbers of trophic species and the total biomass. The critical control parameter is the strength of interaction in the equation (7). The dynamic changes from periodic to chaotic by increasing its strength. In the strong interaction region, the large number of species is sustained via intermittent chaotic dynamics.

In the relatively lower strength regions of Figures 5 (a) and (b), divergences and extinctions of biomass occur repeatedly. In these regions, the system repeats type-r and -u branchings, but seldom shows type-n branching.

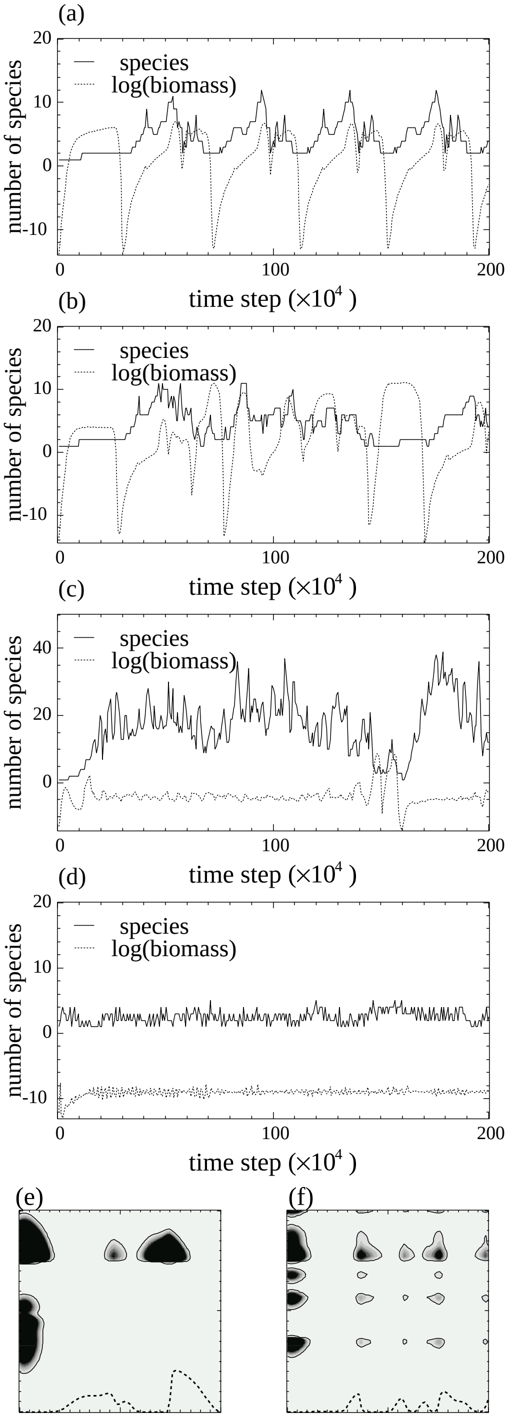

Figure 5: Time evolution of the number of trophic species and the biomass at different strengths of interaction (Ω). (a):$\Omega = 10$,(b):$\Omega = 11$,(c):$\Omega = 20$,(d):$\Omega = 100$. Other parameters used have the same values as in Figure 2 except that $\text{Ł}_0 = 22/\Omega$. (e) is a typical phenotype distribution of (a) and (b), and (f) is a typical phenotype distribution of (c).

Finally, several large clusters of phenotype spread the region, arriving at massive extinction. As a result, the entire food web resets and it starts again from the bottom trophic species that use the inward resource ($L(z)$). The same scenario; an excess reproduction of a particular trophic species, triggers excess reproduction and its distribution is repeated. The associated two-dimensional phenotype space is depicted in Figure 5(e), where four trophic species are expanding without branching. Thus, no food web increases in complexity.

