

Numerical experiments on variation of species diversity in size-dependent evolutionary system

Takanori Sasaki

Department of Earth and Planetary Science,
The University of Tokyo

2005

Contents

1	General Introduction	5
2	Introduction of Numerical Ecology	10
2.1	Implications of Fossil Records	10
2.2	Previous Studies	12
2.3	My Study	17
3	Methods	20
3.1	Outline of the System	20
3.2	Size-Dependent Evolutionary System	24
4	Results	26
4.1	Regulations of Numerical Simulations	26
4.2	Diversity Change in The Food Web System	29
4.3	Effects of Alteration of Evolving System	34
4.3.1	Effects of Alteration of Evolution Timescale	35
4.3.2	Effects of Alteration of Feeding Parameters	37
4.4	Comparing of Size-Dependent/Independent Evolution	38

5	Discussions	43
5.1	Analysis of Maintained State	43
5.1.1	Is Size-dependent Evolution Always Necessary?	43
5.1.2	Alteration of Size-Dependent/Independent Evolution .	45
5.1.3	Implication for Observed Food Web System	45
5.2	Analysis of Interspecies Interactions	46
5.2.1	Apparent Discrepant Results	46
5.2.2	Simplification of Feeding System	46
5.2.3	Map of Interspecies Interactions in Food Web System .	47
5.2.4	Implication for Alteration of Parameter Dimension . .	51
5.3	Punctuated Equilibria	52
6	Conclusions	54
	Acknowledgments	56
	Bibliography	57

List of Figures

2.1	Ecological evolutionary units and evolutionary faunas.	11
2.2	Correlation between body size and metabolic rate.	19
4.1	Overflow on very small species world.	28
4.2	Examples of evolutionary patterns (1)	30
4.3	Examples of evolutionary patterns (2)	31
4.4	Partition of evolutionary pattern of species diversity	32
4.5	Examples of evolutionary patterns (3)	36
4.6	Comparing of size-dependent/independent evolution	40
4.7	Size distributions in food web system	41
5.1	Comparing of size-dependent/independent system stability . .	44
5.2	Examples of evolutionary patterns (4)	48
5.3	Maps of interspecies interactions (1)	49
5.4	Maps of interspecies interactions (2)	50

List of Tables

4.1	Initial Parameters	27
4.2	Effects of altering evolving systems	33

Chapter 1

General Introduction

Over 130 extrasolar giant planets are known to orbit nearby Sun-like stars, including several in multiple-planet systems ¹. These planetary systems are stepping stones for the search for Earth-like planets; the technology development, observational strategies, and science results can all be applied to Earth-like planets. The search for extra-solar Earth-like planets, and possible signatures of biological lifeforms, is one of the most exciting prospects for planetary science in the future; this disciplinary is called "Astrobiology". Astrobiology seeks to understand the origin of the building blocks of life, how these biogenic compounds combine to create life, how life affects - and is affected by the environment from which it arose, and finally, whether and how life expands beyond its planet of origin. None of these questions is by any means new, however for the first time since they were posed, these questions may now be answerable.

By now, I have done research on the origin and evolution of planets using a variety of numerical and analytic methods or some spectroscopic observations

¹California & Carnegie Planet Search, <http://exoplanets.org/>

with Subaru telescope to examine how the planets and the material of planets, which naturally include the building blocks of life on a terrestrial planet, have been produced and evolved (Sasaki et al. 2004, 2005; Sasaki and Abe submitted). Then in the next step, I would like to discuss the ecological system as a kind of astrobiology to examine the general behavior of life. Life developed on Earth, but what about other planets throughout the universe?

Previously, not only an ecologist but other many field scientists have worked on their own studies to understand the same thesis "How life have been developed?".

Paleontologists, evolutionary biologists and perhaps even archaeologists will be called upon to help understand the record of previous life on Earth in a planetary context (e.g. Raup and Sepkoski 1982). Some scientists considered that changes in planetary environments lead or follow periods of change in life (Cloud 1968, 1972; Hoffman et al. 1998). Hoffman et al. (1998) paid attention to negative carbon isotope anomalies in carbonate rocks bracketing Neoproterozoic glacial deposits in Namibia, which suggested that biological productivity in the surface ocean collapsed for millions of years. They explained this collapse by a global glaciation, that is "snowball Earth", and this period ended abruptly when subaerial volcanic outgassing that rose a warming of the snowball Earth to extreme greenhouse conditions. And other scientists investigated the temporal distribution of the major extinctions over the past 250 million years statistically using various forms of time series anal-

ysis (Raup and Sepkoski 1984). They suggested that 12 extinction events showed a statistically significant periodicity with a mean interval between events of 26 million years. Does species complexity arise at a constant rate or does it happen in spurts?

Astronomers, planetary geologists, and paleontologists will be called upon to assess the effect that large impacts have upon life on Earth (e.g. Kaiho et al. 1999). A clear record of bombardment in the early history of the solar system has been found across many planets and moons (Cohen et al. 2000). The lack of impact melt older than 3.92 billion years ago supports the concept of a short, intense period of bombardment in the Earth-moon system at about 3.92 billion years ago. And, even to this day, several years ago, we watched a comet hit Jupiter with many times the force of our planet's collective nuclear arsenal. On Earth it is clear that large ecosystem-busting impacts have occurred with some regularity. Alvares et al. (1980) framed a hypothesis that accounted for the mass extinctions and concentrations of iridium in deep-sea sediments. They considered that impact of a large earth-crossing asteroid, which contained excess of iridium, would inject about 60 times the object's mass into the atmosphere as pulverized rock and a fraction of this dust would stay in the stratosphere for several years and be distributed worldwide. They suggested the resulting darkness would suppress photosynthesis, and the expected biological consequences matched quite closely the extinctions observed in the paleontological record. Are planetary impacts actual component of life's extinction on a planet?

As described above, many phenomenological researches have done to discuss the development of life and gave us many explanations of some biological events. Meanwhile, we still do not understand the mechanisms of diversification or extinction of species under several circumstances. Numerical simulations are absolutely necessary to discuss and answer these questions. Analysis of evolution, diversification, stabilization, and extinction of species should hold the key to understand not only the Earth's ecosystem but also general ecosystems. In field of astrobiology research, biochemists is assigned to the origin of life from the building blocks of life, planetary scientists is assigned to the formation of planet that hold and nurture life, and ecologists is assigned to the behaviour of life on general terrestrial planets.

However, unfortunately no numerical model for meaningful discussion of general ecology is available at the present stage; almost all models have some problem even to describe the terrestrial phenomena of ecosystem, and few studies have investigated the dynamics of numerical models (as will hereinafter be described in detail in Chapter 2). So we first should establish the appropriate ecosystem model and discuss the feature of it as a preliminary step toward general ecology on universe.

Dynamics of an evolving interaction web and food web will be the first subjects of the research. In this master's thesis, I will focus on the evolutionary patterns of hypothetical communities in computer simulations and discuss what will play the important role in diversification and stabilization

of the ecosystem.

Because evolution would be essentially a non-directional phenomenon, the evolution of extra-terrestrial life will most likely be drastically different from the evolution of life on Earth. The different conditions present on different planets will lead extraterrestrial life down different evolutionary pathways. However while life elsewhere in the universe is probably drastically and even unrecognizably different from life on Earth, the same concepts and mechanisms that direct evolution, such as natural selection, will apply. On Earth and beyond, it would be a matter of the survival of the fittest.

Chapter 2

Introduction of Numerical Ecology

2.1 Implications of Fossil Records

The evolution of biodiversity can be seen in the fossil record. Many paleontologists have studied the fossil record and have elucidated the evolutionary patterns of taxonomic diversity throughout the Phanerozoic period in many taxonomic groups (e.g. Larwood 1988; Sepkoski 1984). Sepkoski (1984) examined standing diversity of marine families through the Phanerozoic, and recognized three successive evolutionary faunas (Cambrian, Paleozoic, and Modern); family diversity rose to three progressively higher plateaus during the successive evolutionary faunas (Fig.2.1). Available fossil records have shown that the biosphere on the earth has experienced remarkable fluctuations in the taxonomic diversity since organisms first appeared more than 3.8 billion years ago. The Cambrian Period witnessed one of the most significant events in the history of life, which was an exponential increase in animal diversity and complexity, commonly referred to as the "Cambrian explosion".

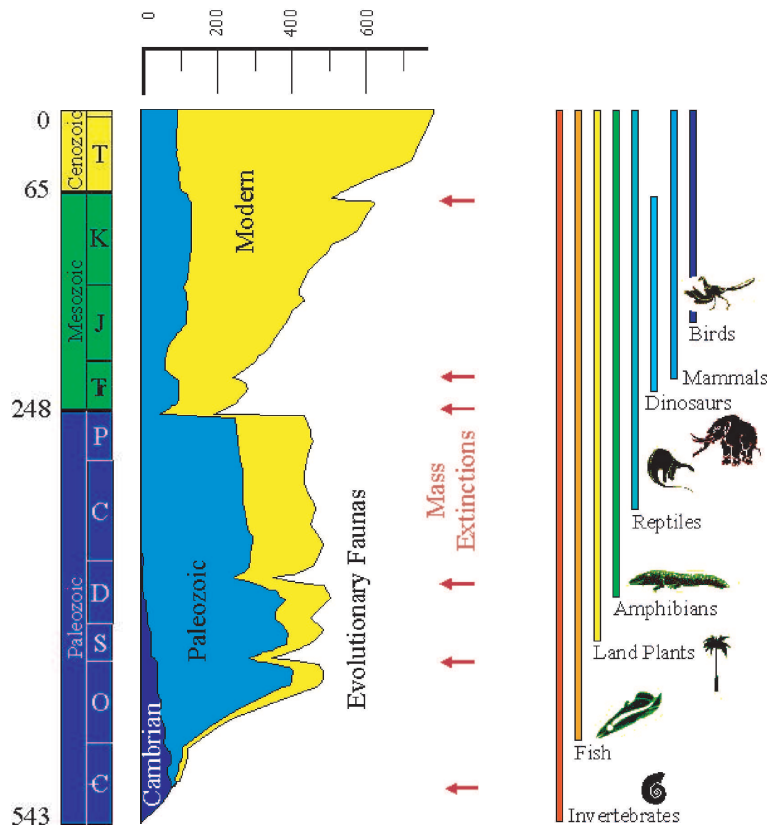


Figure 2.1: Revised ecological evolutionary units and the patterns of Phanerozoic diversity of families recognized by Sepkoski (1984). Centered figure shows the number of marine families at each era estimated from fossil records. Leftward time scale bar is scaled by millions of years ago, and rightward bars show range of available fossil records for some representative species. This figure was adopted from The Milwaukee Public Museum, <http://www.mpm.edu/index.htm>, which is alteration from Sepkoski (1984) originally.

