Perturbation Experiment and Extinction Process in a Prey-Predator Lattice System

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The investigation of perturbation experiments is important not only to forecast the effect of human management but also to understand community interactions. In the present paper, the dynamic processes in a prey-predator system are studied on a two-dimensional lattice. It is known that this system exhibits nonequilibrium phase transition of extinction. By computer we carry out perturbation experiments of extinction, and find that in the extinction process of the prey, the fluctuation enhancement (FM) is clearly observed, where FM means a high variation in extinction process. However, in the case of extinction of the predator, this enhancement is not observed. When prey goes extinct, the dynamic process has a lot of variation compared to the extinction of predator. Moreover, it is found that FM is clearly observed by spatially explicit model..

1. Introduction

Study of perturbation experiments is served for the prediction of ecological managements (Paine, 1966; May, 1973; Pimm, 1993; Tilman & Downing, 1994; Caswell & Cohen, 1995). The most familiar approach to perturbation experiments is the press perturbation, where one or more quantities (such as densities of species) are altered and held at higher or lower levels. It is well known that the response of an ecosystem to a perturbation consists of two parts (Bender, 1984; Yodzis, 1988); that is, *short-* and *long-term* responses. It is well known that the latter response contains indeterminacy (uncertainty) (Yodzis, 1988; Pimm, 1993; Schoener, 1993; Tainaka, 1994a; Schmitz, 1997). The long-term response is much difficult to predict, compared to the short-term response. This indeterminacy comes not only from non-linear but also from indirect effects. In the present paper, we report the indeterminacy in the short-term response. It is difficult to predict the extinction of species.

Recently, coworkers in our laboratory (Tainaka, Hosiyama & Takeuchi, 2000) studied the computer experiments of extinction for contact process (Harris, 1974; Schlogl, 1972; Konno, 1994) that contained a single species. They applied two simulation methods: one was the lattice model (contact process), where interaction was restricted between adjacent lattice points, and the other was the mean-field simulation (MFS) in which long-range interaction was allowed between any pair of lattice points. They found that the so-called *fluctuation enhancement* (Kubo, Matsuo & Kitahara, 1973; Suzuki 1977; Suzuki 1981; Tsuchiya & Horie, 1985) clearly occurred only for the lattice model.

In the present paper, we deal with a more complicated system that contains two species; namely, prey (X) and predator (Y). Various types of prey-predator system have growing interest in various field, such as ecology (Pacheco, et al, 1997; Hance and Van Impe, 1998) and physics (Lipowski & Lipowska, 2000; Droz & Kalski, 2001; Rozenfeld & Alban, 2001). We apply the prey-predator model first introduced by Tainaka and Fukazawa (1992). Each lattice site is labeled by X, Y, or O (vacant site), and interactions are defined by

$$X + O \xrightarrow{r} 2X, \qquad (1a)$$

$$Y + X \longrightarrow 2Y, \qquad (1b)$$

$$Y \xrightarrow{m} O, \qquad (1c)$$

where the reactions (1a) and (1b) respectively mean the reproduction of prey and predation, and (1c) represents the death process of Y. The parameter r is the reproduction rate of prey (r=1), and m is the mortality rate of Y.

This system have revealed the following phase transitions: (i) When a death rate m of predator is higher than m_y, the predator goes extinct. (ii) In

contrast, m decreases and approaches m_x, the prey density becomes zero. The critical values takes $m_x \sim 0$ and $m_y \sim 0.91$ for lattice model and $m_x = 0$ and $m_y = 2$ for mean-field theory. In the limit $m \to 0$, the predator survives for mean-field theory, whereas the survival of predator is still unknown for lattice model (Tainaka 1994; Satulovsky & Tome, 1994; Sutherland & Jacobs, 1994; Nakagiri, Tainaka & Tao 2001).

2. Methods

2-1. Time Evolution

We apply two simulation methods: one is a lattice model and the other is mean-field simulation (MFS). In the former, interaction is restricted between neighboring lattice sites, while in the latter interaction is aloud between any pair of lattice sites. First, we describe the simulation method for the lattice model:

1) Initially, we distribute species on a square lattice; each lattice site is either empty (O) or occupied by prey (X) or predator (Y).

