Patch Dynamics for Prisoner's Dilemma Game: Origin of Golden Rule

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There has been much literature on ecological model of Prisoner's Dilemma game. So far, the strategy of All Cooperate (AC, indicating the "Golden Rule") has been considered to be inferior to other strategies, especially to All Defect (AD, a selfish strategy). However, in the present article, I demonstrate that AC beats AD completely. To this end, I study metapopulation dynamics by applying island and lattice models, where each patch is assumed to be either vacant or composed of a population of AC or AD. It is found that both models exhibit a phase transition: AD completely disappears. For the lattice model, two causes of phase transition are illustrated: i) extinction rate of AD patch becomes high, and ii) colonization rate r of AC becomes low. The former cause is possible to occur, since the AD population gains the least fitness. The latter cause, which cannot be predicted by the island model nor by theory of pair approximation, includes counterintuitive response: AD disappears in spite of the increase of the density of AC patches. Psychological and biological meanings of results are discussed.

1. INTRODUCTION

Many forms of cooperation emerges in human and non-human societies without central authority. A Prisoner's Dilemma game (Axelrod, 1984; Nowak & May, 1992) clearly illustrates that cooperation does occur in situations where individuals tend to look after themselves and their own first. Tit-For-Tat (TFT) and PAVROV (Kraines & Kraines, 1993; Nowak & Sigmund, 1993) may be an effective strategy against an egoist to use. However, they are not a moral standard for a person to follow: TFT and PAVROV are based on "revanchism." Perhaps the most widely accepted moral standard is the "Golden Rule": do unto others as you would have them do unto you. In the context of the Prisoner's Dilemma, the Golden Rule would seem to imply that you should always cooperate. This interpretation suggests that the best strategy from the point of morality is the strategy of All Cooperate (AC). Nevertheless, heretofore, AC has been considered to be inferior to other strategies, especially to All Defect (AD, a selfish strategy). The purpose of the present article is to illustrate that AC completely beats AD in a certain environment.

In the present paper, I apply an idea of "evolutionarily maintainable strategy"(EMS) (Tainaka & Araki, 1999), where EMS is defined by the strategy that gains the highest pay-off (fitness) in a population of a single strategy. It is easily proven from the definition (1) that EMS is represented by AC. Note that EMS differs from "evolutionarily stable strategy"(ESS) (Maynard Smith, 1989); while ESS is not beaten by any other strategy, EMS is invaded by some other strategies. Nevertheless, this outcome does not always hold, especially in a patchy environment: for instance, we consider that a biospecies lives in some patches, and assume that interaction between different patches rarely occurs. The patch occupied by AC will be invaded by a certain strategy, say AD. However, the total fitness gained in the population of the latter strategy is very poor, so that the patch of AD may be extinct during a long time. On the contrary, AC gets the highest fitness in its community. At a local scale, in other words, inside a single patch, AD beats AC, but at a regional (metapopulation) scale, AC may beat AD completely.

In order for a population to survive, it is necessary that the population size is sufficiently larger than the so-called "minimum viable population" (MVP) (Soule, 1987). The MVP size surely differs for different species, whereas recent empirical works for MVP suggest that the MVP size may be very large (Thomas, 1990; Wilcove *et al.*, 1993). Moreover, many authors have pointed out that by the time a species is listed as "endangered", its numbers have fallen well below a sustainable population size (Noss and Murphy, 1995). Hence, it is not so easy for a small population to survive for a long time. Since the strategy EMS gains the largest value of fitness, it is relatively easy to survive. Moreover, individuals of EMS may migrate into another vacant patch and reproduce a new EMS patch (*colonization*).

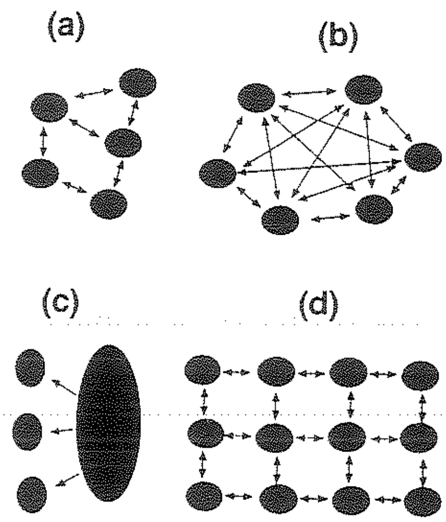

FIG. 1 Several patch models.

