Press Perturbation and Parity Law in a Model Ecosystem

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The spatial pattern dynamics in cyclic ecosystems composed of several species is studied by applying the lattice version of the Lotka-Volterra model. By computer simulation, we carry out press perturbation: the value of birth or death rate of a target species is changed, and held at a higher level. We explore the short- and long-term responses; in particular, we record the population sizes of the target species. It is found that the profile of the parameter dependence is determined by "parity" which is defined by whether each system has an odd or even number of species. When the parity is even, the long-term response becomes similar to the short-term one. On the other hand, in the case of odd parity, the long-term response is counterintuitive: it is just opposite to the short-term one. The spatial pattern formation of endangered species plays an important role in this law.

1 INTRODUCTION

Under various human managements, ecosystems receive perturbations, disturbances,or stresses. There are two ways to carry out perturbation experiment: press and pulse perturbations. We are interested in the latter experiment; that is, the death or birth rate of a target species is altered and held at a higher level. The response of an ecosystem to the press perturbation usually consists of two parts,[1] that is, short- and long-term responses. The former response (less than several generation times) is known to be intuitive (straightforward); for example, when the death rate of a target species is increased, the density of the species decreases. On the other hand, it is known that the latter response (more than 10 generation times) is very difficult to predict.[1-3] Nevertheless, in recent years, coworkers of the authors have dealt with a cyclic system whose food web is represented by a single one-dimensional chain, and found a parity law,[4] where the parity is defined by whether each system has odd or even number of species. When the chain contains odd number of species (odd chain), the long-term response becomes very frequently opposite to the short-term one ("opposite response"). On the other hand, in the case of even chain, the opposite response rarely occurs. In the present article, we demonstrate that the parity law also holds for a more complicated system which contains both odd and even chains.

2 MODEL

We consider a cyclic model composed of n species:

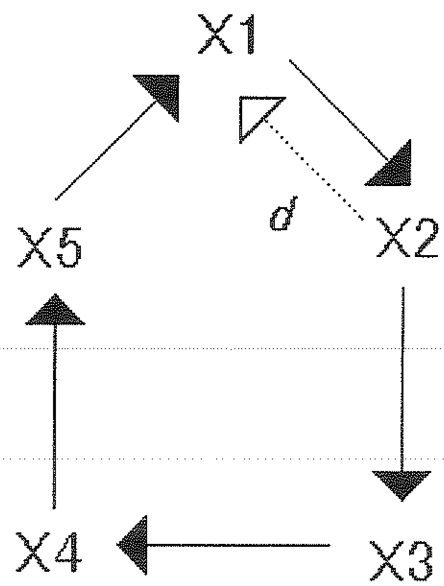

Figure 1: Illustration of system for n=5.

$$X_{i-1} + X_i \;\rightarrow\; 2X_i \quad (1)$$
$$X_2 \;\rightarrow^{d}\; X_1 \quad (2)$$

where X_i means an individual of species i and $i = 1, \cdots n$ ($X_{n+1} \equiv X_1$). The reaction (1) schematically represents that the species i reproduces offspring by eating species $i-1$; especially for $n = 3$, (eq. 1) denotes the Paper-Scissors-Stone (PSS) game[5]. For example, species 1 denotes plant and species 2 (3) represents herbivore (carnivore). Although plant never eats carnivore, it takes chemical components from the dead body of carnivore.

We can regard the reaction (2) as a perturbation which violates the equal balance between species. If

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X_2 dies, it is served for the species 1. Hence, the parameter d means the death rate of species 2 ($d > 0$). Our system (1) and (2) is a generalization of the contact process (CP)[6,7] represented by (2) and $X_1 + X_2 \rightarrow 2X_2$. When n is odd, Our system contains both odd and even chains; for example, if $n = 3$,[8] it contains the odd (PSS) and even (CP) chains.

