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Uncertainty in Dynamic Process to Extinction

Kei-ichi Tainaka, Nariyuki Nakagiri, Tomoyuki Sakata and Tomomi Tao

Abstract: The investigation of perturbation experiments is important not only to forecast the effect of ecological management but also to know community interactions. So far, uncertainty has been well known for perturbation experiments: many authors has reported that long-term response of ecosystem to applied perturbations has been very difficult to predict. In the present article, however, we report the uncertainty even in short-term response. We carry out a computer experiment of extinction, and explore whether the so-called fluctuation enhancement occurs or not, where the fluctuation enhancement means that there are a variety of processes to the extinction. We apply the contact process (CP) on a two-dimensional lattice in which interaction is restricted between adjacent lattice points. We also apply the mean-field simulation (MFS) of CP, where long-range interaction is aloud between any pair of lattice points. Computer simulation reveals that for both CP and MFS, stationary state exhibits the so-called critical slowing-down which denotes that relaxation time diverges near the extinction. It is also found that the fluctuation enhancement occurs in the case of CP. Because of short-range interaction, there are a variety of different processes to extinction.

Keywords: lattice model; ecosystem; uncertainty; perturbation experiments

1 INTRODUCTION

Under various human management, ecosystems receive perturbations or disturbances. The investigation of perturbation experiments is essential to conserve biospecies [Paine, 1966; May, 1973; Tilman and Downing, 1994]. The most familiar approach on perturbation experiment is the press perturbation, where one or more quantities 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. The former response is usually determined by the so-called direct effect which is a straightforward to the cause. On the other hand, the final stationary state (long-term response) is determined not only by direct but also by indirect effect. One of the most striking results is an indeterminacy (uncertainty) of indirect effect [Yodzis, 1988; Tainaka, 1994; Schmitz, 1997]. The long-term response of press perturbation is very difficult to predict. In the present article, however, we report the uncertainty even in short-term response.

In the field of physics, the dynamics of phase transition have been accumulated. There are mainly two types of phase transition: first- and second-order transitions. In the latter case, the value of order parameter continuously changes between both phases, and we can usually observe enhancement of fluctuation [Kubo et al., 1973; Tsuchiya and Horie, 1985] which means that there are a variety of processes for a phase transition. So far, it is thought that the fluctuation enhancement is originated in the so-called critical slowing-down: relaxation time diverges at a stationary state near the phase boundary. On the other hand, extinction in ecosystems can be regarded as a a phase transition, where the order parameter corresponds to the population size (density) of individuals. When the extinction gradually occurs, and when the density is slowly decreased, then we expect that the critical slowing-down and fluctuation enhancement may be observed in this system.

In the present paper, we report that the fluctuation enhancement is not always originated in the critical slowing-down.

When the population size of a species becomes small, the risk of extinction increases. So far, several authors have estimated the risk of extinction, using the following stochastic differential equation
[Lande, 1995]:

\[
\dot{x} = Rx(1 - x/K) + N(x), \quad (1)
\]

where the dot represents the derivative with respect to the time, the variable \( x \) is the population size of a species. The first term in the right hand side of (1) denotes the logistic equation which includes constant parameters \( R \) and \( K \), and the last term in (1) denotes a noise (fluctuation) which usually depends on \( x \). If \( x \) becomes small, the noise term becomes critical. We consider that such an approach has a flaw; namely, the noise term \( N(x) \) is arbitrarily given by authors; especially, the intensity of noise is arbitrary, despite it plays an essential role for risk estimation. However, the noise intensity should be automatically given [Tainaka et al., 2000].

In recent years, lattice models are widely applied in the field of ecology [Nowak et al., 1994; Harada and Iwasa, 1994; Durrett and Levin, 1996]. In the present paper, we apply the contact process (CP) which has been extensively studied from mathematical [Harris, 1974; Liggett, 1985] and physical [Konnos, 1994; Marro and Dickman, 1999] aspects. The CP is a lattice version of logistic equation. Considerable data on CP have been accumulated, but they are mainly related to stationary state. However, we focus on dynamic process of CP.

2 \ MODEL AND METHOD

We consider a simple model ecosystem which contains a single species X. Birth and death processes of X is given by

\[
X + O \rightarrow 2X, \quad (2a)
\]

\[
X \rightarrow m \rightarrow O, \quad (2b)
\]

where \( X \) denotes an occupied site of biospecies and \( O \) is the vacant site. The reactions (2a) and (2b) mean reproduction and death processes, respectively: the parameter \( m \) represents the death rate of \( X \). The reaction (2a) are carried out by two different methods; namely, CP and its mean-field simulation (MFS).