After this explosion, the species diversity increased from one evolutionary fauna to the next, which can be accounted for by the invasion of previously unoccupied environments (Sepkoski 1984).

On the other hand, the fossil record also showed at least five times mass extinction events occurred ever (Sepkoski 1984; Erwin 1993; Hallam and Wignall 1997): which occurred about 450 million years ago, 350 million years ago, 250 million years ago (P-T boundary), 200 million years ago, and 65 million years ago (K-T boundary). These mass extinction events are also showed in Fig.2.1.

Terrestrial ecological system has experienced some biological major incidents (mass explosions and mass extinctions) as described above. While we know such a fact from fossil records, it remains to be seen what triggered these events and how these events occurred. To reveal the mechanism of the events, theoretical biologists have kept up establishing ecological modeling and trying to reproduce real world's events.

2.2 Previous Studies

The relationship between the complexity and stability of an ecosystem has been one of the most fascinating topics in theoretical biology for decades. In the 1950s and 1960s, the proposition that highly complex communities are more stable than simple ones was widely supported (MacArthur 1955). May (1972) challenged this proposition. He considered a large dimensional ecological equation with an n -dimensional random interaction matrix, and

concluded that an ecological system cannot be stable if it is complex. However, there is the discrepancy between the observed complexity of ecosystem in nature and the results of these mathematical studies. While it is found that the stability of a randomly linked food web model tends to decrease with the proportion of links and the number of species, real food webs display a high degree of stability, in spite of being very complex.

The search for what controls the dynamics of taxonomic diversity in a taxonomic group is an important biological and paleontological issue. There are three points of view in what controlled the diversity change: (1) Effects of environmental changes, (2) Effects of stochastic processes, and (3) Effects of biological interactions.

(1) Effects of environmental changes

Many researchers have found that environmental changes may cause changes in biodiversity. It is generally accepted that the major taxonomic diversity changes recorded in the fossil record, especially mass extinctions occurred contemporaneously with catastrophic environmental changes such as meteorite impact (Alvarez et al. 1980; Hut et al. 1987; Sigurdsson et al. 1991), sea level change (Schopf 1974; Simberloff 1974), global climate change (Stanley 1984), large scale volcanic activity (Hallam 1987; Officer et al. 1987), and so on. Several authors also pointed out that the timing of the second and third-order diversity changes are correlated with that of some kinds of environmental change (Kennedy 1977, Hirano et al. 1999).

(2) Effects of stochastic processes

Raup et al. (1973) carried computer simulations to evaluate the effect of stochastic processes on the dynamics of taxonomic diversity. In their system, appearance, extinction, and survival of species were determined by a rolling a dice. Though they revealed that an exceedingly simple stochastic model could produce branching and diversity patterns very like those described in the real world, detailed mechanism of diversity change was not clear, because there was no inter-species interaction and its evolution. Evolution of the system in the study was just changes in the elements of the matrix randomly, however real food webs have features that are ignored in randomly linked models. Their model was criticized by some researchers for failing to reproduce temporal diversity patterns (e.g. catastrophic mass extinctions (Sepkoski 1984; Erwin 1993; Hallam and Wignall 1997)). When one considers long-term biological phenomena as recorded in the fossil record, one must not avoid the evolution of species and the evolution of their interactions.

(3) Effects of biological interactions

The effects of biological interactions on the dynamics of taxonomic diversity have been discussed in empirical analyses of the fossil record, however, there is insufficient information about the actual cause of biological interactions. Empirical and statistical analysis of the long-term taxonomic diversity changes based on the fossil record has a limitation to consider the mechanism of macroevolutionary dynamics. The study of temporal change of biological

communities by experiments or observations of real communities is very difficult, because real communities are often too large and complex for long-term experiments and observations, and temporal changes of interactions among species constituting communities have not been preserved in the fossil record. A computer simulation is a good alternative approach that can be used. If we are able to construct a model biological community on a computer, we can easily investigate changes in interspecific interactions and their effects on diversity changes on an evolutionary timescale. Of course, a community on a computer is not the same as an ecosystem in the real world, however, the analysis of a model community can improve our understanding of the process of temporal changes in taxonomic diversity in the real world.

Following above concepts, Gilpin (1994) carried computer simulations by mixing two hypothetical communities, a random set (so-called random interaction matrix in which species in the system interact randomly) and an assembled set (created by decreasing the number of species from 10 to 5 in a random interaction web). Based on the result, he suggested that communities having experienced extinction have cohesiveness that battle against other communities as a team. And Happel & Stadler (1998) represented evolution with mutations of interaction coefficient. They revealed that strong symbiotic interactions developed through repeats of mutations and that an immigrant easily forces the extinction of other species. These classical ecological theories and hypotheses assume fixed species traits. Species, however, have evolved different phenotypes or strategies in response to interspecific interactions or

abiotic conditions depending on the assembly and evolutionary history of the community.

Tokita & Yasutomi (1999, 2003) have simulated the ecological evolution from a random matrix point of view. In the computer created models, interspecific interactions are assigned randomly. Evolution of the species constituting the interaction web system was modeled by assuming that a randomly chosen species in the system was given a chance of speciation. While they have given us much knowledge for the diversity-stability debate, their model would have an unrealistic assumption such as random matrix ecological system. Although there are many constraints on interspecific interactions in the real world, there is no such constraint in random matrix systems: a land animal can not feed on animals living in the ocean, or it is impossible for any species to increase its biomass infinitely by mutualism without food.

Yoshida (2002, 2003) modeled another interaction web in which each animal species fed on other species according to feeding preference. The food web system evolved via the appearance and extinction of species. Interspecies interactions are decided by the properties of species and change with the evolution of those properties. Their simulations showed the number of prey species decreased and that of predatory species increased with time, and the species became extinct as a result. This result suggested that species extinction often seen in the fossil record were not always connected to an external event; they can be caused by slight changes of interspecies interactions.

2.3 My Study

While Yoshida (2003) seemed to be successful to describe the behavior of real ecosystems, and give us important implications for the evolution of species at last, I will point out two unrealistic assumptions in his model: "one-way evolution" and "randomly chosen evolution".

First, in his model, with evolution, descendant species of predator can feed on prey species more effectively than the ancestor species, and descendant species of prey can have less intensity of predation by predator species than the ancestor species. However, the evolution would not necessarily raise an improvement of the species. It would not be caused by the urge of individual organisms toward something better. So I will assume the random-way evolution without direction in my model.

Second, in his model, speciation occurs for randomly chosen species. However, speciation would depend on the each species property, specifically body size, because smaller species should have faster timescales of the alteration of generations; the relationship between body mass (M) and metabolic rate has an exponent of $3/4$ so that characteristic timescale can scale with body mass as $M^{1/4}$ (Peters 1983, Schmidt-Nielsen 1984, Fig. 2.2). Evolutionary intervals of each species would also scale as the same relationship, so I will assume that speciation occurs at intervals scaled as $M^{1/4}$. While it is known that relative body size of the component species has often been identified as a major determinant of food web structure (Warren & Lawton 1987, Cohen

et al. 1993, Memmott et al. 2000), there is no study to consider the evolutionary timescale for each species. Size-dependent evolution interval would be a quite new idea for ecological modeling.

On the basis of above assumptions, I reconsider an evolving food web model and discuss the mechanism of diversification, stabilization, and extinction of species.

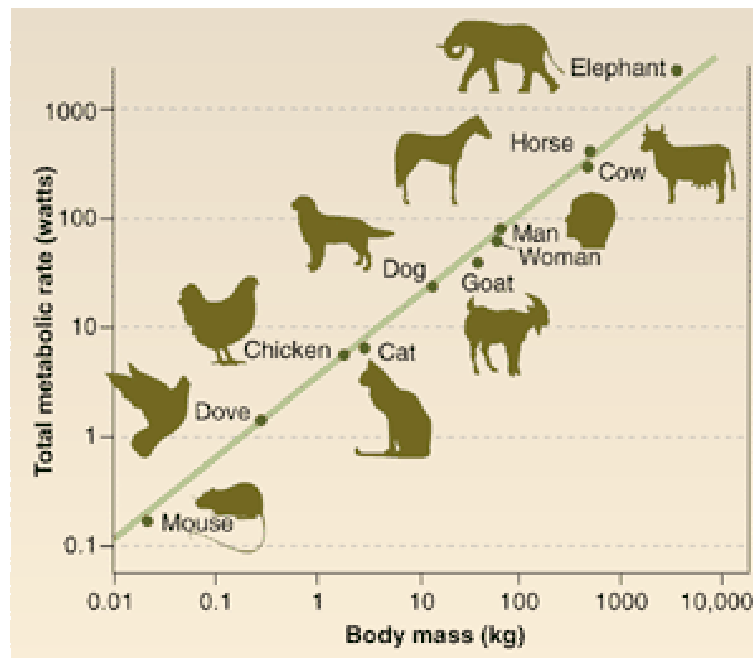


Figure 2.2: The baffling correlation between body size and total metabolic rate. This correlation may stem from nutrient distribution. This figure was adopted from Schmidt-Nielsen (1984).

Chapter 3

Methods

In the following, I defined diversity as the total number of species in the system. I reconsider an evolving food web system model based on mainly Yoshida (2003).

3.1 Outline of the System

I modeled a food web in a closed area (e.g. a separate continent) where interspecific interaction, speciation and extinction occur. Assuming that immigration from a distant continent is very rare, the appearance of new clades is neglected. The main routine in this computer simulation of a hypothetical interaction web system is the calculation of the biomass of each species in the system by using the following multidimensional Lotka-Volterra equations (Lotka 1925; Volterra 1926):

$$\frac{dM_i}{dt} = M_i \left(r_i + \sum_{j=1}^n a_{ij} M_j \right) \quad (3.1)$$

where M_i is the total biomass of species i ; r_i is the intrinsic growth rate of species i ; n is the number of species in the system and a_{ij} is the effect of

species j on species i .