We apply a method of lattice Lotka-Volterra model (LLVM)[4-8] to the system (1)and(2), where we assume $3 \leq n \leq 8$. We briefly describe this method. 1) Each lattice site is occupied by a single individual of one of n species. 2) The system evolves in the following two steps. i) We perform the reaction (1); choose one lattice site randomly, and then specify one of eight neighbor sites (*Moore neighborhood*). Let the pair react according to (1). ii) Next, we perform the reaction (2): choose one site randomly. If the site is X_2, then it becomes X_1 by the rate d.

3 THEORIES

3.1 Master Equation

The basic equations for the system are

$$\dot{P_2} = P_{12} - P_{23} - dP_2 \qquad (3)$$
$$\dot{P_i} = P_{i-1,i} - P_{i,i+1}; \quad (for \quad i \geq 3) \qquad (4)$$

where P_i is the density of species i ($i = 1, \cdots, n$), the dots denote the derivative with respect to the time t which is measured by the unit of the Monte Carlo step, and P_{jk} denotes the probability density finding a species j at a site and a species k at a neighbor of that site ($j, k = 0, \cdots, n$). Note P_{jk} differs from the conditional probability. The relations

$$P_{jk} = P_{kj}, \quad \Sigma_j P_{kj} = P_k, \qquad (5)$$

and

$$\Sigma_k P_k = 1 \qquad (6)$$

thus hold.

3.2 Mean-Field Theory

It is well known that the first approximation is the mean-field theory (MFT): if the reactions (7)and(8) take place between any pair of individuals, the population dynamics can be represented by MFT which is equivalent to the Lotka-Volterra model. The steady-state solution for MFT can be obtained by setting all the time derivatives to be zero, and substituting

$$dP_2 = P_2(P_1 - P_3) - dP_2 \qquad (7)$$
$$dP_i = P_i(P_{i-1} - P_{i+1}); \quad (for \quad i \geq 3) \qquad (8)$$

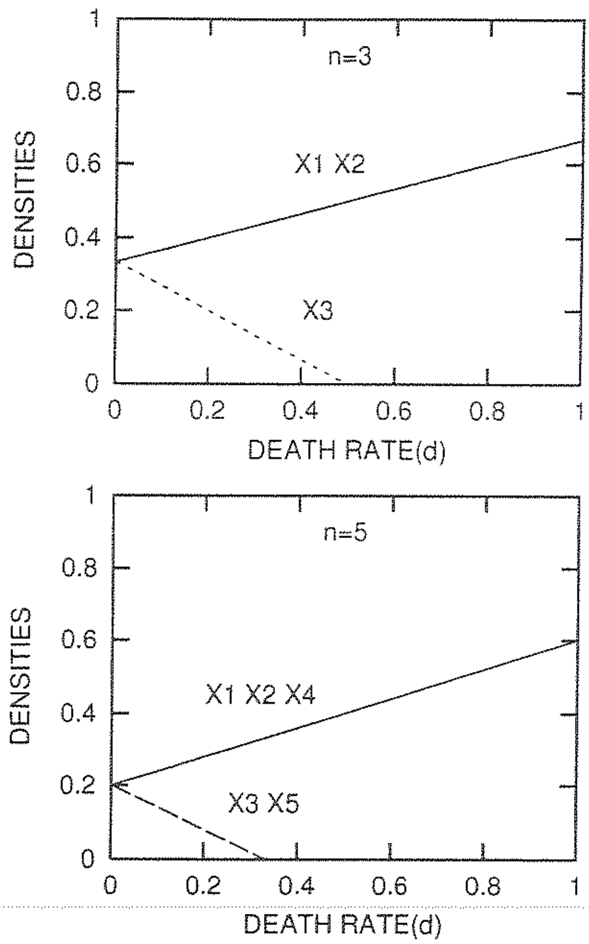

Figure 2: The steady-state densities are shown against the death rate d in the case of odd parity ($n = 3, 5$) by MFT.