The Simulation method for CP is defined as follows:

1) Initially, we distribute individuals on square lattice; each lattice site is either empty (O) or occupied by an individual (X).

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

(i) First, we perform two-body reaction (2a): Choose one lattice site randomly, and then specify one of four neighboring sites. If the pair of sites are X and O, then O is changed into X.

(ii) Next, we perform one-body reaction (2b). Choose one lattice point randomly; if the site is occupied by X, the site will become O by a probability (rate) \( m \).

3) Repeat step 2 by \( L \times L \) times, where \( L \times L \) is the total number of lattice points. This step is called as Monte Carlo step [Tainaka, 1988.]. We assume that the value of \( L \) is 100.

4) Repeat step 3) until the system reaches a stationary state. Here we employ periodic boundary conditions.

Now we consider the computer experiment of extinction caused by the sudden increase of the value of \( m \). In other words, we carry out perturbation experiments of phase transition. It is known that CP exhibits a phase transition at a critical point \( m = m_c \). The value of \( m_c \) is \( m_c \sim 1.213 \) on square lattice. The phase transition resembles the second-order transition; at the critical point, the steady-state density continuously changes from non-zero value to zero. The experiment is performed as follows: Before the perturbation \( (t < 0) \), our system stays in a stationary state at \( m = m_1 \), where the species X exists \( (m_1 < m_c) \). After \( t = 0 \), the death rate \( m \) is suddenly increased, and held at \( m = m_2 \) \( (m_2 > m_c) \). Because of this perturbation, the system eventually reaches the extinct phase. We repeat the same experiment (from \( m_1 \) to \( m_2 \) \) many time, and record the time dependence of species density.

3 \ CRITICAL SLOWING-DOWN

In this section, we explore the dynamics in stationary state to know the initial condition of perturbation experiment. In Fig. 1, typical examples of stationary state for CP is illustrated, where black
and white denote the lattice sites of X and O, respectively. We obtain the average $A(t)$ and variance $V(t)$ of density $x(t)$ which are defined by

$$A(t) = \frac{1}{T} \int_0^T x(t) dt, \quad (3a)$$

$$V(t) = \frac{1}{T} \int_0^T |x(t) - A(t)|^2 dt. \quad (3b)$$

It is known that the variance $V(t)$ in stationary state has been increases with the decrease of steady-state density $A(t)$ [Marro and Dickman, 1999]. The variance diverges near the critical point $m_c$. Such a phenomenon is caused by the so-called “critical slowing-down” (divergence of the relaxation time). The similar result is obtained for MFS.

$$\dot{x} = Rx(1 - x/K), \quad (4)$$

where the dot represents the derivative with respect to the time $t$ which is measured by the Monte Carlo step, and the quantities $R$ and $K$ are defined by

$$R = 2 - m, \quad K = 2(1 - m)/2. \quad (5)$$

The steady-state solution of logistic equation (4) can be obtained by setting the time derivative in (4) to zero. It is well known that non-trivial solution ($x = K$) for $m < 2$ is stable, and that phase transition occurs at $m_c$ = 2: for $m \geq m_c$ (or $m < m_c$), species cannot (or can) exist. Moreover, the logistic equation explains the critical slowing-down near $m = m_c$. When the difference $x(t) - K$ is much smaller than unity, we have from (4) that

$$x(t) - K \propto \exp(-|m_c - m|t). \quad (6)$$

Hence, we see that the relaxation time $1/|m_c - m|$ diverges in the limit $m \to m_c$. If $m = m_c$, we obtain power-law decay. Because of critical slowing-down, the variance in stationary state diverges near $m = m_c$.

4 Results of Perturbation Experiments

4.1 Results of MFS

Perturbation experiment is repeatedly performed from $m_1$ to $m_2$, where $m_2 > m_c$ and $m_1 < m_c$. We prepare $N$ kinds of initial patterns (ensembles) which are in stationary state at $m = m_1$; each of them has the density $x_i(0)$ ($i = 1, 2, \ldots N$). The value of $x_i(0)$ is almost equivalent to the steady-state density at $m = m_1$. We obtain the dynamics $x_i(t)$ for $t > 0$ in order to calculate the ensemble average $\bar{A}(t)$ and the variance $V(t)$ which are defined by

$$\bar{A}(t) = \frac{1}{N} \sum_i x_i(t), \quad (7a)$$

$$V(t) = \frac{1}{N} \sum_i [x_i(t) - \bar{A}(t)]^2. \quad (7b)$$

In both methods of CP and MFS, the stationary state near the critical point $m_c$ exhibits the critical slowing-down. Since the variance in stationary state increases with the decrease of steady-state density, it is expected that fluctuation enhancement [Kubo et al., 1973; Tsuchiya and Horie, 1985] (extreme increase of $V (t)$) occurs in the transient state of dynamic process.