With this set of equations, I calculated the dynamics of the total biomass of each species using a computer. In the computer, the interaction web system is represented in a matrix form; this matrix a_{ij} is then called the "interaction matrix." The calculation was done using the following equations:

$$M_i(t + \Delta t) = M_i(t) + M_i(t) \left(r_i + \sum_{j=1}^n a_{ij} M_j(t) \right) \cdot \Delta t \quad (3.2)$$

where $M_i(t)$ is the total species biomass of species i at a given time step t ; and Δt is equal to a thousandth of one time step. The biomass of species $M_i(t)$ represents the proportion of each species in carrying capacity (this value is 5000). And time step Δt represents the alternation of generations for the minimal species. Using this equation, the fluctuation of biomass of each species is calculated at each time step. When the total biomass of a species becomes lower than its individual bodyweight (w_i) as a result of the calculation of the biomass, the species becomes extinct. When the total biomass in the system exceed 5000 after the calculation of biomass at each step, the biomass of each species was normalized, so that the total biomass of the system was equal to 5000. This normalization implied that the carrying capacity of the system was 5000.

The system consists of both animal and plant species. Plant species are able to grow without feeding on other species. The value of r in plant species is set to 100. On the other hand, that in animal species is given as a mass-

dependent number described below.

For simplicity, carnivorous and parasitic plants are not considered in the present study. My assumption is that a predatory animal species can feed on other prey animal species only when the bodyweight of the predatory species is larger than that of the prey species, although there can be exceptions to this in the real world. This assumption is based on the observation that most predators are larger than their prey (Warren & Lawton 1987, Cohen et al. 1993, Pahl-Wostl 1997, Neubert et al. 2000, Jennings et al. 2001). Animal species are free of bodyweight constraints when they feed on plant species.

Each species has the following characteristics: defense property (D), offense property (A), and feeding range (P). These parameters are used to construct interspecific interactions. Both A and D are arrays consisting of 10 elements. The values of each element of A and D , and the value of P are given by random numbers uniformly distributed in $[0, 100]$ and $[0, 10]$ ranges, respectively.

The construction of a food web is explained in detail in the following case example where species i feeds on species j . If the defense properties of species j (D_j) meet the feeding preferences of species i , which is determined by A_i and P_i , species i can feed on species j . In my model, this judgement is made by counting the number of elements of D that satisfy the following condition:

$$A_i[k] - P_i \leq D_j[k] \leq A_i[k] + P_i \quad (3.3)$$

where $A_i[k]$ is the k th element of A of species i . If the number of elements n is greater, the interaction with i and j will increase. In this case, also considering the ingestion efficiency of energy i.e. mass ratio between prey and predator, the a_{ij} value is given by the following equations:

$$a_{ij} = 0.01 \cdot n \cdot \frac{w_j}{w_i} \quad (3.4)$$

and a_{ji} is set to $-a_{ij}$.

In the real world, neighboring plant species often hamper each other's growth in competition for light, soil resources and germination sites. I assumed that plant species tend to hinder each others growth when they can interact each other. The judgement of how plant species i reduces the growth rate of another plant species j is made by the same method as the case of animal species. If species i reduces the growth rate of species j , the growth rate of a_{ji} is set by

$$a_{ji} = -0.001 \cdot n \quad (3.5)$$

otherwise, a_{ij} is set to 0.

The diagonal elements of an interaction matrix have negative values that represent intraspecific competition. While intrinsic growth rate r_i represents energy gain by photosynthesis for plant or energy loss by metabolism for animal, the diagonal elements of an interaction matrix a_{ii} represents energy loss by sharing sunlight or food in a same species community. When species i is a plant species, the diagonal element a_{ii} is set to -0.001 , and when species i is an animal species, a_{ii} is set to -0.01 . The values (0.01 or 0.001) of

a_{ij} depend on energy conversion efficiency of each species in fact, however, to simplify I set them constant value in this model. And energy conversion efficiency of animal species is assumed to be larger than that of plant species.

3.2 Size-Dependent Evolutionary System

In general, the larger the species, the longer the life. This relationship holds true with remarkable precision: Life timescale tends to lengthen, and metabolism slows down, in proportion to the animal's body weight. Many characteristics of organisms vary with body size, as described by allometric equations of the form

$$Y = Y_0 \cdot M^b \quad (3.6)$$

where Y is the dependent variable, M is body mass, b is a power exponent and Y_0 is a normalization constant that varies with the nature of Y and with the kind of organism. Studies of animals suggest that many variables scale with quarter-powers of mass, for example $b = \frac{3}{4}$ for metabolic rate, and $\frac{1}{4}$ for lifespan (Peters 1983, Schmidt-Nielsen 1984).

I give each species the additional parameter τ_i , characteristic time, which is used to determine the interval of speciation:

$$\tau_i = \left(\frac{w_i}{0.03} \right)^{\frac{1}{4}} \quad (3.7)$$

And the value of r_i in animal species, the metabolic rate of the species, is given by

$$r_i = -2 \cdot \left(\frac{w_i}{0.03} \right)^{\frac{3}{4}} \quad (3.8)$$

In this system, a new species appears only via speciation of mature species. Speciation of species occurs at intervals of 5000 time steps for plant species, and $30000 \times \tau_i$ time steps for animal species. A subpopulation of the species is separated from the main population and becomes a new species. Characteristics of a new species are set by adding slight changes to those of its ancestor species. These changes are given by random numbers drawn from Gaussian distributions (G^1) with a mean of 1.0 and a standard deviation of 0.1. When species d is born from species i , the values of w_d , P_d , and each element of A_d and D_d are set to $w_i + w_i \cdot G$, $P_i + 1.0 \cdot G$, $A_i + 10.0 \cdot G$, $D_i + 10.0 \cdot G$, and the values of r_d of animal species and τ_d are determined by the same equations above. The total biomass of species d is set to 5% of that of species i , and interaction coefficients of species d are decided by using the same method as mentioned above.

¹I apply the Gaussian random number function in *Numerical Recipes in C*, Cambridge University Press.

Chapter 4

Results

4.1 Regulations of Numerical Simulations

At the beginning of a run, a food web comprising of 50 animal species and 50 plant species was constructed. Using the random function (R^1), initial values of each parameters are given by the formula shown in Table 4.1. Runs with 10000000 steps were iterated 10 times. Only the data of animal species were analyzed in the present study. Due to the constraint of computational capacity, the simulation was aborted if the number of species reached beyond 1000, and this case is called "overflow" of species.

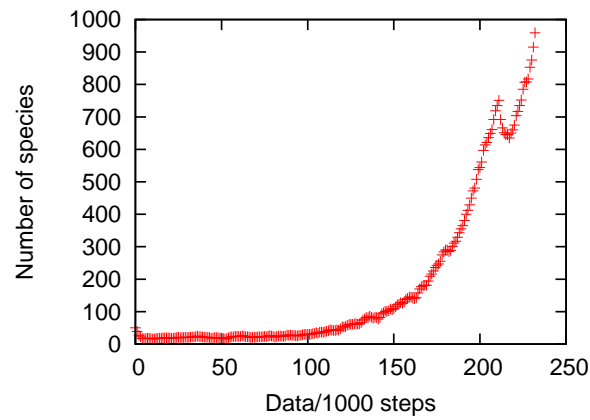
In my numerical system, the smaller species is, the faster it will evolve. Then once very small species is generated, the world will be filled with the small species soon (Fig. 4.1). This result would be consistent with real living world. Very small species (like bacteria) have enormous amount of variety in fact. However, In this case, because the number of species go beyond the numerical limit (=1000 species) in a minute, the analysis of diversity

¹I apply the random number function in *Numerical Recipes in C*, Cambridge University Press.

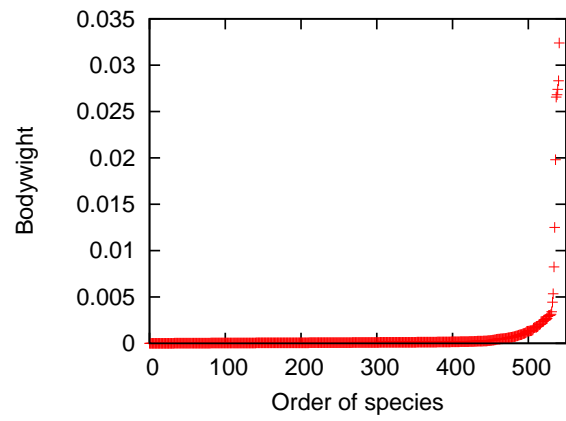
Table 4.1: Initial values of each species parameters in the system

	animal species	plant species
Biomass (M)	10	10
Bodyweight (w)	$0.03R$	$0.03R$
Intrinsic growth rate (r)	$-2(w/0.03)^{\frac{3}{4}}$	100
Defense property (D)	$100R$	$100R$
Offense property (A)	$100R$	$100R$
Feeding range (P)	$10R$	$10R$
Characteristic time (τ)	$(w/0.03)^{\frac{1}{4}}$	0

Parameters of animal species and those of plant species are shown respectively. R is the random function.



(a)



(b)

Figure 4.1: (a) Temporal change of species diversity in the food web system plotted every 1000 steps, and (b) bodyweight of each species in ascending order at 200000 step.

change of species cannot be made by the simulation, so that lower limits of bodyweight of species was fitted to 0.003 in following simulations.

4.2 Diversity Change in The Food Web System

The results of the present study had two kinds of diversity pattern, and each result was not greatly affected when initial values of most species characters were altered, as the values of characters changed through the evolution of species. Within the first 100 steps of each simulation, the diversity in the system decreased to fewer than 20 species, then after this stage, two diversity patterns were observed. The first pattern was characterized by the overflow of species, I call this phenomenon a "overflow pattern" (Figs. 4.2(a) and 4.2(b)). And the other pattern was characterized by the following sequence: the diversity drastically increased to several hundreds of species, then drastically decreased, and after the decline, the diversity maintained several dozen of species with a small degree of fluctuations, I call this phenomenon a "maintain pattern" (Figs. 4.3(a) and 4.3(b)). In the 10 simulations performed, the overflow and maintain pattern appeared 4 and 6 times, respectively (Table 4.2). The maintain pattern was partitioned into 4 stages roughly in Fig. 4.4. Stages II, III, and IV will be called "increasing stage", "decreasing stage", and "stable stage" in this paper.