2) The reactions in (1) are performed in the following two steps:

(i) First, we perform two-body reactions (1a) and (1b): Choose one lattice site randomly, and then specify one of four adjacent sites. Let the pair react according to (1a) and (1b). For example, if these sites are X and O, then the latter site is changed into the former one by the rate r ($r = 1$). We employ the periodic boundary condition.

(ii) We perform a single particle reaction (1c). Choose one lattice point randomly; if the site is occupied by Y, that site will become O by a probability (rate) m.

In the case of lattice model, each individual on a lattice site is assumed not to move: this assumption is applicable for plant, and may be approximately valid even for animals, provided that the radius of action of an individual is much shorter than the size of the entire system.

Next, we describe the method of mean-field simulation (MFS). Almost all procedures of lattice model are not changed in MFS, but the algorithm of two-body reactions is changed as follows: two lattice sites are randomly and independently chosen.

2-2. Perturbation Experiment

The system (1) exhibits a phase transition or extinction as described before. In this paper, we set $r = 1$, and change the value of parameter m. Then

the phase transition point have been obtained as follows: $m_x = 0$ and $m_y = 2$ for mean-field theory and $m_y \sim 0.0$ and $m_y \sim 0.9$ for square lattice model. The experiment is performed as follows: Before the perturbation ($t < 100$), our system stays in a stationary state at $m = m_1$, where both species X and Y coexist ($m_x < m_1 < m_y$). After $t = 100$, the phase transition (extinction) is brought about: the death rate m is suddenly increased or decreased, and held at $m = m_2$, where $m = m_2$ is a value near m_x or m_y. We repeat the same experiment (from m_1 to m_2) many times (N times), and record the time dependence of species density.

We prepare N kinds of initial patterns (*ensembles*), and obtain the densities $x_i(t)$ and $y_i(t)$ for $t > 200$. We calculate the ensemble average $A(t)$ and the variance $V(t)$ which are defined by

$$A(t) = \frac{1}{N} \sum_i x_i(t) \qquad (2)$$

$$V(t) = \frac{1}{N} \sum_i [x_i(t) - A(t)]^2. \qquad (3)$$

These equations are for the prey; for the predator, $x_i(t)$ in above equations must be replaced by $y_i(t)$. Our question is whether the enhancement of variation (fluctuation) occurs, in other words, whether the values of $V(t)$ in dynamical process extremely increase compared to those in stationary state.

3. Mean-Field Theory and MFS

3-1. Mean-Field Theory

If the total number of lattice sites is infinite, the population dynamics for MFS is represented by mean-field theory:

$$\dot{x} = 2rx(1 - x - y) - 2xy, \qquad (4a)$$

$$\dot{y} = 2xy) - my, \qquad (4b)$$

where x and y are the densities of species X and Y, respectively, and the dots denote the derivative with respect to the time t which is measured by the unit of the Monte Carlo step (Tainaka, 1988). Setting all the time derivatives in (4) to be zero, we find the stationary solution ($r = 1$):

$$x_s = m/2, \quad y_s = (2 - m)/4. \qquad (5)$$

where x_s and y_s are steady state densities of x and y, respectively. From (5), we find that the critical values are expressed by $m_x = 0$ and $m_y = 2$. It is

known that stationary solution (5) is asymptotically stable for $0 < m < 2$.

Next, we prove the critical slowing-down (divergence of relaxation time). There is a close relation between critical slowing-down and fluctuation enhancement. Assume that the system initially stays near stationary state. We expand x and y around the steady-state densities:

$$x = x_s + X, \quad y = y_s + Y, \qquad (6)$$

where X and Y are small values ($X << 1$, $Y << 1$). Inserting above equations into (4) and collecting terms to the first order of X and Y, we get

$$\dot{X} = -2(2 + m)X - 2mY, \qquad (7a)$$

$$\dot{Y} = (2 - m)X/2, \qquad (7b)$$

From these equations, we have

$$X(t) \propto \exp(-\mid \lambda \mid t), \qquad (8a)$$

$$Y(t) \propto \exp(-\mid \lambda \mid t), \qquad (8b)$$

where the relaxation time $1/\lambda$ satisfies

$$\lambda^2 + (2 + m)\lambda + m(2 - m) = 0. \qquad (9)$$

Eqs. (8) and (9) denotes the critical slowing-down: the relaxation time diverges ($\lambda \to 0$) in the limit $m \to m_x$ or $m \to m_y$. Since the critical slowing-down is associated with fluctuation enhancement, we perform experiments of phase transition (extinction).