On the other hand, the larger interaction strength evolves into a regular lattice on the two-dimensional phenotype space (Figure 5(f)). The excess reproduction of trophic species is suppressed by forming a laterally-inhibiting network. The organized food web continues expanding outwards. At the outside of the food web, sub-networks based on the bottom trophic species become extinct. At the same time, new networks based on the new bottom trophic species are created in the inside of the food web. Because the speed of this extinction and expansion of the network is stabilized, the total biomass and the numbers of all trophic species are maintained dynamically. This picture is well demonstrated in Figure 5(c). It is interesting to note that the system has a much larger number of species in Figure 5(c) rather than in (a) and (b): even the entire biomass is suppressed in the case of (c). However, a big extinction is aperiodically induced in Figure 5(c). When the interaction strength is much larger, the amplitude of biomass changes is suppressed and shows more stable oscillations. Instead, the food web at this stage cannot sustain a large number of species because of the shortage of biomass.

Whether a system shows periodic, chaotic or other dynamics is mostly determined by the parameters. Practically, the interaction strength Ω determines the kinds of branchings. The maximum predation level M has asimilar effect to Ω.

In the next section, we study how the entire dynamics depend on interaction strengths and other ecological parameters.

Interaction Strengths and Mutation Rates

By changing parameter values, we measured the long time averages of the number of species, and the speciation and extinction rates.

1)Interaction Strength (Ω): (Fig. 6)

A larger strength of interaction leads to a smaller biomass without temporal oscillation. Because it is difficult to sustain species, the number of species becomes smaller. On the other hand, the smaller interaction strength delays the increase in the number of predators. Therefore, this can produce a large biomass but with an unstable temporal oscillation that easily leads to extinction. The number of species is suppressed.

With a middle strength (around 20), the average number of species attains a maximum value having the same

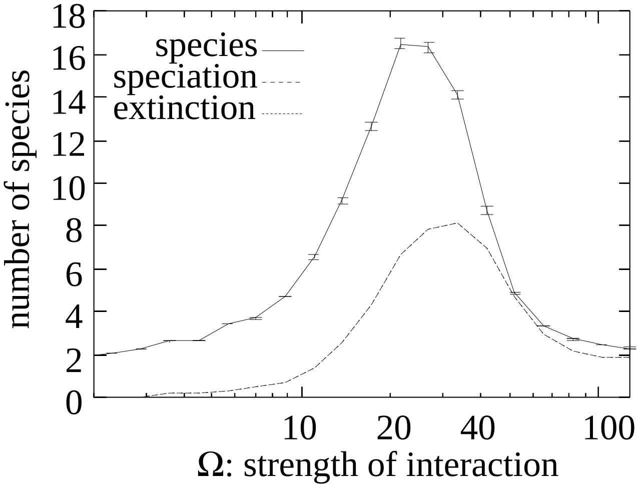

Figure 6: A relation between the strength of interaction (Ω) and the numbers of trophic species. An average number of species, extinction and evolutionary branching through a long time-step ($6 \cdot 10^5$) is computed. The relative amounts of extinction and branching almost coincide over this wide range. Model parameters: $L_0 = 22/\Omega$, and the others are used with the same values as in Figure 2.

temporal variation as the biomass. When the number of species attains a maximum value, the extinction and speciation rates also become maximum, as is seen in Figure 6. Note that those two rates have almost equal average values. This reflects that the food web temporally collapses to the initial state so that it reorganizes the entire network, or the food web with balanced speciation and extinction.

2) Mutation rates (Fig.7)

When the mutation rates of two traits (D_u, D_r) are set at the same, the number of species gets larger. In general, when D_r is less than D_u, a system holds more species than in the opposite situation. A similar argument can be found given by Ikegami and Kaneko (T.Ikegami & K.Kaneko 1990). The entire biomass (Fig. 7(b)) becomes larger when the absolute values of D_u and D_r are smaller and the asymmetry is larger.