The results of maintain pattern are consistent with the fossil record; we can see that many clades diversified rapidly at the beginning of a new geologic

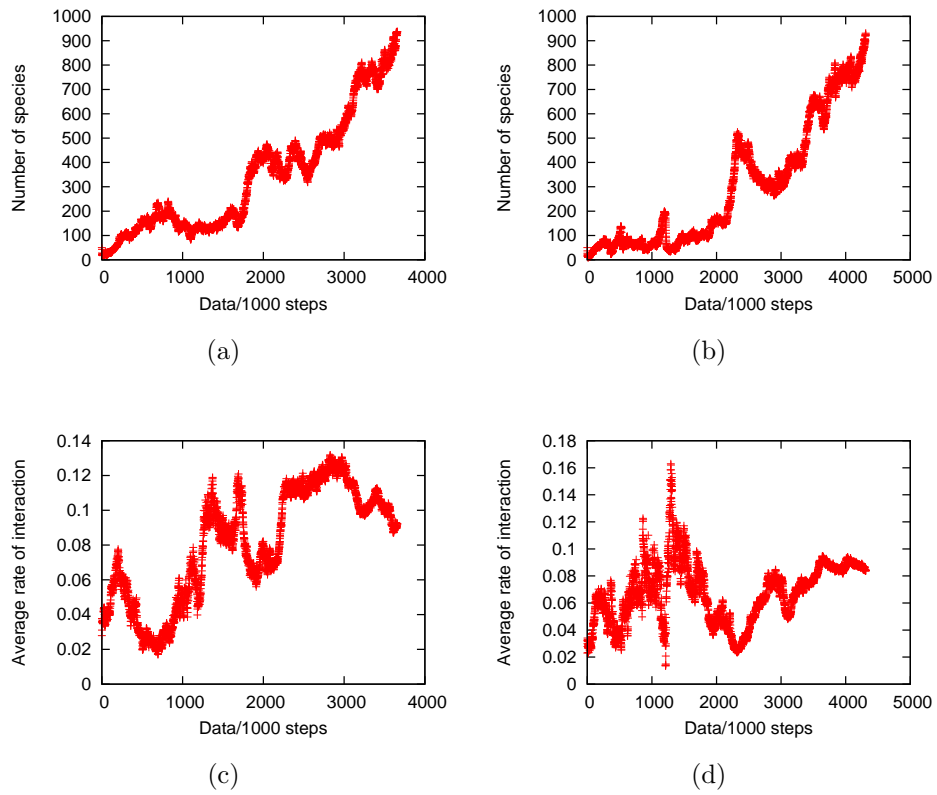


Figure 4.2: Examples of evolutionary patterns for the overflow pattern: (a) and (b) species diversity, and (c) and (d) average rate of interaction between each species.

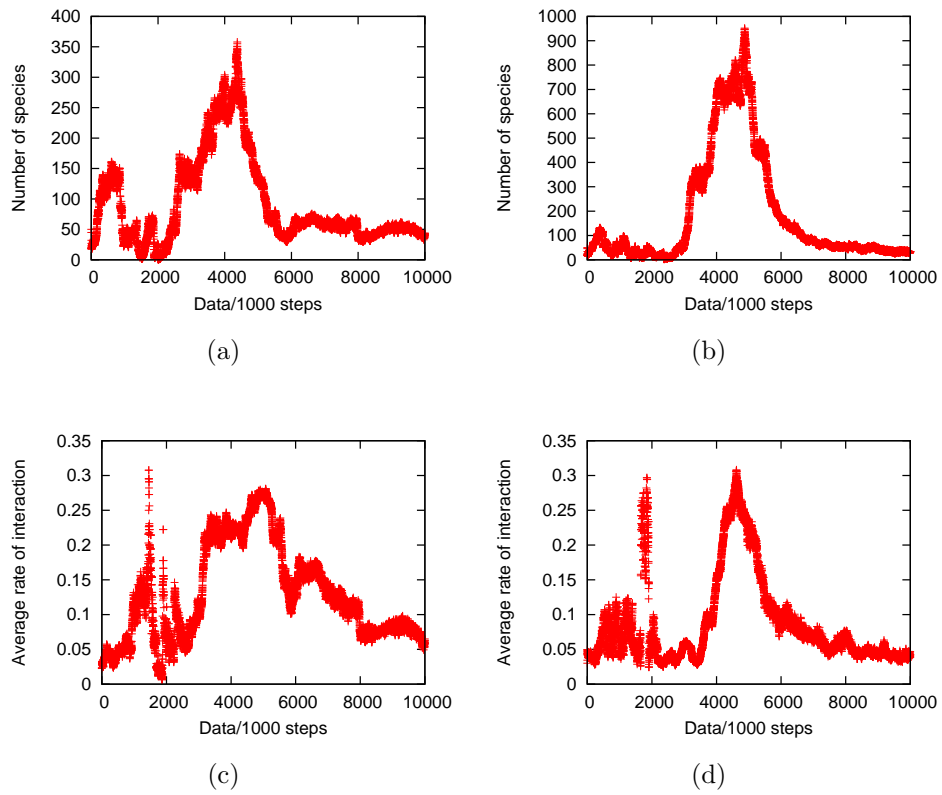


Figure 4.3: Examples of evolutionary patterns for the maintain pattern: (a) and (b) species diversity, and (c) and (d) average rate of interaction between each species.

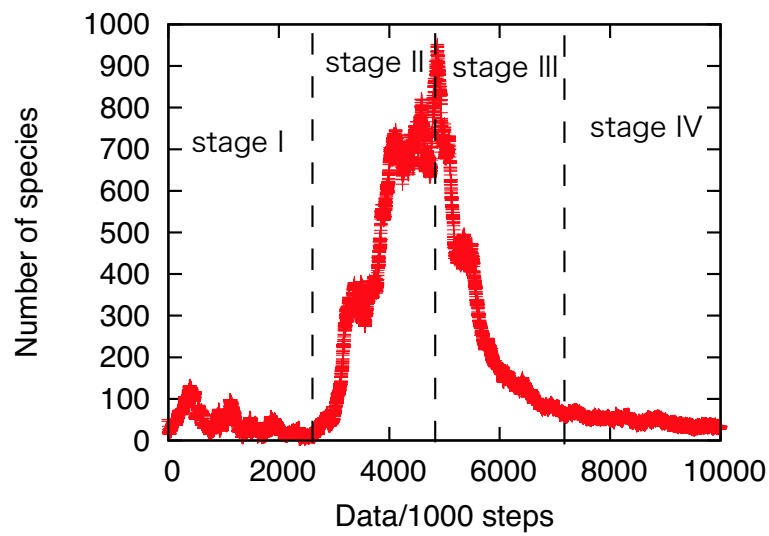


Figure 4.4: Partition of evolutionary pattern of species diversity for the main-tain pattern: stage II, increasing stage; stage III, decreasing stage; stage IV, stable stage.

Table 4.2: Effects of altering evolving systems

	Maintain	Diversity	Limit C
Current version	6/10	53.4	0.31
... Interval of speciation is halved	1/10	25	0.19
... Interval of speciation is doubled	9/10	45.7	0.27
Dimensions of A and D are decreased to 2	4/10	50.2	0.25
... Feeding range P is fixed to 2	3/10	73.3	0.23
... Feeding range P is fixed to 8	4/10	182.5	0.45

Results of 10 runs of each case are shown. Maintain, number of times that maintain pattern occurred; Diversity, means of ten runs of total species diversity in the system at the end of run; Limit C, means of ten runs of connectance maximum values that gave rise to a decline of diversity of species.

era like after the Cambrian explosion and at the end of the Cretaceous mass extinction (Gould et al. 1977). And they also are consistent with a picture of "punctuated equilibria"; the history of evolution is a story of homeostatic equilibria, disturbed only rarely by rapid and episodic events of speciation (Eldredge and Gould 1972).

As well as diversity, I investigated the average connectance rate of interaction between each species, which was defined as the ratio of the number of non-zero elements to the total number of elements in the interaction matrix except the diagonal elements that represent intraspecific competition at each time step. In the case of the overflow pattern, the connectance was kept to low value about 0.1 (Figs. 4.2(c) and 4.2(d)). On the other hand, in the case of the maintain pattern, the high connectance (0.2-0.25) gave rise to a rapidly decline of diversity of species (Figs. 4.3(c) and 4.3(d)). These results are consistent with May (1972), which found that the stability of a randomly linked food web model tends to decrease with the proportion of links of species. My results, which showed the same connectance (0.2-0.25) raise decline of diversity independent of initial values of species characters, also indicate that the limiting value of connectance would exist.

4.3 Effects of Alteration of Evolving System

To consider what affected the diversity of species or evolutionary patterns of the system, I altered interval of speciation (see Eq. 3.7) and some parameters of species. To be more precise, I halved and doubled interval of speciation,

decreased dimensions of A and D to 2, and fixed feeding range P to 2 and 8 (Table 4.2).

4.3.1 Effects of Alteration of Evolution Timescale

The evolution timescale had a large effect on the determination of evolutionary patterns. Qualitatively, slower evolution results in occurrence probability of maintain pattern (Table 4.2). However, the limiting connectance was not affected by the evolution timescale (in the system that interval of speciation is halved, however, only one case showed the maintain pattern. Thus, this case is not statistically significant). The diversity of species declined when the connectance exceeds about 0.2, and the connectance also declined subsequently in any case. Assuming that these declination represent natural selection, the following explanation could be derived: these results indicate that number of species increased too far before the system was stabilized in the faster evolution system, that is, a timescale of stabilization of the system was longer than a that of natural selection in the food web system. It means too fast evolution cannot stabilized the system. Comparing the maintain evolution pattern between in the slow and fast evolution, the stage II and III is shorter in the latter case (Figs. 4.5(a) and 4.5(b)). In the fast evolution system, the period of increasing stage and the decreasing stage was shorter than that of slow evolution system.