If n is even ($n = 2k$), above equations never give any non-trivial stationary solution; species 2 goes extinct. If n is odd ($n = 2k + 1$), we can get a stationary solution; by setting all the time derivatives in (3) and (4) to be zero, and substituting (6), we have

$$P_{2m} = P_1 = (1 + \frac{n-1}{2}d)/n \qquad (9)$$
$$P_{2m+1} = (1 - \frac{n+1}{2}d)/n \qquad (10)$$

In Figure 2, the steady-state densities are depicted against d for several odd values of n. We consider the following press perturbation: the value of d is altered from zero to a non-zero value of d. We can describe the long-term response of this experiments in mean-field: First, species 2 is regarded as a target species. Recall that parameter d means a death rate of species 2. MFT shows the following parity law: (i) When n is even, the density of

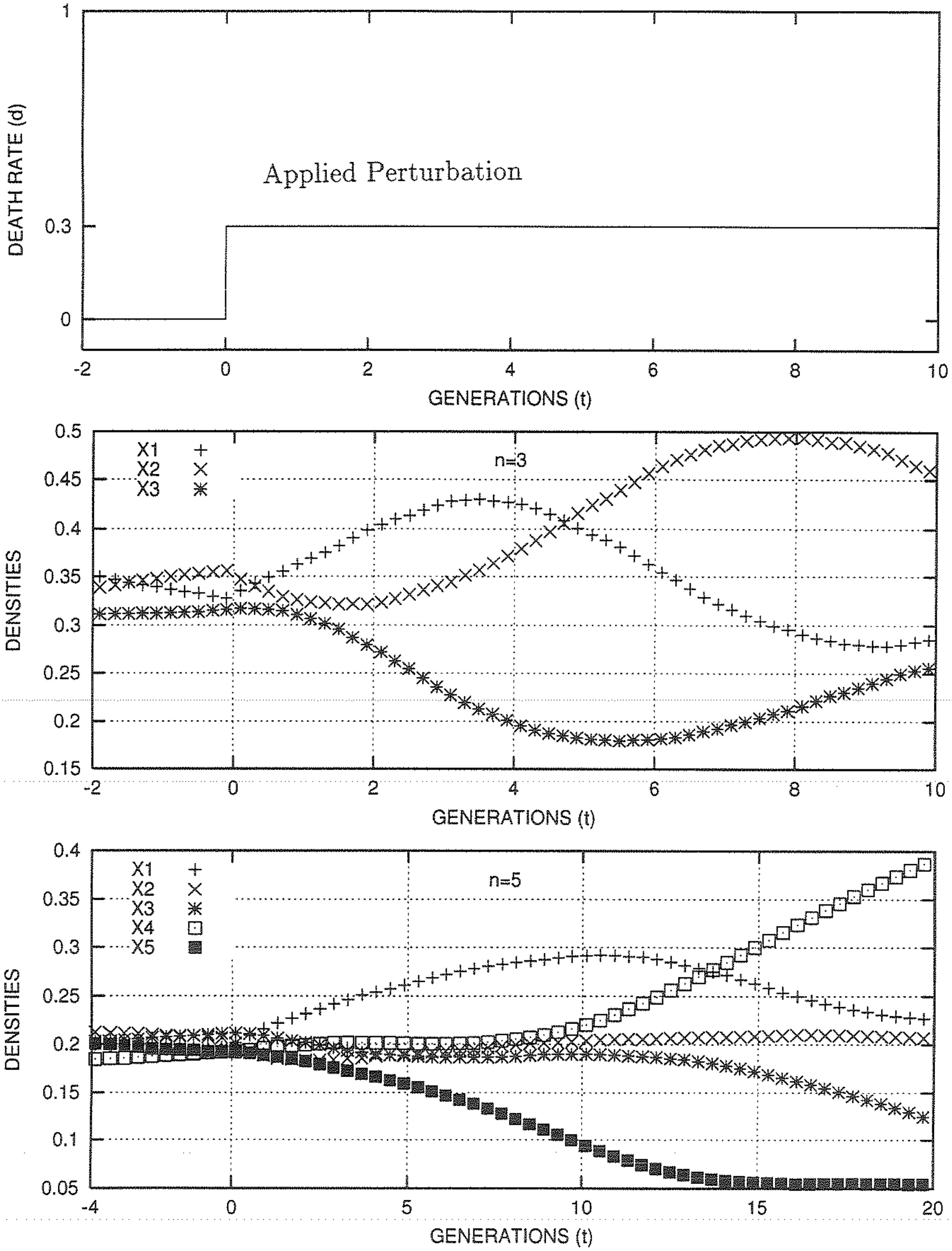

Figure 3: Short-term response for the lattice model ($n = 3, 5$). The value of d is suddenly increased from 0.0 to 0.3 at $t = 0$.