A relation between biomass and species diversity

A large biomass does not necessarily imply a maximal number of species. In Figure 8, the relationship between the number of species and the biomass is depicted. The number of species forms a convex function of the biomass. This convex form is observed over a wide range of parameter values (e.g. mutation rates and the interaction strength). Figure 8(a) is computed from Figure 5(d), which shows a sharp peak around 0.1. Here the biomass is well distributed over the trophic species and the hole in the network caused by sub-extinction will soon be compensated for by the new network.

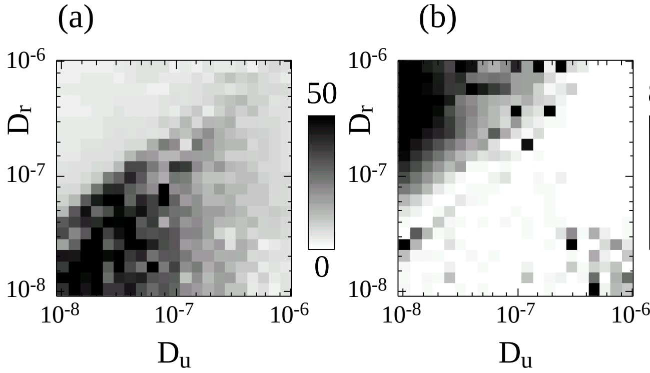

Figure 7: The effect of mutation rates on the numbers of trophic species (a) and of biomass (b). Horizontal and vertical axes are mutation rates of the utilizer trait u and resource trait r, respectively. Model parameters: $\Omega = 13.0, L_0 = 20/\Omega$, and the others are used at the same values as in Figure 2.

This convex shape is also observed in different parameter changes such as mutation rate (Fig. 8(a)) and interaction strength.

A case of $\tilde{F} = UR/(U + R/M)$

Instead of using F, we analysed a model equation with $\tilde{F}$. In this case too, type-r, -u and -n were observed. By these branchings, development and sudden extinctions of trophic species occur (Fig.9 (a)). As a result, the mutation rate produces the same effect on the average number of trophic species and biomass.

However, we could not observe a dynamic stable state as in Figure 5(c). Instead, a nearly fixed phenotype distribution lasts for a long time in the region of $D_u > D_r$ (Fig.9 (b)). It seems that many different organizations can be possible in this stable phase.

Some oscillating phases that hold stable phenotypic distribution also appear in Figures 9(c) and (d). These phases tend to collapse by oscillationary divergence. After the extinction, a new food web structure becomes reorganized.

Discussions

In this model, we have studied the evolution of "trophic species", which are functional groups of taxa consisting of species sharing the same predators and prey in a food web. The concept of trophic species is sometimes criticized but is widely accepted, and structural food web studies can reduce biases in the data by using it (Williams & Martinez 2000).

We distinguish two different time scales in the present simulations. A longer time scale corresponds to an evolutionary food web scale, which is determined by successive large extinctions. A shorter time scale corresponds

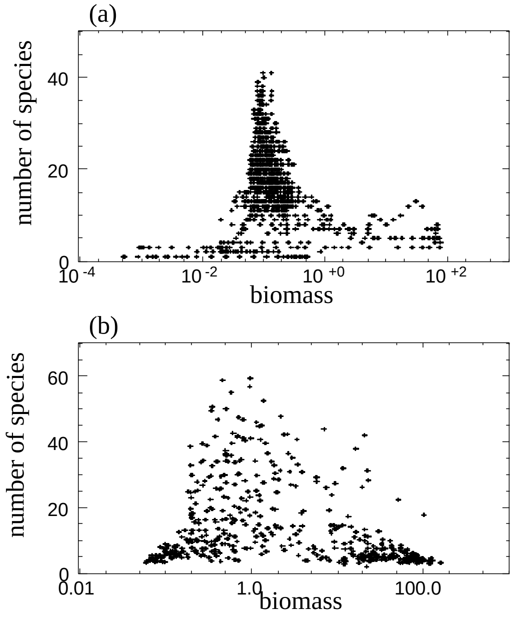

Figure 8: A relationship between biomass and the number of trophic species. (a) generated from Fig. 5(d), and (b) from Fig. 6.