Several models at the regional (metapopulation) scale have been presented (Hanski & Gilpin, 1997; Maynard Smith, 1989). I use the island (Levins, 1969) and lattice models (Fig. 1). The Lotka-Volterra equation (LVE) (Hofbauer & Sigmund, 1988) is applied to the former, and "lattice Lotka-Volterra model" (LLVM) (Tainaka, 1988; 1993; Matsuda, *et al.*, 1992) is applied to the latter.

2. Model and Method

2.1 PATCH MODEL

We assume that a target biospecies lives in a patchy environment, and that interaction between different patches rarely occurs. In each patch, the Prisoner's Dilemma game is played by a pair of individuals. Then, a single patch will be dominated by a certain strategy in a relatively short period. Each patch is assumed to be either vacant or composed of a population of All Cooperate (AC) or All Defect (AD). We study the following cyclic system:

$$\mathrm{AD} + \mathrm{AC} \xrightarrow{p} 2\mathrm{AD}, \qquad (1a)$$

$$\mathrm{AC} + \mathrm{O} \xrightarrow{r} 2\mathrm{AC}, \qquad (1b)$$

$$\mathrm{AD} \xrightarrow{d} \mathrm{O}, \qquad (1c)$$

where O represents a vacant patch. Above system is based on the actual moves of Prisoner's Dilemma game. The first reaction (1a) denotes the following meaning: If few individuals of AD migrate into a AC patch, then the population size of AD (AC) immediately increases (decreases) in this patch. The AC patch is easily invaded by AD. The parameter p thus means the probability (rate) that the invasion of AD occurs. The second reaction (1b) means the colonization of AC: if some individuals of AC migrate into a vacant site, its population size may grow up. Namely, the process (1b) denotes the reproduction of AC patches. The last reaction (1c) represents the extinction of a habitat of AD. Since the AD population gains the least value of fitness, it is very hard for this population to survive for a long time. The parameters r and d respectively denote the colonization (reproduction) rate of AC and the extinction (death) rate of the AD patch. When the size of minimum viable population (MVP) of the target species is large, then d takes a large value. The model (1) is essentially equivalent to the prey-predator (host-parasite) model in an ecosystem (Hofbauer & Sigmund, 1988; Tainaka & Fukazawa,1992; Tainaka, 1994; Satulovsky & Tome, 1994; Sutherland & Jacobs,1994); the strategies AC and AD respectively correspond to prey and predator.

2.2 SIMULATION METHODS

First, I explain the simulation method of the lattice model (LLVM):

1) Initially, we distribute two kinds of strategies, AC and AD, over some square-lattice sites; each lattice site is, therefore, labeled by one of three states (AC, AD, or O).

2) Reactions (1) are performed in the following two processes.

(i) First, we perform two-body reactions, namely, reactions (1a) and (1b). Choose one lattice site randomly, and then specify one of four nearest-neighbor sites. Let them react according to (1a) and (1b). For example, if you pick up a pair of sites labeled by AC and AD, the former site will become AD by a probability (rate) p. Here we employ periodic boundary conditions.

(ii) The process (1c) is performed. Choose one lattice site randomly: if the AD site is picked up, it will become O by the rate d.

Next, I explain the simulation method for the island model. The above steps 1) and 2) are the same for this model, but the process *(i)* at step 2) should be replaced. *(i)'*: Choose two lattice sites randomly and independently, and let them react according to (1a) and (1b). Hence, spatial dimension becomes meaningless for the island model. When the number of total lattice sites (L^2) is sufficiently large, the population dynamics is expressed by a Lotka-Volterra equation (LVE).