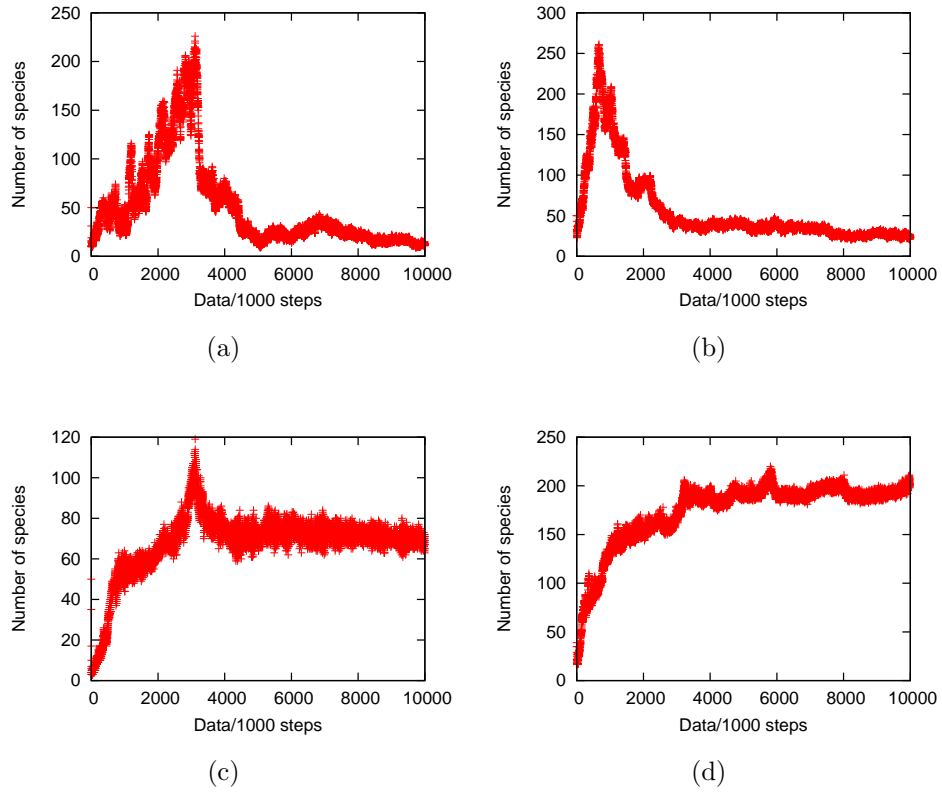


Figure 4.5: Examples of evolutionary patterns of species diversity for cases: (a) interval of speciation is halved, (b) interval of speciation is doubled, (c) dimensions of A and D are decreased to 2 and feeding range P is fixed to 2, and (d) dimensions of A and D are decreased to 2 and feeding range P is fixed to 8.

4.3.2 Effects of Alteration of Feeding Parameters

The range of the feeding zone P value and the dimensions of A and D had a large effect on the behaviour of the system (Table 4.2 and Figs. 4.5(c) and 4.5(d)): species diversity increased gradually not so rapidly in the beginning, then stabilized at high diversity with passing little or no decreasing stage. This result shows that these parameters related directly to the construction of interspecific interactions.

The species diversity in the system related positively to the P value (Table 4.2). This is seemed to be inconsistent with May (1972), because it suggests high connectance system hold high species diversity. I will provide an explanation for that in section 5.2 later.

On the other hand, the dimensions of A and D affected the increasing stage. As compared Figs. 4.5(a) and 4.5(b) to Figs. 4.5(c) and 4.5(d), while in default version's system that has 10 dimensions of A and D , the number of species increased to several hundreds first, then decreased to several dozens or a few hundreds, there were little or no decreasing stage in the 2 dimensional system. It would due to the availability of parameter space, that is, free spaces exist everywhere in the large dimensional system. So many species could spread large spaces and continue to increase the diversity over the long term in the increasing stage. However, maintained diversity at the end of the simulation was larger in the smaller dimension than the larger one. I will discuss the issue in the Discussions chapter later

4.4 Comparing of Size-Dependent/Independent Evolution

Effects of size-dependent speciation frequency is a most important idea for this study, because no study considered the evolutionary timescale for each species to modeled complicated food web system. To examine the effects of that, simulations of size-independent evolutionary system just like previous studies were carried out and compared to my study's results.

First, the interval of speciation was transformed to size-independent form; any species evolve the same interval of 5000 time steps. The species diversity fluctuated randomly. Then, in many cases, the species became extinct in time (Figs. 4.6(c) and 4.6(d)). Size distribution of species in the food web system was also greatly affected by the change of speciation frequency. While size distribution of size-dependent system was followed a power law distribution, that of size-independent system was plotted approximately as a linear function (Figs. 4.7(a), (b) and 4.7(c), (d)).

Next, additionally, metabolism of species (see Eq. 3.8) was transformed to size-independent form; any species burn up its energy at the same rate as that the intrinsic growth rate $r = -2$, that is in this model, larger species can live with on the same amount of food as smaller species. The species diversity was contained to very low (around 10 species) and fluctuated randomly, then the species became extinct soon (Figs. 4.6(e) and 4.6(f)). Size distribution was plotted as a linear function like the model that has size-independent

speciation frequency (Figs. 4.7(e) and 4.7(f)). The difference of species diversity between these two models would be due to the presence of large species. Because of the same metabolic rate for any species, larger species was easier to survive and eat out more small species than size-dependent metabolism model, so species diversity of the total food web system was kept to lower.

Moreover, I also carried out simulations that evolution time scale was doubled to check the speciation frequency could not affect the species diversity just like the results of Section 4.1. Temporary change of species diversity and the size distribution of that model were showed in Figs. 4.6(g), (h) and 4.7(g), (h). As anticipated from the previous results, the species diversity was very low at the value approximately the same as the former model (size-independent speciation frequency and metabolic rate), and the size distribution was also similar to that. However, the fluctuation of species diversity became a little larger because evolutionary rate was set to faster value and more species appeared at a shorter timescale.

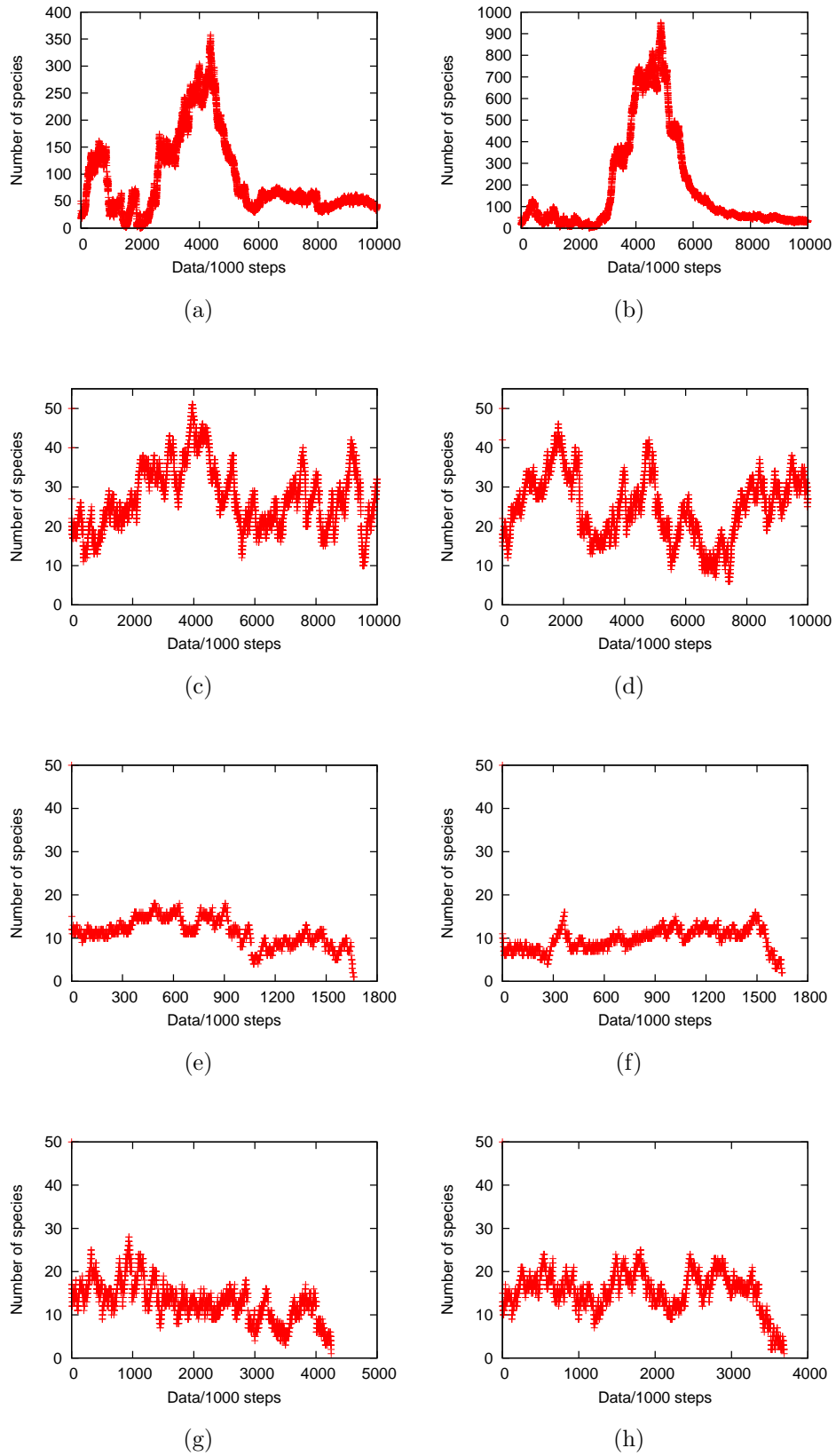


Figure 4.6: Figure caption is in the following page.