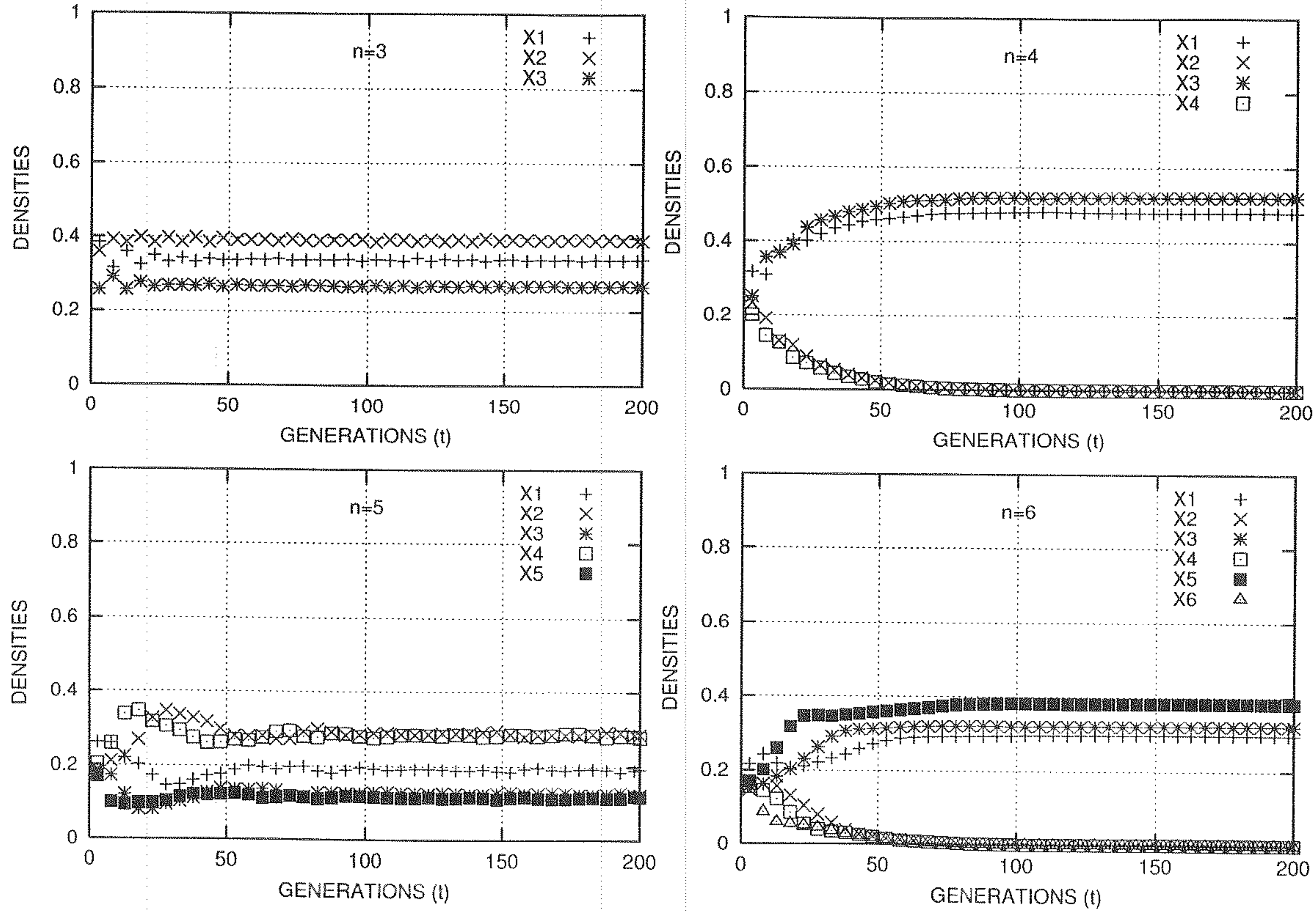

Figure 4: The long-term response for the lattice model (n = 3 - 6). The short- and long-term responses are entirely different from each other. The latter response is determined by the parity law.