3-2.   Results for MFS

Results for MFS are described. If the size L of lattice is finite, the deterministic equation (4) should be modified by the effect of fluctuation. In the present paper, we never use a stochastic equation, but directly estimate the fluctuation (variation) by computer simulation. In Fig. 1, a typical result of a phase transition is illustrated ($N = 100$ and $L^2 = 10^4$), where the perturbation is applied for $t \geqq 100$ (the value of death rate m of predator is jumped from $m_1 = 0.5$ to $m_2 = 0.02$. Here the time dependencies of both $A(t)$ and $V(t)$ are respectively plotted in the upper and lower figures.. It is found from upper figure that the prey X goes extinct by the perturbation. The lower figure (Fig. 1) shows the fluctuation enhancement: the variation $V(t)$ of predator suddenly increases. We carry out various experiments for the extinction of both prey and predator. In most cases,

no fluctuation enhancement is observed: the value of $V(t)$ is monotonically decreases. However, when m_2 is near the extinction point of prey, we can detect the enhancement of fluctuation. Namely, there are many processes for the extinction of prey.
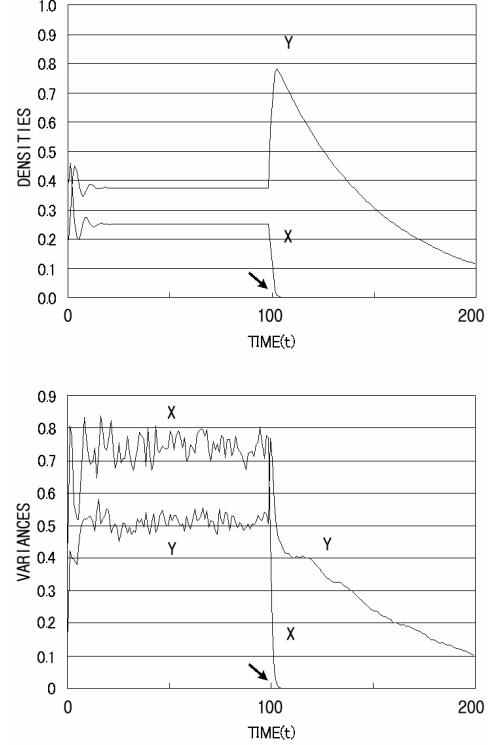

Fig.1 A typical result of perturbation experiment for MFS. The time dependencies of average $A(t)$ and variance $V(t)$ for both species are depicted in the upper and lower figures, respectively. The value of $V(t)$ is increased by a factor of 10^4. At time $t = 100$, the value of death rate m is suddenly decreased from 0.5 to 0.02. We repeat the similar experiment 1000 times ($N = 1000$) on a square lattice of $L^2 = 10^4$ sites.
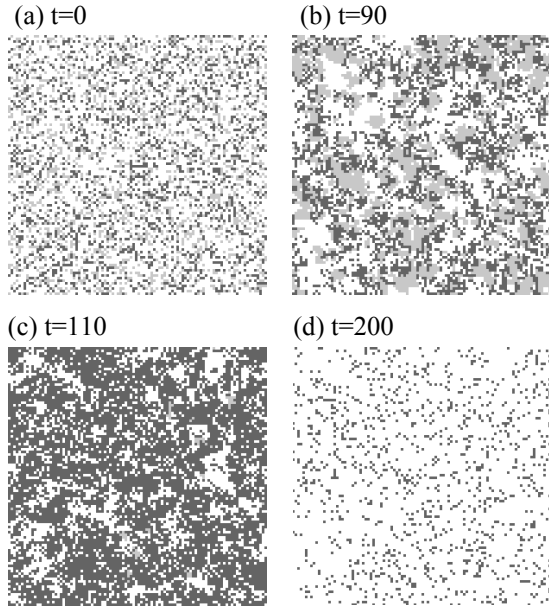
(a) t=0   (b) t=90