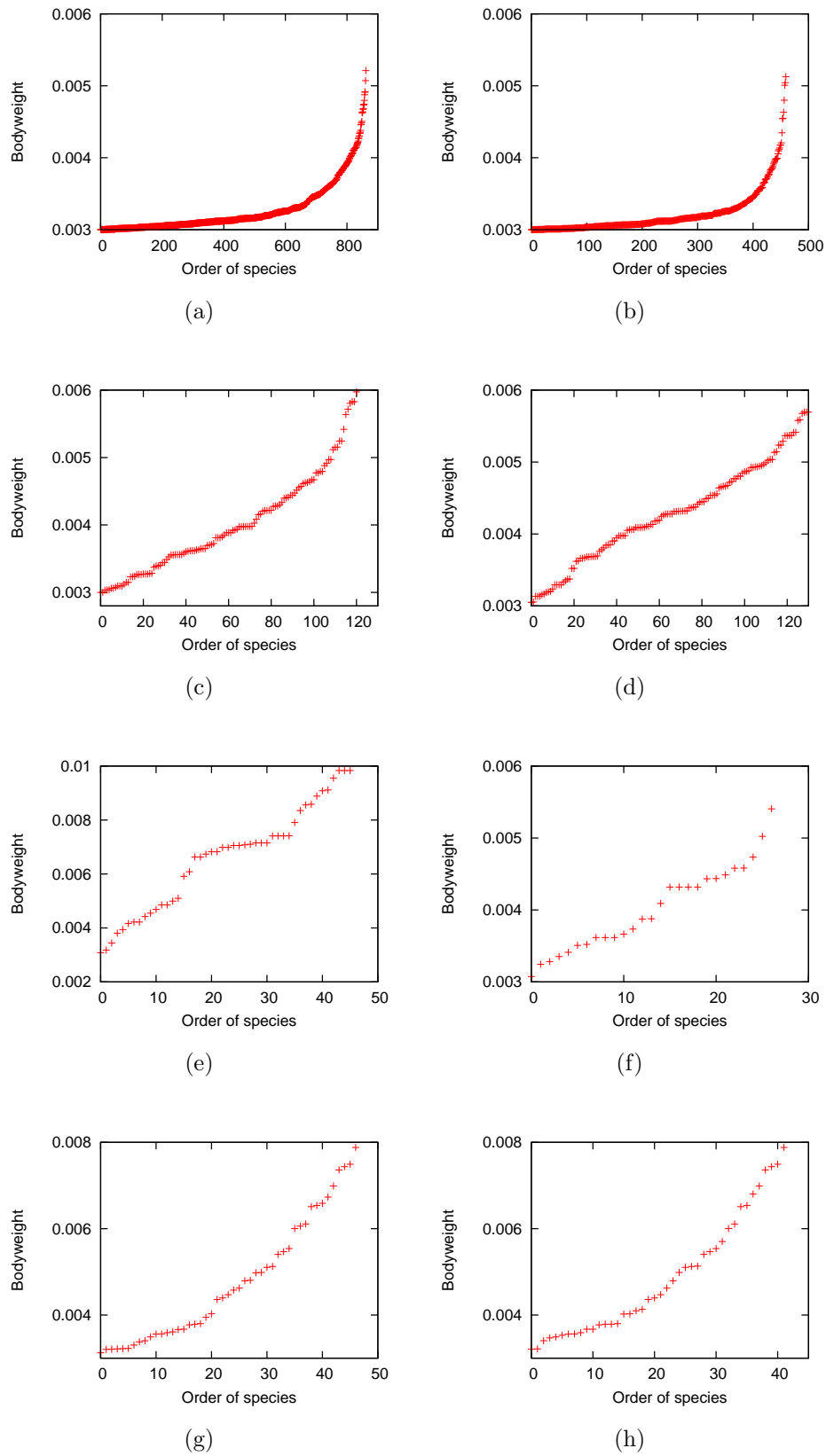


Figure 4.7: Figure caption is in the following page.

Figure 4.6: Examples of evolutionary patterns of species diversity for cases: (a) and (b) size-dependent evolution, (c) and (d) size-independent evolution interval, (e) and (f) size-independent evolution interval and metabolic rate, (g) and (h) evolution timescale is doubled for the model (e) and (f).

Figure 4.7: Size distributions of each food web system. Bodyweight of each species was plotted in ascending order. (a), (b), ..., (h) represent the same system as Fig. 4.6.

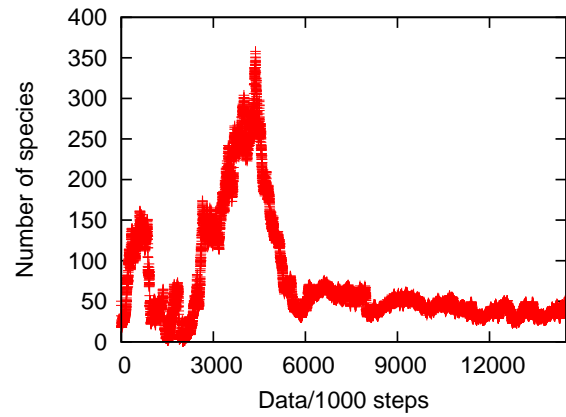
Chapter 5

Discussions

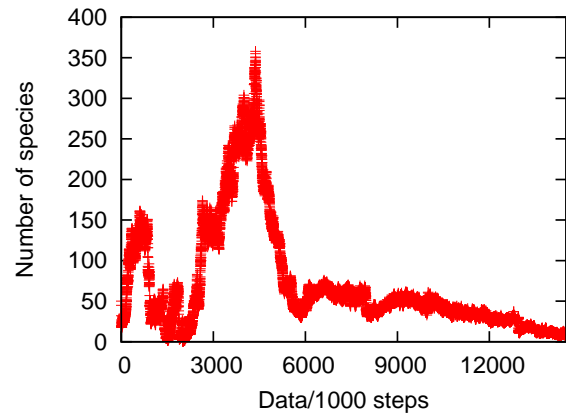
5.1 Analysis of Maintained State

5.1.1 Is Size-dependent Evolution Always Necessary?

The results of my numerical experiments indicates that size-dependent evolutionary system gave us solutions that have the similar behavior of evolution of species such as (increasing stage - decrease stage - stable stage) pattern irrespective of altering the evolution timescale or some parameters of species. However, size-independent evolutionary system never evolved like that, and never maintained high diversity. Therefore, at least, size-dependent evolutionary system is considered to be necessary to go through the evolutionary pattern (increasing stage - decreasing stage - stable stage) for a food web system. Then, the next question is, whether size-dependent evolutionary system is also necessary to maintain high species diversity in the system after entering a period of stability? To examine that, evolutionary system changed from size-dependent to size-independent after entering a maintain stage (at 10000000 time step), and compared the result to size-dependent system (Fig. 5.1).



(a)



(b)

Figure 5.1: Examples of evolutionary patterns of species diversity for cases: (a) size-dependent evolutionary system and (b) the system that size-dependent system was replaced with size-independent system after entering a maintain stage.

5.1.2 Alteration of Size-Dependent/Independent Evolution

Species diversity gradually decreased and then the species became extinct soon for the case that evolutionary system transformed from size-dependent system into size-independent system at 10000000 time step (Fig. 5.1(b)). To be specific, while size-dependent evolutionary system maintained about 50 species with low standard deviation after at 10000000 time step, size-independent evolutionary system reduced the diversity constantly and relegated the species to extinction for about 4500000 time steps (10000000 time step to 14500000 time step). It shows that size-independent evolutionary system causes the collapse of species diversity in the food web system even after the system has been stabilized, that is, size-dependent evolutionary system is also necessary at all times to maintain the food web system. Therefore, saying from another viewpoint, the state that smaller species evolve and increase its diversity faster than larger species is required to maintain the species diversity.

5.1.3 Implication for Observed Food Web System

This results imply that size-dependent evolutionary system should be observed in the real world if our food web system is stabilized and maintain the species diversity for a long term. In other words, power law size distribution of species as shown in Figs. 4.5(a) and (b) (not linear size distribution as shown in Fig. 4.5(c), ..., (h)) should be observed in the stabilized system. I

have not come across detailed study of size distribution of species for global food web system, however, present study would provide a new point of view on ecology. I believe analysis of size distribution of present species and extinct species, which is investigated from fossil records, will be important to examine the evolution of species diversity and extinction events in the animal history.

5.2 Analysis of Interspecies Interactions

5.2.1 Apparent Discrepant Results

As described in section 4.1, The species diversity in the system correlated positively to the P value (Table 4.2), and maintained diversity at the end of the simulation was larger in the smaller dimension system than the larger one (Table 4.2), those are seemed to be inconsistent with May (1972) that showed high connectance system cannot hold high species diversity. What are their apparent discrepant results indicate for the food web system? I analyze the state of interspecies interactions in the system, and examine these problems in this section.

5.2.2 Simplification of Feeding System

For the sake of simplicity, It is assumed that the predator species can feed the prey species when all elements of D of prey species j satisfy the following condition:

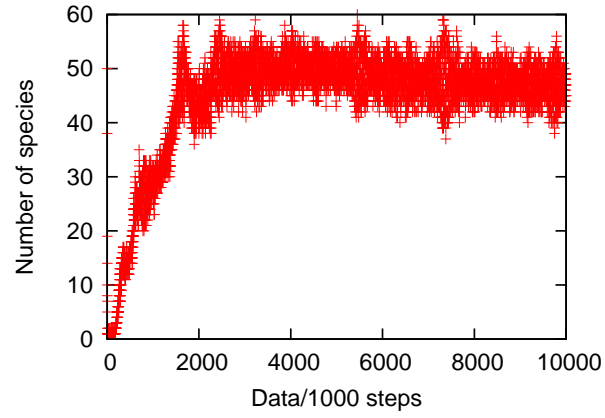
$$A_i[k] - P_i \leq D_j[k] \leq A_i[k] + P_i \quad (5.1)$$

where $A_i[k]$ is the k th element of A of predator species i . In other words, if prey species lives in predator species' feeding zone ($A \pm P$) in all aspects, the prey species are preyed on. It's just a black-and-white rule of the food web system. In order to give a graphic representation of interspecies interactions, 2 dimensions A and D system are dealt with here. I have confirmed that species diversity in the system behaved in much the same way as the system dealt in the previous sections (Fig. 5.2), that is, the behaviour of evolution is independent of dimensions of A and D .