to a within-food web developmental time scale, where new trophic species are synthesized on the local portions of the phenotypic space. The term *evolvability* usually implies inheritance of genetic potential to produce new characteristics over a longer time scale. The term ecological diversity means to develop a food web network in a shorter time scale. An advantage of our model is that evolvability and ecological diversity are studied in the same model. Both evolvability and diversity require a certain degree of instability in the system. Evolvability needs to destabilize the established food web to introduce new trophic species and thus introduce a new form of a food web into the system. Under a certain range of interaction strengths with the condition of mutation rates, $\mu_u < \mu_r$, large diversity is developed. Thus, predators should have larger mutation rates than prey to produce diversity. A similar condition has been reported for host-parasitoid systems (T.Ikegami & K.Kaneko 1990). In the wide parameter range of our model, a system autonomously breaks down its own food web structure to synthesize a new food web. In other words, instability that generates a local species branching event will finally lead to a large scale instability that resets the entire food web.

Evolutionary branching of the trophic species in the present model is categorized into three types. Type-u is branching as a competitor (or predator), which corresponds to previous models for evolutionary branching through niche-shift for new resources by intra-species competition (Doebeli 1996; M. Kawata 2002). On the other hand, type-r and type-n are branchings produced by predator-prey interaction, that is inter-species competition. Previous models for evolutionary branching by predator-prey interaction have shown that, at one time, a single pair of predator-prey systems splits into two pairs (four populations) or a single prey splits into two preys exploited by the same predator (three populations) (Savill & Hogeweg 1998; Doebeli & Dieckmann 2000). Type-n can generate more than two species at a time, because a single pair of predator-prey system splits effectively into six trophic species (two preys and four predators) at one time. This type of speciation might be possible in real populations, which have both resource competition and intra-guild predation.

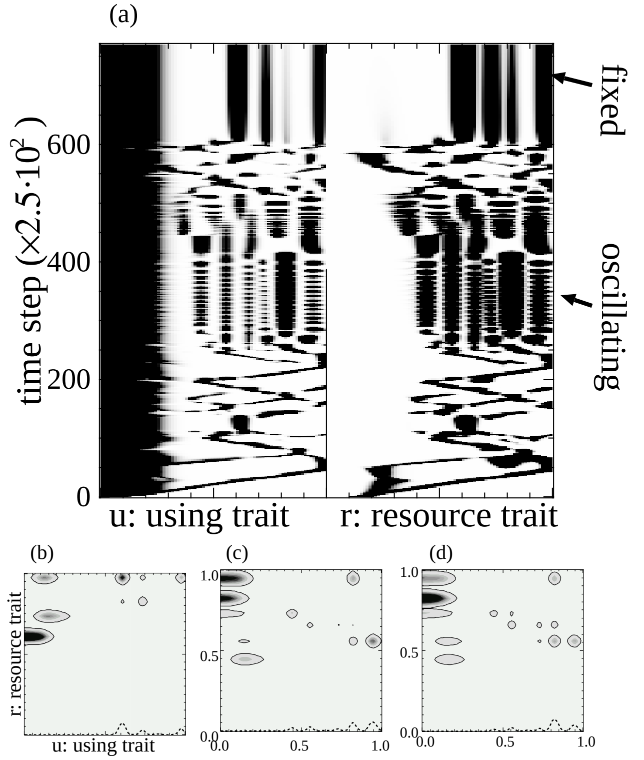

Figure 9: Evolutionary dynamics with $\tilde{F}$. (a) Time evolution of distributions of traits u(left) and r(right). A phenotype distribution in a stable phase (b), and in that of the oscillating phase ((c) & (d)). Model parameters: $M = 10.0, \Omega = 10.0, D_u = 8.45 \cdot 10^{-8}, D_r = 9.0 \cdot 10^{-8}, c = 0.1, d = 1.0, K = 1.0 \cdot 10^4, \varepsilon = 1.0 \cdot 10^{-9}, \epsilon = 1.0 \cdot 10^{-2}, L_0 = 300/\Omega, \mu_L = 0, \sigma_L = 0.08, \Delta t = 4.0 \cdot 10^{-3}$

Based on our model simulations, we suggest the following insights into the relationships between 1) interaction strength and stability, and 2) biomass and species-diversity.