3. Result of Island Model

The basic equations for the island model are

$$\dot{P}_{\mathrm{AC}} = 2(-pP_{\mathrm{AC}}P_{\mathrm{AD}} + rP_{\mathrm{AC}}P_{\mathrm{O}}), \qquad (2a)$$

$$\dot{P}_{\mathrm{AD}} = 2pP_{\mathrm{AC}}P_{\mathrm{AD}} - dP_{\mathrm{AD}}, \qquad (2b)$$

$$\dot{P}_{\mathrm{O}} = -2rP_{\mathrm{AC}}P_{\mathrm{O}} + dP_{\mathrm{AD}}, \qquad (2c)$$

where the dots denote the derivative with respect to the time t which is measured by the Monte Carlo step (Tainaka, 1988), and P_i is the density of strategy i (i =AC, AD, O). Note that the following relation hold:

$$\Sigma_i P_i = 1. \qquad (3)$$

Each term in (2) comes from each reaction in (1). For example, the first term in the right-hand side of (2a) is originated in the reaction (1a), where the factor 2 denotes that there are two ways for the left-hand side of (1a); that is, AC+AD and AD+AC. Similarly, the second term of (2a) comes from (1b), and so on. The relation (2) is called the Lotka-Volterra equation (LVE). In the below, we set $p = 1$: even when p takes another value, the basic equations of $p = 1$ is unchanged by selecting a suitable time scale.

The steady-state solution can be obtained by setting all the time derivatives in (2) to be zero: it follows that

$$P_{\mathrm{AC}} = \frac{d}{2}, \quad P_{\mathrm{AD}} = \frac{r(1-P_{\mathrm{AC}})}{1+r}, \quad P_{\mathrm{O}} = \frac{1-P_{\mathrm{AC}}}{1+r}. \qquad (4)$$

According to the linear stability analysis the densities of both strategies reach the stationary values (4) in the case $d < 2$ (stable focus). When $d \geq 2$, we have $P_{AC} = 1$ and $P_{AD} = 0$. Hence, LVE exhibits a phase transition between a phase where both AC and AD survive ($d < 2$), and a phase where AD is extinct ($d \geq 2$). The phase boundary is represented by $d_0 = 2$. Namely, AC beats AD completely, when $d \geq 2$. Recall that d denotes the extinction rate of AD patch. The extinction of AD may occur, since the AD population gains the least value of fitness. On the other hand, AC goes extinct, only if $d \to 0$, or only if the size of MVP is sufficiently small.

So far, the number of total lattice sites (L^2) was assumed to be sufficiently large. In this case, the average densities (4) in final stationary state never depend on both densities P_{AC} and P_{AD} at $t = 0$ (initial condition). Now, we consider the case that L^2 takes a small value. Then, the dynamics becomes a stochastic process, and it depends on the initial condition; either strategy AC or AD which has a lower density in stationary state tends to go extinct. Equation (4) reveals that $P_{AC} < P_{AD}$ for $d < 2r/(1+2r)$: when d takes a small value, AC often goes extinct. It is, however, emphasized that AD cannot survive without AC (except for $d \to 0$); in other words, AD immediately goes extinct after the extinction of AC. On the contrary, in the case of a large value of d, the strategy AD often goes extinct. After this extinction, AC occupies the whole patches. Note that AC can survive in the absence of AD. It is, therefore, concluded that for a small value of L^2, the strategy AD cannot survive except for the limiting case $d \to 0$.

4. Result of Lattice Model

4.1 BASIC EQUATIONS

The basic equations for LLVM are

$$\dot{P}_{AC} = -2P_{AC,AD} + 2rP_{AC,O}, \qquad (6a)$$

$$\dot{P}_{AD} = 2P_{AC,AD} - dP_{AD}, \qquad (6b)$$

$$\dot{P}_{O} = -2rP_{AC,O} + dP_{AD}, \qquad (6c)$$

where $P_{i,j}$ denotes the two-body density finding a strategy i at a lattice site (patch) and a strategy j at its adjacent site (i, j =AC, AD, O). Here we put $p = 1$. Note $P_{i,j}$ differs from the conditional probability. The relations

$$P_{i,j} = P_{j,i}, \quad \Sigma_j P_{i,j} = P_i \qquad (7)$$

thus hold. The basic equation (6) for the lattice model cannot be solved. The first and crude approximation to solve (6) is the mean-field theory:

$$P_{i,j} = P_i P_j.$$

Inserting above equation into (6), we have the basic equations (3) for the island model.