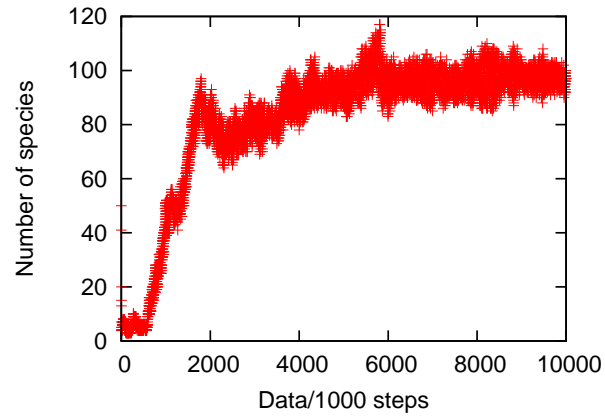
5.2.3 Map of Interspecies Interactions in Food Web System

Figures 5.3 and 5.4 show "maps" of interspecies interactions in the food web system; Fig. 5.3 represents the case that feeding range P is set to 2, and Fig. 5.4 represents the case P is set to 8, respectively. Each figure shows the parameter place $((x, y) = (D[1], D[2])$ and $(x, y) = (A[1], A[2])$; for details to figure caption of Fig. 5.3) where animal species (blue star) and plant species (green star) live, and also shows a feeding zone of each animal species (red square). Bigger animal species can feed smaller animal species and all plant species, if those prey species place in the predator's feeding zone. And, you can follow temporal changes of interspecies interactions, and see the maintained states for the food web systems in Figs. 5.3 and 5.4.

Both Figs.5.3(c) and 5.4(c) show that there are much more green stars (plant species living place) are inside red squares (feeding zone of each animal

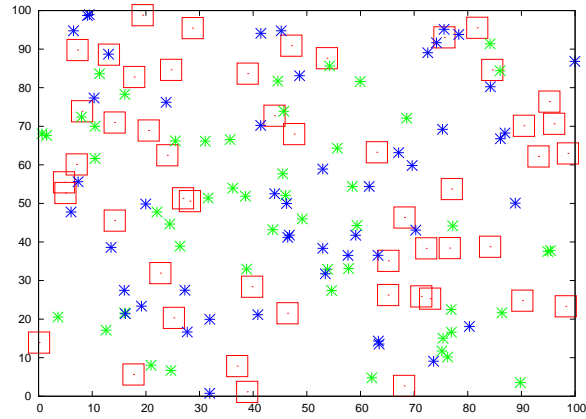


(a)

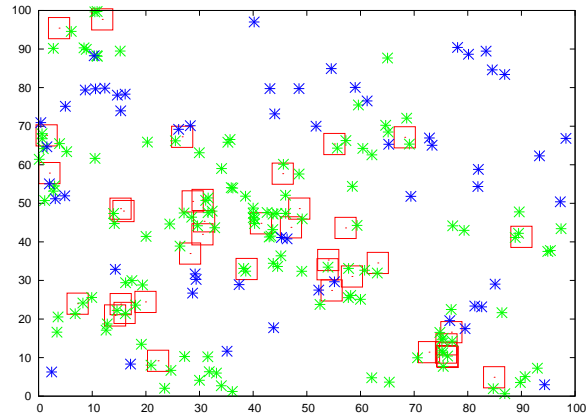


(b)

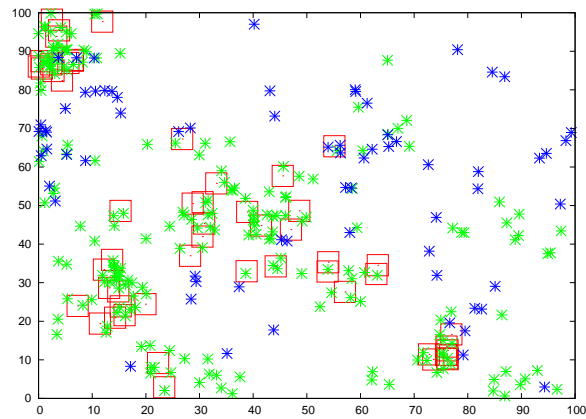
Figure 5.2: Examples of evolutionary patterns of species diversity for cases: (a) dimensions of A and D are decreased to 2 and feeding range P is fixed to 2 and (b) dimensions of A and D are decreased to 2 and feeding range P is fixed to 8.



(a)



(b)



(c)

Figure 5.3: Maps of interspecies interactions in the food web system for the case of $P = 2$. Blue star: animal species living parameter place $((x, y) = (D[1], D[2]))$; Green star: plant species living parameter place $((x, y) = (D[1], D[2]))$; Red square: feeding zone of each animal species $((x, y) = (A[1] \pm 2, A[2] \pm 2))$. (a) Initial state, (b) midterm state, and (c) final state of the simulation.

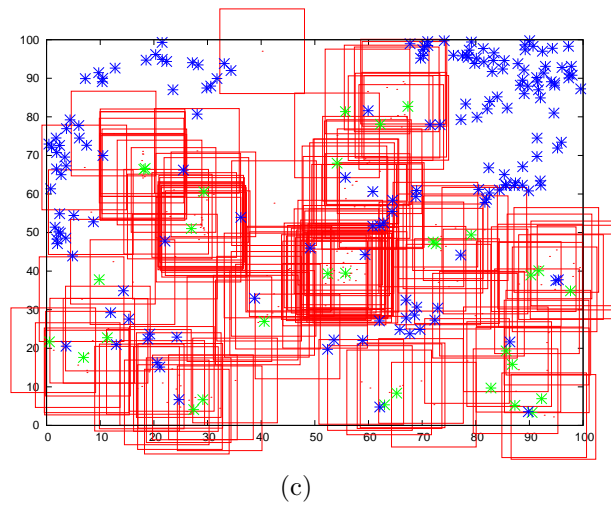
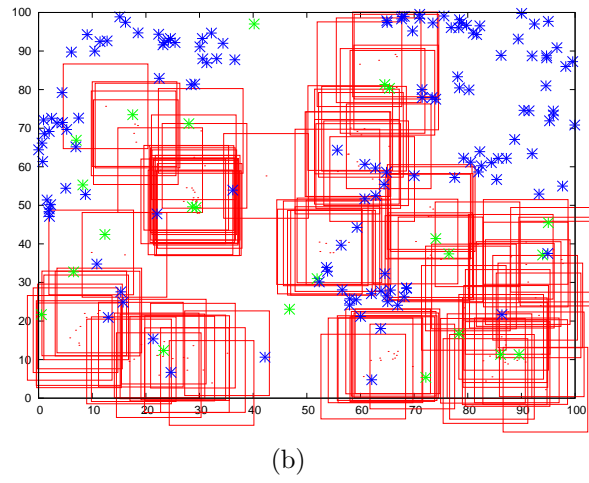
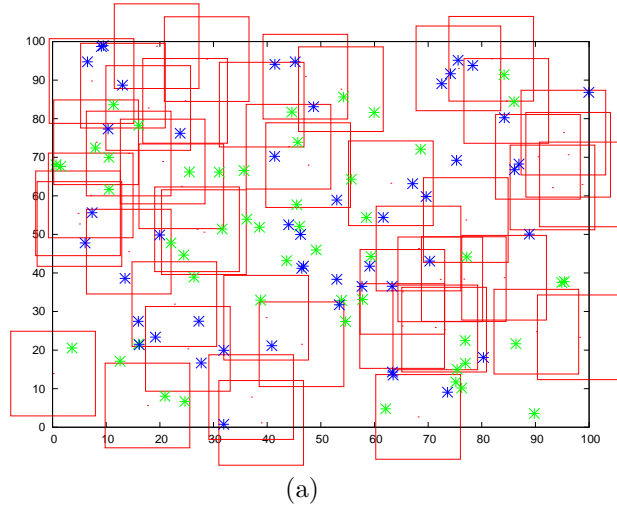


Figure 5.4: Maps of interspecies interactions in the food web system for the case of $P = 8$.

species) than blue stars (animal species living place). This seems to indicate animal species feed on a plant species more than animal species. On the contrary, it would mean that animal species are easy to grow at places where no animal species is feeding. And both cases have some concentration of feeding zone, and free places that are not in use in the parameter place. Especially in the case of smaller feeding zone (Fig. 5.3), more free parameter spaces exist. In the case of larger feeding zone, parameter space was used up across the board, relatively. Thus more species, those had a large variety of parameters A and D , could exist in the latter case than in the former case. Because of that, the species diversity at the stable stage in the system related positively to the P value.

5.2.4 Implication for Alteration of Parameter Dimension

The result, that maintained diversity at the end of the simulation was larger in the smaller dimension system than the larger one (Table 4.2), could be explained from the same viewpoint. In larger dimension system, many free parameter space would exist. It means that species cannot expand to broad parameter places and thus cannot increase its diversity in larger dimension system. As compared to smaller dimension system, distance between each feeding zone is large, relatively. Then, it is difficult for animal species to change feeding zone from successive feeding zone to other one by slight change of properties through evolution. Therefore, the species diversity in the larger

dimension system was smaller than that of the smaller dimension system in present study. On the contrary, considering invasion or new-production of species that use free parameter spaces, the species diversity could increase more.

5.3 Punctuated Equilibria

Paleontology's view of speciation has been dominated by the picture of "phyletic gradualism" (Moore et al. 1952). It holds that new species arise from the slow and steady transformation of entire populations. Under its influence, they sought unbroken fossil series linking two forms by insensible graduation as the only complete mirror of Darwinian processes; they ascribed all breaks to imperfections in the record.

On the other hand, the theory of allopatric (or geographic) speciation suggests a different interpretation of paleontological data (Raup & Stanley 1971). If new species arise very rapidly in small, peripherally isolated local populations, then the great expectation of insensibly graded fossil sequences is a chimera. A new species does not evolve in the area of its ancestors; it does not arise from the slow transformation of all its forbears. Many breaks in the fossil record are real.

Then, considering of the fossil records objectively, Eldredge & Gould (1972) concluded that the history of life is more adequately represented by a picture of "punctuated equilibria" than by the notion of phyletic gradualism. The history of evolution is not one of stately unfolding, but a story of home-

ostatic equilibria, disturbed only rarely by rapid and episodic events of speciation such as mass extinction and mass explosion. My present study also showed extinction just after the beginning of the simulation (mass extinction), rapidly increasing (mass explosion) and following rapidly decreasing (natural selection) of the species diversity, and then stabilization (long-term equilibrium state) finally. I have not consider environmental variations in the present evolutionary system, however, environmental variations could affect the behaviour of evolution. Especially, very large environmental variations like the mass extinction events could collapse the food web system once, and then the system could re-evolve (go through the same evolutionary route, increasing stage - decreasing stage - stable stage) again. Thus, although present simulation showed only one transient stage (increasing stage - decreasing stage) respectively, multiple transient stages could be reproduced if environmental variations are considered in the numerical system (and could reproduce multiple evolutionary fauna like Cambrian-Paleozoic-Modern fauna (Fig. 2.1)). Considering environmental variations built into the evolutionary system is an important issue in the future study of numerical ecology.

