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Interspecific Segregation and Phase Transition in a Lattice Ecosystem with Intraspecific Competition

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Abstract: Many empirical studies of ecological community indicate the coexistence of competing species is extremely common in nature. However, many mathematical studies show that coexistence of competitive species is not so easy. In the present article, we focus on the segregation of habitat (microhabitat). If habitats of species are spatially separated, they can coexist easily: under the habitat segregation, net competition does not work between species. We study a lattice ecosystem composed of two competitive species. The dynamics of this system is found to be asymptotically stable. In this system both species can coexist, because intraspecific competition is stronger than interspecific competition. It is found that this system exhibits a phase transition: if the mortality rate of both species increases, they go extinct. Our main result shows a self-organized isolation of microhabitat; that is, at the phase transition point, the living regions of both species are naturally and completely separated from each other. In this critical state, each species independently forms clusters, and the shape of each cluster greatly varies with time proceed. Such a phase transition occurs, even though (i) there is no special condition in space, and (ii) the intraspecific competition is stronger than interspecific competition. We conclude that such segregation comes from an inherent nature of species. Despite no attraction acts between individuals, each species forms clusters. This conclusion suggests that all biospecies may have some mechanism that naturally causes the isolation of habitats.

Keywords: Habitat segregation; Lattice model; Competition; Lotka-Volterra model

1. INTRODUCTION

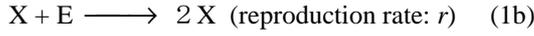
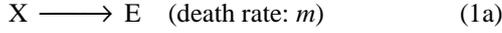
Lattice models are widely applied in the field of ecology (Nowak, et al., 1994; Harada & Iwasa, 1994; Nakagiri, et al., 2001). Spatial distribution of individuals usually differs from randomness. In most cases, individuals of the same species form clumping patterns; they huddle together. Non-randomness in spatial distribution influences on evolutionary argument. In the present paper, we demonstrate that a habitat segregation naturally occurs. Although intraspecific competition is stronger than interspecific one, these species live separately. Because of segregation, the competition between species almost disappears.

We deal with a lattice system called “Lotka-Volterra model (LLVM)” (Tainaka, 1988; Matsuda, et al., 1992). The simulation method of this system is similar to that of the so-called Lotka-Volterra model. The difference between both

simulation methods is very simple. Namely, in the case of LLVM, interaction is restricted to occur between adjacent lattice points (local interaction), whereas in the Lotka-Volterra model interaction globally occurs between any pair of lattice points (global interaction). For this reason, the Lotka-Volterra model is a mean-field theory of LLVM; in other words, LLVM is a lattice version of Lotka-Volterra model. The investigation of spatial model (LLVM) enables us to give useful information for population dynamics in living systems. Non-randomness of spatial distribution strongly effects on the dynamics.

The LLVM model is an extension of the contact process (CP) which contains a single species. The CP model, presented by Harris in the field of mathematics (Harris, 1974), is a lattice version of the logistic equation. This model has been

extensively studied from mathematical (Durrett, 1988) and physical (Katori & Konno, 1991; Marro & Dickman, 1999) aspects. The contact process is defined by birth and death processes of a species X on a lattice space. Each lattice site is either empty (E) or occupied (X). The site X means an individual or a sub-population (occupied patch). Birth and death processes are respectively given by

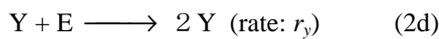
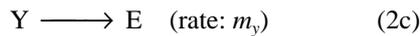
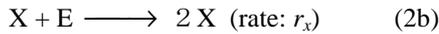
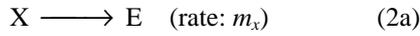


The processes (1a) and (1b) simulate death and reproduction, respectively. The reaction (2) occurs between adjacent lattice sites.

We develop the contact process to deal with competition between two species. Moreover, intraspecific competition is also assumed. Hence, any pair of individuals located in a short distance compete with each other. It is found that this system exhibits habitat segregation: living regions of both species are automatically separated. Although the intraspecific competition is stronger than the interspecific one, habitat segregation occurs.

2. The Model

Consider two competing species X and Y . Our model is defined by



and



The reactions (2a) - (2d) are the same meaning as in the contact process. The last two reactions represent the intraspecific competition. The parameters c_x and c_y mean competition rates. In this model, interspecific competition occurs to get the empty site E.

We describe the simulation method:

1) Initially, we distribute individuals on the square lattice; the initial distribution is not important, since the system evolves into a stationary state. The final equilibrium points are qualitatively the

same, though spatial pattern changes dynamically. It is an attractor.

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

(i) we perform two-body reactions (2b), (2d), (2e) and (2f). Choose one lattice site randomly, and then randomly specify one of four neighboring sites. Let the pair react according to two-body reactions. For example, if the pair of sites are (X, E) or (E, X), then E is changed into X according to the reaction (2b).