1) Interaction Strength vs. Stability

Evolution of trophic species in our model may correspond to a travelling wave phenomenon in the phenotype space. The stability of the trophic species is sustained when there exists a time lag between the growth of prey and that of predators, as it generates a traveling waves of prey chased by predators. Thus, each species maintains its population evolving directionally. This time lag increases when the interaction strength is weak (a small Ω).

However, a weak interaction rate tends to destabilize the whole food web and results in relatively small diversity. By contrast, there are studies reporting that weak interaction has a stabilizing effect to maintain high diversity by dumping the population dynamics of the food web (McCann 2000; Neutel, Heesterbeek, & de Ruiter 2002). This paradox may arise because we are concerned with dynamic stability through the directional evolution of each trophic species. On the other hand, these empirical studies do not concern evolutionary dynamics, but population dynamics.

2) Biomass vs. Species-Diversity

Another important result is that the number of trophic species becomes maximum at a medium biomass. We argue that this dependency on the biomass can be explained as follows. When the amount of biomass is low, the system simply cannot afford to have any higher order niches, and the number of species may be suppressed. On the other hand, the system may develop a large biomass only when plant species are prospering in the absence of predators. Thus, the number of trophic species is kept lower. Only the mid range of biomass corresponds to a rich and complex food web network. There are many empirical studies investigating the relationships between biomass or productivity and species diversity. Most of them (Abramsky & Z 1984; Tilman & Pacala 1993; Leibold 1999; Ritchie & Olff 1999; Waide *et al.* 1999; Dodson, Arnott, & Cottingham 2000; Gaston 2000) report the same tendency as our results here: that diversity peaks at intermediate productivity or biomass. However these empirical researches were focused on a restricted range of trophic levels in the whole food web; on the other hand, we investigated the relationship at a higher level between the whole biomass of a food web and the numbers of trophic groups, each of which may contain several species. This interesting concordance beyond scale difference in a food web might imply a universal restriction on the relationship between biomass and diversity.

A criticism of the present model is that to represent a resource by a single dimension is an extreme simplification. Indeed, our simplification from actual multidimensional niche-space should be reducing some aspects of real evolutionary dynamics. For example, in our model, when two pairs of arms-racing predators and preys are approaching each other in the phenotype space they always collide. On the other hand, they may not collide if there is enough distance between the pairs in the direction of another niche-axis. Thus, an extension of the present model to take multidimensional traits into account may be necessary. However, as food webs are assembled in the same way in our model, assigning each species on one dimensional niche-axis helps explain many characteristics of real complex food webs (Williams & Martinez 2000) and may provide a certain assurance that the evolutionary dynamics of food webs are also described sufficiently in our simple rule.

To make the present model closer to real food webs, the introduction of mating mechanisms is important. This provides a certain viscosity with populations by gene-flow between phenotypes, which will converge each mating group as a “species” under ecological definition and will provide more realistic evolutionary dynamics of a food web consisting of those species. Another extension will be to improve a new form of resource flow $F(z)$. As we have described, the new form of $\tilde{F}(z)$ certainly provides more rich evolutionary pathways. It is also interesting to note a connection between the present model and the approaches based on the replicator equations (K.Hashimoto & T.Ikegami 2001; T.Ikegami & K.Hashimoto 2002). For example, the notion of keystone species should also be examined in the present model.

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