4.2 DEPENDENCE OF d

Simulations for lattice model (LLVM) are carried out for various values of the parameters d and r (Tainaka and Fukazawa, 1992). It is found from the simulation that the population dynamics exhibits the stable focus as predicted by the island model (LVE). The lattice system evolves into a stationary state, where the population size of both strategies becomes constant in time. In Fig. 2, the steady-state densities of P_{AC} and P_{AD} are respectively plotted against d. The PA theory in these figures is described in Appendix. It is found from Fig. 2 that the phase transition occurs as predicted by the island model (LVE); the strategy AC occupies the whole patches, when d exceeds a critical value d_0. However, this figure reveals that the density of the AC patch (AD patch) for LLVM is significantly higher (lower) than the prediction of island model; the critical value for LLVM ($d_0 \sim 0.9$) is much smaller than the prediction of LVE ($d_0 = 2$). Moreover, in the case of lattice model, we notice a *counterintuitive* response never seen in island model: even if the value of d decreases and approaches zero, the density P_{AD} decreases.

4.3 DEPENDENCE OF r

Next, we fix d, and change the parameter r (Tainaka, 1994). In Fig. 3, the steady-state densities of P_{AC} and P_{AD} is plotted against the colonization rate r of AC, where we set $d = 0.6$. This figure reveals the following results:

i) The density of AC (P_{AC}) increases in spite of the decrease of r. In particular, when r approaches r_0 from above ($r_0 \sim 0.17$), the AC population abruptly increases.

ii) The density P_{AD} for the lattice model (LLVM) is much lower than the prediction of LVE or PA. Especially, when $r \leq r_0$, AD disappears (extinct phase). Thus, r_0 represents the critical value between the survival and extinct phases.

Such a phase transition is never explained by LVE nor PA. We notice that the phase transition is caused by a counterintuitive situation: AD completely disappears, even though the number of AC patch abruptly increases. This counterintuitive response indicates the superiority of AC in the Prisoner's Dilemma game.

4.4 CLUSTER FORMATION

Spatial pattern is also self-organized into a quasi-stationary state, but the configuration of patch distribution dynamically varies. To know the spatial correlation, we define the ratio of joint probabilities as follows (Tainaka & Fukazawa,1992):

$$R_{i,j} \equiv P_{i,j}/P_i P_j. \qquad (7)$$

For the random distribution, we have $R_{i,j} = 1$. The quantity $R_{i,j}$ represents how the distribution is deviate from the random distribution. In particular, $R_{i,i}$ represents the clumping degree of strategy i: when $R_{i,i} > 1$ ($R_{i,i} < 1$), the distribution of this strategy is clumped (uniform).

The relation between $R_{AC,j}$ and d is depicted in Fig. 4. It is found that the values of $R_{AC,j}$ are remarkably different from those of random distribution (unity). Especially, when d approaches zero,