(ii) we perform one-body reactions (2a) and (2c). Choose one lattice point randomly; if the site is occupied by X (or Y), the site will become E by the rate m_x (or m_y). In a real simulation, the maximum mortality $\max\{m\} = 2$. When $m = 2$, we perform mortality reaction twice.

3) Repeat step 2) $L \times L = 10,000$ times, where $L \times L$ is the total number of lattice points. This is the Monte Carlo step (Tainaka, 1988).

4) Repeat step 3) until the system reaches a stationary state.

3. Mean-field theory

If the global interaction is allowed between any pair of lattice sites, the population dynamics of our system (2) is given by the mean-field theory:

$$\frac{dx}{dt} = -m_x x + r_x x e - c_x x^2 \quad (3a)$$

$$\frac{dy}{dt} = -m_y y + r_y y e - c_y y^2 \quad (3b)$$

where x , y and e are the densities of the sites X, Y, and E, respectively ($e = 1 - x - y$). The above equations can be rewritten by

$$\frac{dx}{dt} = R_1 x (K_1 - x - ay) / K_1 \quad (4a)$$

$$\frac{dy}{dt} = R_2 y (K_2 - x - bx) / K_2 \quad (4b)$$

Here the parameters satisfy the following relations:

$$R_1 = r_x - m_x, \quad R_2 = r_y - m_y, \quad (5)$$

$$K_1 = \frac{r_x - m_x}{r_x + c_x}, \quad K_2 = \frac{r_y - m_y}{r_y + c_y}, \quad (6)$$

$$a = \frac{r_x}{r_x + c_x}, \quad b = \frac{r_y}{r_y + c_y} \quad (7)$$

The equations (4a) and (4b) are called the Lotka-Volterra model, and its result is well known. Final stationary states are classified into four classes, depending on the values of parameters: namely, (i) both X and Y coexist, (ii) X only survives, (iii) Y only survives, and (iv) both go extinct. The condition for the coexistence is given by

$$K_x > aK_y \text{ and } bK_x < K_y. \quad (8)$$

This is explicitly expressed by

$$\frac{r_x(r_y - m_y)}{r_y + c_y} < r_x - m_x < \frac{(r_y - m_y)(r_x + c_x)}{r_y}. \quad (9)$$

It is therefore necessary for the coexistence that intraspecific competition is stronger than interspecific one; in other words, the competition rates (c_x and c_y) should take large values for the coexistence. If $c_x=c_y=0$, then the condition (9) is not satisfied.

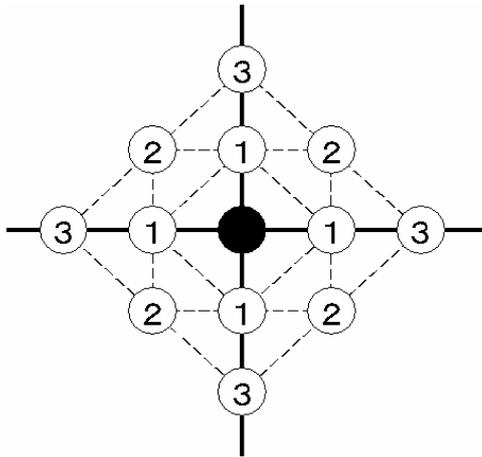


Fig. 1. Schematic illustration of distance. The numerals in circles denote the distance (r). The nearest neighbour corresponds to $r=1$, and the next nearest neighbour is represented by $r=2$, and so on.

4. Correlation Function

It is obvious that the Lotka-Volterra model has no information on the spatial distribution of individuals. Main aim of this article is to analyze spatial distribution. Species in nature usually form a non-random pattern. A typical example of such non-randomness is a clumping pattern. To know the degree of clumping, it is convenient to define correlation function on a lattice space. Let $F(r,jk)$ be the correlation function, where r is the distance between a pair of individuals and j or k represents a species ($j,k=X$ or Y). For example $F(2,XX)$ means the probability finding X at the distance $r=2$ apart from a X individual. Thus correlation

functions mean local densities. Note that they are scaled by overall densities. In the case of lattice system, the distance takes discrete values. We can prove $F(r,XY) = F(r,YX)$. In Fig. 1, we make clear the meaning of distance r . The shortest distance ($r=1$) means the nearest neighbour, and $r=2$ means the next nearest neighbour, and so on. The shortest distance is most important, since the correlation function is usually a decreasing function of distance. Previously, one of authors defined $F(1,XX)$ as the clumping degree of X (Tainaka and Nakagiri, 2000), and $F(1,XY)$ as the degree of symbiosis (coexistence) of both species (Tainaka, et al. 2003). In the case of present article, it may be necessary to calculate F not only for the shortest distance but also for several values of distance. This is because our model (2) contains the intraspecific competition; that is reactions (2e) and (2f). For example, it is expected that $F(1,XX)$ takes a smaller value compared to $F(2,XX)$ because of the competition: If a pair of adjacent sites are occupied by X, then one site will be changed into E according to the reaction (2e).