(c) t=110   (d) t=200

Fig.2 A typical result of perturbation experiment for lattice model. The perturbation is applied for t $\geqq$ 100. (a) initial random pattern, (b) stationary state, (c) transient state after perturbation, (d) spatial pattern near new stationary state. The colors grey, black and white represent prey, predator and empty, respectively. In (c), the population size of predator increases. In (d), the prey is almost extinct.
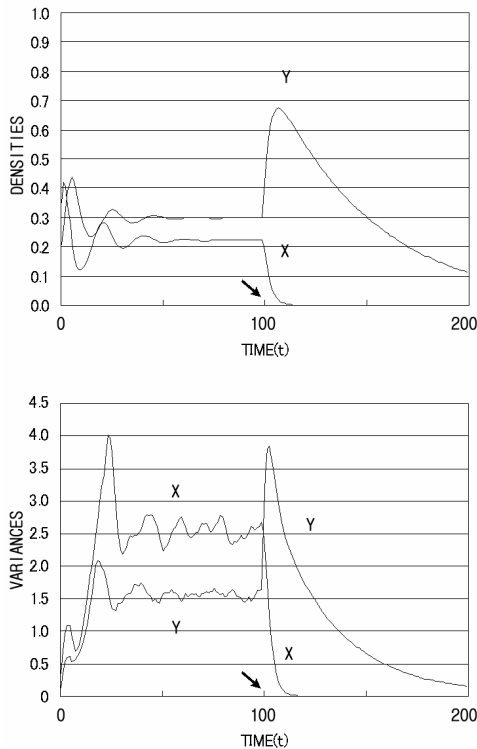

Fig.3 The same as Fig.1, but for lattice model. The mortality rate m is jumped from $m_1 = 0.3$ to $m_2 = 0.02$.

4.   Results for Lattice Model

Simulation results for lattice model are described. First, we carry out perturbation experiments of predator extinction. In Fig. 2, typical spatial patterns are illustrated, where grey, black and white represent prey, predator and empty, respectively. The perturbation is applied for t $\geqq$ 100: the mortality rate m is jumped from $m_1 = 0.3$ to $m_2 = 0.02$. The initial random pattern (a) naturally evolves into a stationary state (b). When the perturbation is applied, the population size of prey (predator) decreases (increases). Finally, the prey goes extinct by the perturbation. In (c), the population size of predator increases. In (d), the prey is almost extinct. Figure 3 displays the time dependencies of both A(t) and V(t). We find from Fig. 3 that the fluctuation enhancement clearly takes place in the transient process to extinction: the variance of predator is suddenly increased just after the perturbation. Namely, the population dynamics of predator has a lot of processes. It should be noted that the peak of variance becomes clear, compared to the mean-field simulation (MFS). According to various experiments, the fluctuation enhancement occurs, only when the prey goes extinct. If the predator becomes extinct the values of V(t) for both prey and predator is monotonically decreased.

5.   Discussions

Perturbation experiments of phase transition (extinction) are carried out for two-dimensional prey-predator model. The death rate m of predator is suddenly increased or decreased from m_1 to m_2, where m_1 represent an existing state ($m_x < m_1 < m_y$) and m_2 takes a value near one of extinction points (m_x or m_y). When m_2 takes a value near the extinction point m_x of prey, then the enhancement of variation (fluctuation) in dynamic processes takes place (Figs. 1 and 3). On the other hand, for the extinction process of predator, no fluctuation enhancement takes place. Our study reveals the following results:

(a) the fluctuation enhancement was clearly observed for lattice model (CP), compared to the mean-field simulation (MFS).

(b) the fluctuation enhancement was never directly associated with the critical slowing down: the critical slowing down was observed for both lattice model and MFS, whereas the fluctuation enhancement emerged only for lattice model.

(c) No fluctuation enhancement can be observed for the species which goes extinct. It emerges for surviving species.

(d) We can observe *asymmetry* in the fluctuation enhancement: in the case of extinction of predator, no fluctuation enhancement is observed, while in the extinction process of prey, the enhancement occurs.