Fig. 1: Snapshots of typical stationary patterns for CP. The value of annihilation rate $m$ is below the critical point $m_c$ ($m_c \sim 1.2$), so that species X can survive. (a) $m = 0.3$, (b) $m = 1.0$. Black and white denote the lattice sites of X and O, respectively. It is worth while nothing that species X goes extinct for the higher values than $m_c$.

In the case of MFS, we can prove the critical slowing-down. If the total sites is infinitely large ($L \to \infty$), the dynamic equation for MFS becomes
We carry out perturbation experiments of extinction in mean-field simulation (MFS). In Fig. 2, a typical result of perturbation experiment is displayed; the time dependencies of both average \( A(t) \) and the variance \( V(t) \) are plotted. It is found from computer simulation that the fluctuation enhancement never takes place for various values of \( m_1 \) and \( m_2 \); especially when \( m_2 \) takes a value much larger than \( m_c \), the value of \( V(t) \) rapidly decreases with time.

![Fig. 2: The result of perturbation experiment in the mean-field limit. The time dependencies of both average \( A(t) \) and variance \( V(t) \) defined by (7a) and (7b) are displayed, where the value of \( V(t) \) is multiplied by 200. At time \( t = 0 \), the annihilation rate \( m \) is jumped from 1.0 to 2.1. We repeat the similar experiment 100 times (\( N = 100 \)) with different initial patterns. The system has \( 10^4 \) lattice sites.](image)

In the below, we give an explanation for the fact that fluctuation enhancement never occurs in the mean-field limit. From (7b), we have

\[
V(t) = \frac{1}{N} \left[ \sum_i x_i(t)^2 - \frac{1}{N} \left( \sum_i x_i(t) \right)^2 \right]
\]

\[
= \frac{1}{N^2} \sum_{i > j} \left[ x_i(t) - x_j(t) \right]^2.
\]

It follows that

\[
\dot{V} = \frac{2}{N^2} \sum_{i > j} (x_i - x_j)(\dot{x}_i - \dot{x}_j).
\] (8)

The dynamics for \( t > 0 \) is assumed to be determined by the logistic equation (4), where both parameters \( R \) and \( K \) are negative (\( m_2 > 2 \)). Let \( x_i(t) \) and \( x_j(t) \) be two solutions of (4) whose initial values are slightly different from each other. Here we put

\[
x_i(0) > x_j(0).
\]

From (4), we have

\[
\dot{x}_i - \dot{x}_j = R(x_i - x_j)[1 - (x_i + x_j)/A],
\] (9)

Note that \( x_i(t) \neq x_j(t) \) for \( t > 0 \) because of the uniqueness of the solution to (4) and \( x_i(t) > x_j(t) \) for all \( t > 0 \). Hence, the right-hand side of (9) is always negative, and the difference \( x_i(t) - x_j(t) \) decreases as the time proceeds. It is therefore proved from (8) that the variance \( V(t) \) always decreases.

Strictly speaking, this proof is insufficient, since the dynamics for a finite value of \( L \) is described by some stochastic differential equation, such as (1). Nevertheless, the logistic equation (4) well explains that i) critical slowing-down occurs, and ii) enhancement of fluctuation does not occur.

### 4.2 Result of CP

The basic equation of CP for \( L \to \infty \) becomes;

\[
\dot{x} = (P_{XO} + P_{OX}) - mx \quad (10a)
\]

where \( P_{ij} \) is the probability density finding a state \( i \) at a site and a state \( j \) at a nearest neighbor of the former site \((i, j) = X, O\). Note the difference from the conditional probability; the relations

\[
P_{ij} = P_{ji}, \quad \Sigma_j P_{ij} = P_i \quad (10b)
\]

Unfortunately, (9) cannot be solved; nevertheless, it is known that the phase transition occurs at \( m = m_c \),

\[
m_c \sim 1.2 \text{ for } d = 2.
\]

We carry out similar perturbation experiment for CP: the value of annihilation rate \( m \) is jumped from \( m_1 \) to \( m_2 \) (\( m_1 < m_c \) and \( m_2 > m_c \)). In Fig. 3, the time dependencies of both average density \( A(t) \) and the variance \( V(t) \) are plotted, where we put \( m_1 = 0.3 \) and \( m_2 = 1.3 \). It is found from Fig. 3 that the fluctuation enhancement takes place. Even though the average density decreases, the variance \( V(t) \) increases at intermediate stage of phase transition. Note that such a phenomenon is not always observed for all experiments. Fig. 4 illustrates the time dependencies of both \( A(t) \) and \( V(t) \) for the cases of \( m_2 = 2.0 \) and \( 5.0 \). As the value of \( m_2 \) increases, the enhancement of fluctuation disappears.