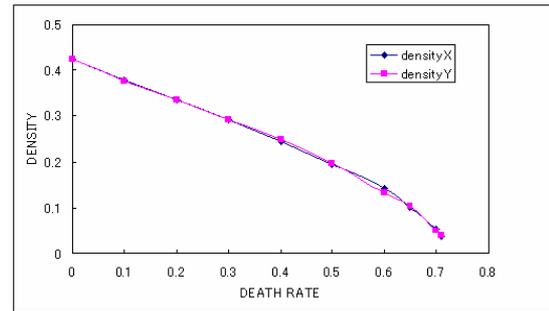


Fig. 2. The steady-state densities of species X and Y are depicted against the mortality rate of both species. Both densities take almost the same value.

5. Result of Lattice Model

The population dynamics for lattice model is consistent with the prediction of mean-field theory. The system evolves into a stationary state. Four types of stationary states are observed: namely, (i) both X and Y coexist, (ii) X only survives, (iii) Y only survives, and (iv) both go extinct. If $c_x=c_y=0$,

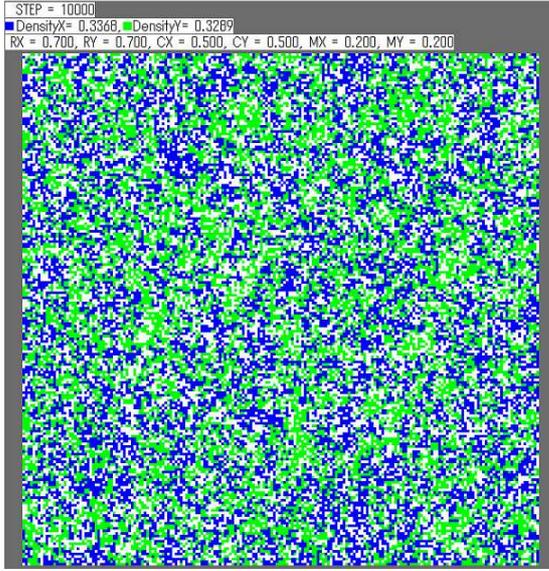


Fig. 3. A typical stationary pattern in the case of high densities. The mortality rate of both species is 0.2 which is relatively a small value.

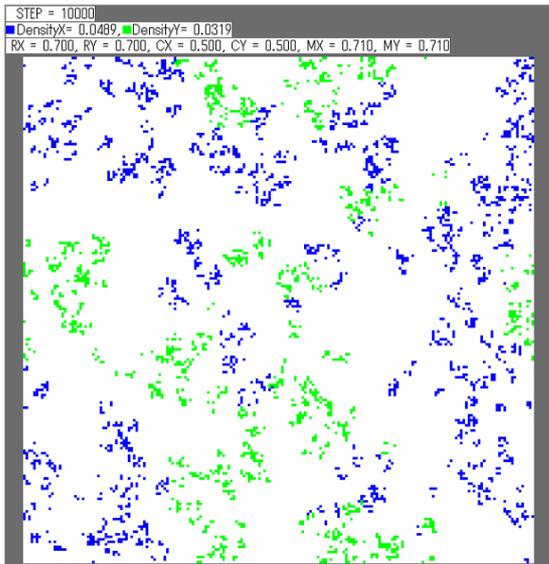


Fig. 3. A Same as Fig. 3, but densities of both species are low. The mortality rate of both species is 0.71 which is a large value. This situation is near the extinction threshold. Interspecific segregation occurs.

both species cannot coexist. With the increase of the values of c_x and c_y , both species become to survive together. In the present paper, we focus on the coexistence phase. There are six parameters: at first, we consider a symmetrical case: $r_x=r_y$, $m_x=m_y$ and $c_x=c_y$. We change the values of mortality rates

(c_x and c_y), and fix the other parameters. In Fig. 2, steady-state densities of both species are depicted against the mortality rate. This figure reveals that the densities decrease with increasing the mortality rate. Heretofore, the results are qualitatively predicted by the mean-field theory.

Spatial pattern exhibits specific properties. In Figs. 3 and 4, typical spatial distributions of species are illustrated, where the mortality rate of both species is 0.2 for Fig. 3 and 0.71 for Fig. 4. Indeed, the densities decrease with increasing the mortality rate. We also find from Fig. 4 that a kind of habitat segregation occurs: the species X and Y live separately.