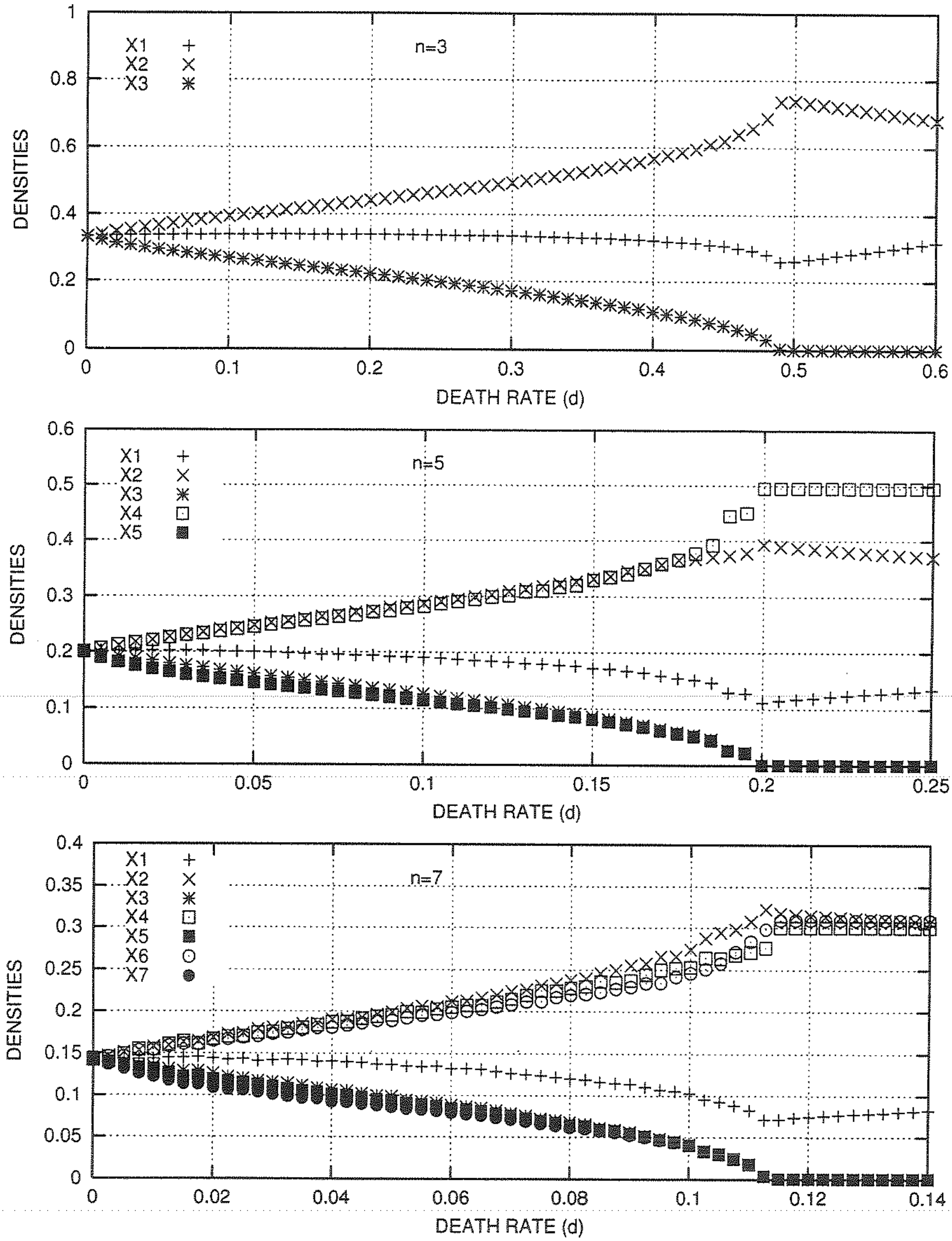

Figure 5: Same as Fig. 2, but for the lattice model ($n = 3, 5, 7$).

species 2 (P_2) decreases and goes extinct. (ii) When n is odd, P_2 increases with the increase of d. Hence, the long-term response for odd number of n becomes counterintuitive. Second, species 1 is regarded as a target species; d means the birth rate of species 1. In this case, MFT never predicts the parity law: (i) When n is even, P_1 increases. (ii) When n is odd, P_1 increases. No counterintuitive responses thus occurs.

4 RESULT OF LATTICE MODEL

The results of lattice model (LLVM) support the parity law. We study perturbation experiment by computer simulation. We change the death rate of a target species, and record the density of all species. Before the perturbation ($t < 0$), the system is assumed to remain in a stationary state of $d = 0.0$. At $t = 0$, the death rate is suddenly changed from $d = 0.0$ to $d = 0.3$.

In Figure 3, typical examples of short-term response are shown. When t takes a small value, P_2 (P_1) always decreases (increases). Such a short-term response can be proven from the basic equation.[8] The long-term response is depicted in Figure 4. From this figure we find that the long-term response exhibits the parity law: when the system contains even number of species (n is even), then the species 2 becomes extinct ($P_2 = 0$). On the contrary, when n is odd, the steady-state density of the species 2 is increased by the perturbation (opposite response).

In Figure 5, the steady-state densities of all species are plotted against the death rate d. Indeed, we can confirm that the steady-state density P_2 increases with d.

5 CONCLUSION

We have developed model ecosystems which reveal the parity law. The parity, a rough property of an ecosystem, is relevant for the prediction of long-term response. The lattice model of LLVM shows the parity dependence for both species 1 and 2, whereas MFT fails for the species 1. In the case of odd parity, our system has both odd and even chains; with increasing d the latter should prevails the former. However, simulation reveals that the odd chain always prevails regardless of the value of d.

We discuss the mechanism of parity dependence. If the density of species j (a target species) is assumed to be directly increased by an applied perturbation, the density of their prey (species $j-1$) of species j will be decreased by an indirect effect. Similarly, the density of species through a cyclic chain. Provided that the parity of the chain is even, the density of species j is again increased by an indirect effect. Since the direct and indirect effects are consistent, the long-term response becomes the same direction as the direct response. However, in the case of odd parity, the direct and indirect effects on species j are mutually inconsistent. Our results indicate the importance of the indirect effect for the long-term response.

The parity law is useful for the prediction of model systems, but it is still suspicious whether this law does hold in real ecosystems. Our model shows that a long-term response is very frequently opposite to the short-term one. Heretofore, very little literature is known for the perturbation experiment of long-term response (more than 10 generation times). The study of long-term response may be important in ecosystems.

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