![Fig. 3: Perturbation experiment for CP. The value of \( m \) is jumped from 0.3 to 1.3 (\( N = 100 \) and \( L = 100^2 \)). Both average \( A(t) \) and variance \( V(t) \) are depicted against time, where the value of \( V(t) \) is increased by a factor of 70.](image)
From (11), we have steady-state density. On the other hand, (11) leads to enhancement of variance thus increases as density decreases. In stationary state the system more or less stays in stationary state; the in stationary state becomes contagiously (uniformly). The basic equation (10) for CP that near the critical point \( x \) becomes rapidly high \((12)\) of particles. If \( m \) takes a value near the critical point \( m_c \), then the fluctuation enhancement in dynamic processes takes place (Fig. 3).

\[
R_{XX} \equiv P_{XX}/x^2 \quad (11)
\]

in stationary state [Tainaka, 1994]. When the distribution of particles is just random, we have \( R_{XX} = 1 \). When \( R_{XX} > 1 \) \((R_{XX} < 1)\), they distribute contagiously (uniformly). The basic equation (10) in stationary state becomes \( P_{XO} = mK/2 \). On the other hand, (11) leads to \( P_{XX} = K - P_{XO} \). From (11), we have \( R_{XX} \propto K^{-1} \). It is well known for CP that near the critical point \( m \rightarrow m_c \), the steady-state density \( K \) satisfies \( K \propto (m_c - m)^{\beta} \), where \( \beta \) is a positive constant. It follows that

\[
R_{XX} \propto (m_c - m)^{-\beta}. \quad (12)
\]

When \( m \) approaches \( m_c \), the degree of clumping of \( X \) becomes rapidly high \((R_{XX} \rightarrow \infty)\). The enhancement of \( V(t) \) may be caused by the clumping behavior (12) of particles. If \( m_2 \) is not so large, the system more or less stays in stationary state; the variance thus increases as density decreases.

5 Conclusions

Study on the process to biospecies extinction is very important for conservation biology. In the present article, we study perturbation experiments of phase transition (extinction), and report the uncertainty originated in critical phenomenon. The annihilation rate \( m \) of particle is suddenly increased from \( m_1 \) to \( m_2 \), where \( m_1 < m_c \) and \( m_2 > m_c \). The density \( x \) of particle (order parameter) is thus changed from a positive value to zero. We estimate the fluctuation in population size (density) which is automatically generated. Simulation is carried out by two different methods: CP and its mean-field version. In the latter case, the fluctuation enhancement does not occur. On the other hand, when the method of CP is applied, and when \( m_2 \) takes a value near the critical point \( m_c \), then the fluctuation enhancement in dynamic processes takes place (Fig. 3).

We can propose an experiment of cultivation of bacteria. The cultivation are carried out on two kinds of nutrient media; that is, agar and fluid media. To the former model, we apply the basic contact process (CP) in which the growth process (1a) occurs within a short range: offspring are reproduced at a neighboring site of mother. On the other hand, in the fluid medium, solution is always stirred, so that offspring are randomly distributed in the medium. Thus this medium corresponds to the mean-field simulation (MFS) of CP. The reaction (1b) means the death processes of bacteria In actual experiment, (1b) is realized under UV light or radioactive rays. The parameter \( m \) represents the intensity of light (rays). We carry out the experiment of extinction caused by the sudden increase of the value of \( m \). Our results predict that there are a variety of different processes to extinction in the case of agar medium (CP).

So far, the enhancement of fluctuation has been observed in some physical systems [Kubo et al., 1973; Tsuchiya and Horie, 1985]. However, our system has distinct properties never seen in the previous works:

i) The fluctuation enhancement is not always originated in the critical slowing-down: it is not observed in the mean-field limit (Fig. 2).

ii) Previously, the order parameter was increased from zero to a positive value, whereas the present paper reports the just opposite case: the order parameter (density) is decreased. If the order parameter would increase, the variance \( V(t) \) often increased; examples are the exponential growth and logistic equation.

Our results suggest that for the fluctuation enhancement, not only the critical slowing-down but also the clumping behavior of particles are essential. The
latter property has an important meaning in ecology, since almost all species spatially form a clumped distribution. Especially, when a species becomes endangered, the degree of clumping usually increases. This is due to the inherent nature of biological species: offspring is produced in the neighborhood of parents. In the system (2), we regard X as a biospecies, and m as the death rate. Even if the density x approaches zero, the conditional probability Fxx/x never vanishes (12). The fluctuation enhancement ecologically means that there are a variety of processes to extinction of a species. It is not easy to predict the extinction process of species.

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