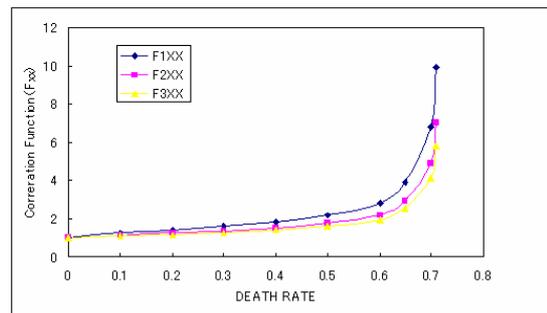


Fig. 5. The results of correlation functions $F(r,XX)$, where $r=1,2,3$. These values mean the degree of clumping. If distribution of individuals is random, the correlation functions take unity. The top curve denotes the case of $r=1$. When the distance r becomes large, the correlation function tends to become small. The values of $F(r,XX)$ diverge near the extinction threshold. Namely, the degree of clumping of each species becomes extremely large near extinction.

We analyze the segregation by the use of correlation function. Figures 5 and 6 show the correlation functions $F(r,XX)$ for $r=1,2,3$. In the case of Fig. 5, the correlation functions are plotted against the mortality rate (death rate). In Fig. 6, they are plotted against the steady-state density (log-log plot). The functions $F(r,XX)$ represent the degree of clumping. If $F(r,XX)$ takes a large value, then the species X is clumped. It is found from Fig. 5 that the degree of clumping increases with the increase of the mortality rate. Such a profile is also observed for the species Y, because our system is unchanged for the exchange of X and Y (symmetrical case). Figure 6 reveals that the correlation functions satisfies the same power law;

when the steady-state densities approach zero, they diverge; namely, $F(r,XX)$ approaches infinity.

In Fig. 7, $F(r,XY)$ for $r=1,2,3$ are plotted against the steady-state densities. This figure implies that the degree of coexistence decreases with the increase of the mortality rate. In particular, if the densities of both species become zero, both species live separately.

6. Conclusions and Discussions

We have developed the spatial explicit model which is a lattice version of the Lotka-Volterra competition model. The population dynamics of our model is well predicted by the Lotka-Volterra model. It is obvious that the Lotka-Volterra model has no information on the spatial distribution of individuals. Our system evolves into a stationary state. Depending on the values of mortality rates, the stationary pattern exhibits a kind of phase transition: when the densities of both species become zero, the habitat segregation completely occurs.

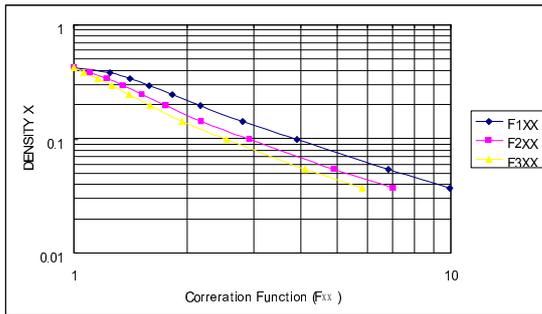


Fig. 6. The relation between the correlation functions displayed in Fig. 5 and the densities plotted in Fig. 2 (log-log plot). The plots are almost on lines. This means a kind of power law; when the steady-state densities approach zero, the degree of clumping of each species diverges.

Our system (2) contains the interspecific competition; namely, both species X and Y compete to get the empty site (E). This type of competition also exists for the individuals of the same species (intraspecific competition). Our system further contains the other type of intraspecific competition; that is, reactions (2e) and (2f). Although intraspecific competition is stronger than interspecific one, the degree of clumping of each species infinitely increases near the extinction

threshold. The results of correlation functions (Figs. 5, 6 and 7) demonstrate the phase transition of habitat segregation. With decreasing the densities of species X and Y, both species live separately.

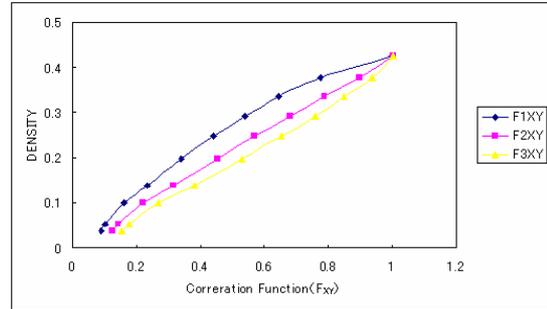


Fig. 7. The results of correlation functions $F(r,XY)$, where $r=1,2,3$. These values indicate the degree of coexistence. The values of correlation functions become zero near the extinction threshold.

Heretofore, we dealt with the symmetrical case: that is, the system does not change with respect to the reversal of species X and Y. It should be noted that the result of habitat segregation is almost unchanged in asymmetrical cases. If a species is endangered, the degree of clumping becomes large. Finally, we discuss the origin of habitat segregation. The enhancement in clumping degree may be originated in the fact that offspring are located near their mother. For this reason, many species potentially have the mechanism of habitat segregation.

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