The results (a) and (b) are also observed for the contact process (Tainaka, et al, 2000). However, the results (c) and (d) are never seen in the previous works:

We discuss the mechanism of the asymmetry between prey and predator. The mean-field theory (4) predicts some information for the asymmetry: the final densities (x, y) for $t \rightarrow \infty$ become $(1, 0)$ for $m = m_y = 2$, whereas they are given by $x = 0$ and $0 \geqq y \geqq 1$ in the case $m = m_x = 0$. Thus, uncertainty factor for $m = 0$ may be greater than that for $m = 2$.

It should be emphasized that the fluctuation enhancement is clearly observed for the lattice model. We consider that the spatial pattern is one of important factors for the emergence of fluctuation enhancement. In Fig. 5, typical spatial patterns in stationary state are displayed [(a): $m = 0.04$ and (b): $m = 0.88$], where grey, black and white denote the lattice sites of X, Y and O, respectively. In the case of (a), prey faces extinction, whereas in (b), the predator is endangered. For both patterns, the densities of the endangered species almost take the same value (0.03), whereas we notice that prey is more clumped than predator. The stationary patterns in Fig. 5 suggest that the asymmetry is originated in the clumping behavior of species. In other words, by the clumping pattern of prey, the multiplicity of extinction process is emphasized.

We explore the degree of clumping of both species X and Y in stationary state. To this end, we obtain the ratios R_{XX} and R_{YY} defined by (Tainaka & Fukazawa, 1992; Tainaka, 1994)

$$R_{XX} \equiv P_{XX}/x^2, \quad R_{YY} \equiv P_{YY}/y^2, \qquad (10)$$

where P_{ii} is the probability density finding a state i at a site and a state j at a nearest neighbor of the former site ($i =$X, Y).

When the distribution of species is just random,

we have $R_{ii} = 1$. When $R_{ii} > 1$ ($R_{ii} < 1$), the spatial distribution of species i is clumped (uniform). In Fig. 5, the degree of clumping P_{ii} is depicted against the death rate m of predator ($I = $ X, Y). From this figure, we find the following results:

i) Very near the extinction point m_x (or m_y), the clumping degree of endangered species X (or Y) diverges.

ii) Considerably near the extinction points, in the case of endangered prey, the clumping degree takes a higher value than that in the case of endangered predator (see also Fig. 4).

The result i) can be observed for both species, whereas the result ii) indicates the difference between prey and predator, Hence, the latter may be important for the fluctuation enhancement. Non-random distribution, more precisely, clumping behavior, may play an important role for the enhancement.
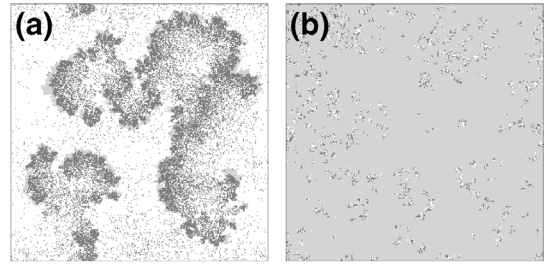

Fig.4 Snapshots of typical stationary patterns. (a): $m = 0.04$, and (b): $m = 0.88$. The colors grey, black and white represent prey, predator and empty, respectively. In (a) the prey faces extinction, whereas in (b) the predator is endangered. Although the densities of both endangered species almost take the same value (0.03), the prey in (a) is more clumped than predator in (b).
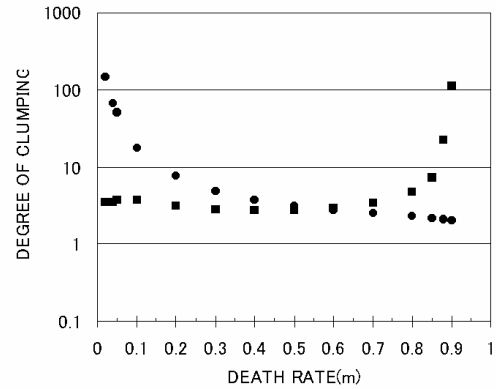

Fig.5 Degree of clumping in stationary state. The values of clumping degree for both species are

obtained by equations (10). The circles and squares denote the results of prey and predator, respectively.

6. Acknowledgments

7. References

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