Chapter 6

Conclusions

By adopting the size-dependent evolutionary system for numerical experiments on variation of species diversity in the food web system, I derived a particular evolutionary pattern: (1) rapidly decrease of species diversity like mass extinction, (2) rapidly increase like mass explosion, (3) rapidly decrease like natural selection, which was observed especially in larger parameter dimension model, then (4) equilibrated state that maintained over the long term. And I confirmed that size-dependent evolutionary system is stable whereas size-independent evolutionary system raises the fluctuation and extinction of species diversity. The results implied that considering the size-dependent system would be essential in establishing food web numerical model.

For meaningful discussions of general ecology, it is necessary to improve the numerical model of food web system in future. Considering environmental variations, which represent fluctuations of a planet's surface or external disturbing, would be important to discuss long-term life history. And also, we should consider precise energy balance between prey and predator in the

system, precise meaning of species' parameters, precise way of evolution (interval of speciation or range of fluctuation of parameters), and so on. I wish present study serve as a starting point toward making proper numerical models and understanding of general ecological system in the universe.

Acknowledgments

I would like to express my sincere appreciation to my supervisor Dr. Y. Abe. His advice and comments that have guided this study properly. And many discussions with him improve not only this thesis but also my philosophy of research.

I would like to thank Dr. H. Kayane, Dr. E. Tajika, and other members in Earth and Planetary System Science Seminar for fruitful suggestions and comments. I would also like to thank Prof. S. Sasaki, R. Machida, K. Hamano, and the other members in L Seminar for their constructive comments on this study.

I would like to thank H. Genda for many advice on research in all aspects. Finally, I would like to thank S. Watanabe, T. Ishii, T. Konishi, T. Yuuki, Y. Uehara, and other members of the Department of Earth and Planetary Science for making my everyday life a great time.

Bibliography

- [1] Alvares, L. W., Alvarez, W., Asaro, F. & Michel, H. V. 1980 Extraterrestrial cause for the Cretaceous-Tertiary extinction: experimental results and theoretical interpretation. *Science*, **208**, 1095.
- [2] California & Carnegie Planet Search, <http://exoplanets.org/>.
- [3] Cloud, P. 1968 Atmospheric and hydrospheric evolution on the primitive Earth. *Science*, **160**, 729.
- [4] Cloud, P. 1972 A working model of the primitive Earth. *Amer. J. Sci.*, **272**, 537.
- [5] Cohen, J. E., Pimm, S. L., Yodzis, P. & Saldana, J. 1993 Body sizes of animal predators and animal prey in food webs. *J. Animal Ecology*, **62**, 67.
- [6] Cohen, B. A., Swindle, T. D. & Kring, D. A. 2000 Support for the lunar cataclysm hypothesis from lunar meteorite impact melt ages. *Science*, **290**, 1754.
- [7] Eldredge, N. & Gould, S. J. 1972 Punctuated Equilibria: An Alternative to Phyletic Gradualism in *Models in Paleobiology*, Freeman.

-
- [8] Erwin, D. H. 1993 *The great Paleozoic crises*, Columbia University Press.
- [9] Gilpin, M. E. 1994 Community-level competition: asymmetrical dominance. *Proc. Natl. Acad. Sci. USA*, **91**, 3252.
- [10] Gould, S. J., Raup, D. M., Sepkoski, J. J., Schopf, T. J. M. & Simberloff, D. S. 1977 The shape of evolution: a comparison of real and random clades. *Paleobiology*, **3**, 23.
- [11] Hallam, A. 1987 End-Cretaceous mass extinction event: Argument for terrestrial causation. *Science*, **238**, 1237.
- [12] Hallam, A. & Wignall, P. 1997 *Mass extinctions and their aftermath*, Cambridge University Press.
- [13] Happel, R. & Stadler, P. F. 1998 The evolution of diversity in replicator networks. *J. Theoretical Biology*, **195**, 329.
- [14] Hirano, H., Toshimitsu, S., Matsumoto, T. & Takahashi, K. 1999 Bioevents and paleoenvironmental changes in Mid-Cretaceous (in Japanese). *Fossil*, **66**, 47.
- [15] Hoffman, P. F., Kaufman, A. J., Halverson, G. P. & Schrag, D. P. 1998 A Neoproterozoic snowball Earth. *Science*, **281**, 1342.

-
- [16] Hut, P., Alvarez, W., Elder, W. P., Hansen, T., Kauffman, E. G., Keller, G., Shoemaker, E. M. & Weissman, P. R. 1987 Comet showers as a cause of mass extinctions. *Nature*, **329**, 118.
- [17] Jennings, S., Pinnegar, J. K., Polunin, N. V. C. & Boon, T. W. 2001 Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *J. Animal Ecology*, **70**, 934.
- [18] Kaiho, K., Kajiwarra, Y., Tazaki, K., Ueshima, M., Takeda, N., Kawahata, H., Arinobu, T., Ishiwatari, R., Hirai, A. & Lamolda, M. A. 1999 Oceanic primary productivity and dissolved oxygen levels at the Cretaceous/Tertiary boundary: Their decrease, subsequent warming, and recovery. *Paleoceanography*, **14**, 511.
- [19] Kennedy, W. J. 1977 Ammonite evolution. in *Patterns of Evolution: As Illustrated by the Fossil Record*, Elsevier.
- [20] Larwood, G. P. 1988 *Extinction and Survival in the Fossil Record*, Clarendon Press.
- [21] Lotka, A. J. 1925 *Elements of Physical Biology*, Dover, New York.
- [22] MacArthur, R. H. 1955 Fluctuations of animal populations and a measure of community stabilities. *Ecology*, **77**, 762.
- [23] May, R. M. 1972 Will a large complex system be stable? *Nature*, **238**, 413.

-
- [24] Memmot, J., Martinez, N. D. & Cohen, J. E. 2000 Predators, parasitoids and pathogens: species richness, trophic generality and body size in a natural food web. *J. Animal Ecology*, **69**, 625.
- [25] Moore, R. C., Lalicker, C. G. & Fischer, A. G. 1952 *Invertebrate Fossils*, McGraw-Hill.
- [26] Neubert, M. G., Blumenshine, S. C., Duplisea, D. E., Jonsson, T. & Rashleigh, B. 2000 Body size and food web structure: testing the equiprobability assumption and the cascade model. *Oecologia*, **123**, 241.
- [27] Officer, C. B., Hallam, A., Drake, C. L. & Devine, J. D. 1987 Late Cretaceous and paroxysmal Cretaceous/Tertiary extinctions. *Nature*, **326**, 143.
- [28] Pahl-Wostl, C. 1997 Dynamic structure of a food web model: comparison with a food chain model. *Ecological Modeling*, **100**, 103.
- [29] Peters, R. H. 1983 *The Ecological Implications of Body Size*, Cambridge University Press.
- [30] Press, W. H., Teukolsky, S. A., Vetterling, W. T. & Flannery, B. P. 1988 *Numerical Recipes in C*, Cambridge University Press.
- [31] Raup, D. M., Gould, S. J., Schopf, T. J. M. & Simberloff, D. S. 1973 Stochastic models of phylogeny and the evolution of diversity. *J. Geology*, **81**, 525.

-
- [32] Raup, D. M. & Sepkoski, J. J. 1982 Mass extinctions in the marine fossil record. *Science*, **215**, 1501.
- [33] Raup, D. M. & Sepkoski, J. J. 1984 Periodicity of extinctions in the geologic past. *Proc. Natl. Acad. Sci. USA*, **81**, 801.
- [34] Raup, D. M. & Stanley, S. M. 1971 *Principles of Paleontology*, Freeman.
- [35] Sasaki, T., Sasaki, S., Watanabe, J., Sekiguchi, T., Yoshida, F., Kawakita, H., Fuse, T., Takato, N., Dermawan, B. & Ito, T. 2004 Mature and fresh surfaces on the new-born asteroid Karin. *Astrophys. J.*, **615**, L161.
- [36] Sasaki, T., Kanno, A., Ishiguro, M., Kinoshita, D. & Nakamura, R. 2005 Search for nonmethane hydrocarbons on Pluto. *Astrophys. J.*, **618**, L57.
- [37] Sasaki, T. & Abe, Y. Imperfect equilibration of Hf-W system by giant impacts: mechanisms and consequences. *Earth and Planet. Sci. Lett.*, submitted.
- [38] Schmidt-Nielsen, K. 1984 *Scaling: Why Is Animal Size so Important?*, Cambridge University Press.
- [39] Schopf, T. J. M. 1974 Permo-Triassic extinctions: Relation to sea-floor spreading. *J. Geology*, **82**, 129.
- [40] Sepkoski, J. J. 1984 A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinction. *Paleobiology*, **10**, 246.

-
- [41] Sigurdsson, H., D'Hondt, S., Arthur, M. A., Bralower, T. J., Zachos, J. C., van Fossen, M. & Channel, J. E. T. 1991 Glass from the Cretaceous/Tertiary boundary in Haiti. *Nature*, **349**, 482.
- [42] Simberloff, D. S. 1974 Permo-Triassic extinctions: Effects of area on biotic equilibrium. *J. Geology*, **82**, 267.
- [43] Stanley, S. M. 1984 Temperature and biotic crises in the marine realm. *Geology*, **12**, 205.
- [44] Tokita, K. & Yasutomi, A. 1999 Mass extinction in a dynamical system of evolution with variable dimension. *Phys. Rev. E*, **60**, 682.
- [45] Tokita, K. & Yasutomi, A. 2003 Emergence of a complex, symbiotic and stable ecosystem in replicator equations with extinction and mutation. *Theoretical Population Biology*, **63**, 131.
- [46] Volterra, V. 1926 Fluctuations in the abundance of species considered mathematically. *Nature*, **118**, 558
- [47] Warren, P. H. & Lawton, J. H. 1987 Invertebrate predator-prey body size relationships: an explanation of upper triangularity in food webs and patterns in food web structure. *Oecologia*, **74**, 231.
- [48] Yoshida, K. 2002 Long survival of 'living fossils' with low taxonomic diversities in an evolving food web. *Paleobiology*, **28**, 464.

-
- [49] Yoshida, K. 2003 Dynamics of evolutionary patterns of clades in a food web system model. *Ecological Research*, **18**, 625.