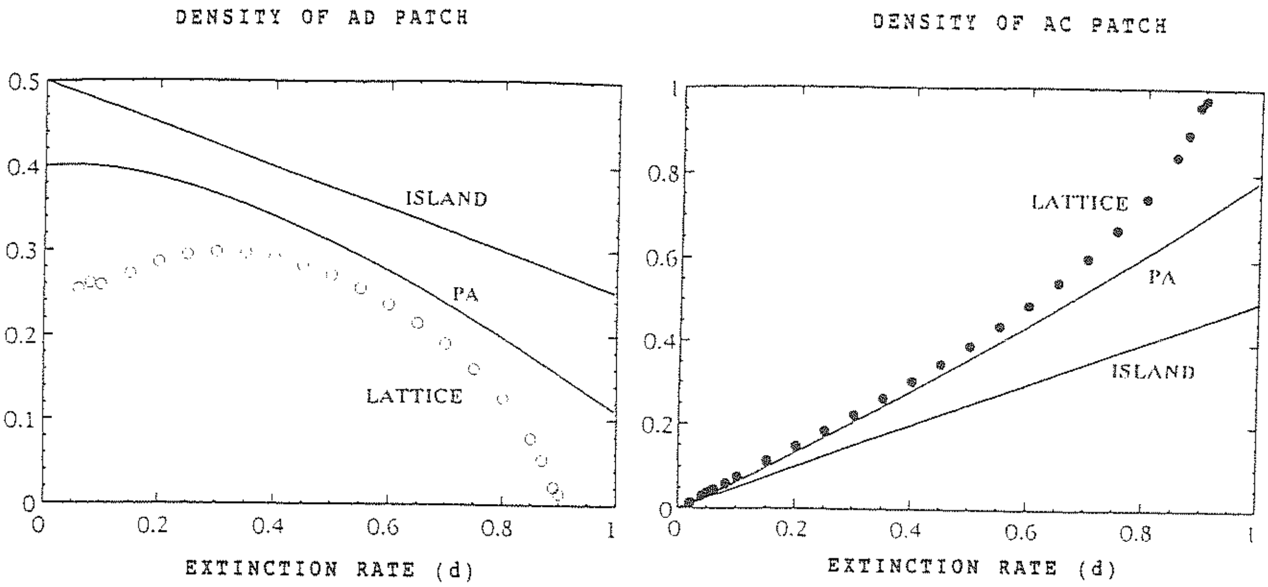

FIG. 2 The steady-state densities of AD and AC patch are plotted against the extinction rate (d) of AD patch ($r = 1$). Each plot is obtained by the long-time average in the period $200 < t \leq 1000$ with the square lattice (100×100), where the time t is measured by the Monte Carlo step. The symbols ISLAND and PA by the solid curves represent the island model and pair approximation (see Appendex), respectively.

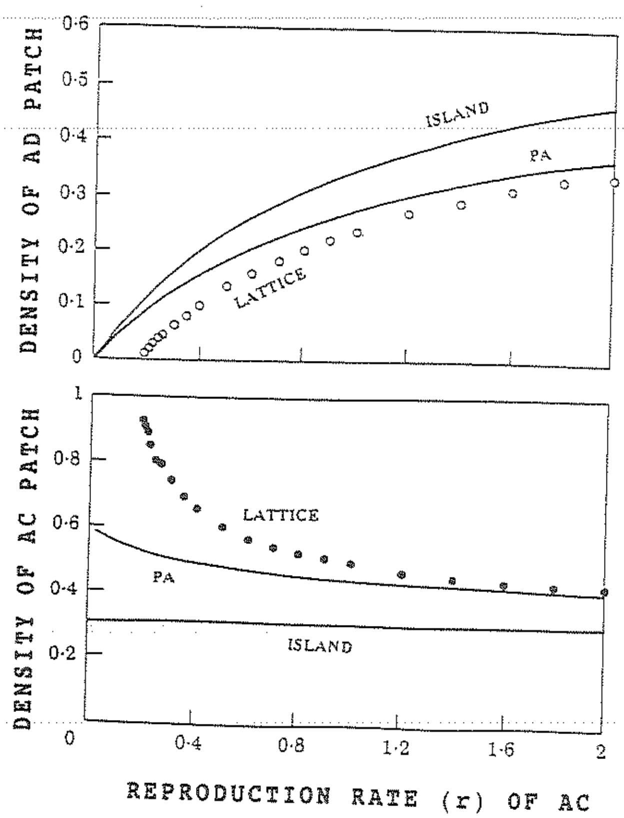

FIG. 3 The steady-state densities are plotted against the reproduction (colonization) rate of AC (r), where we put $d = 0.6$. The symbols ISLAND and PA represent the same meanings as described in Fig. 2.

the quantity $R_{AC,AC}$ becomes much larger than unity and satisfies

$$R_{AC,AC} \propto d^{-\alpha}\,;\, \alpha \sim 1. \tag{8}$$

This result means that the degree of contagiousness of AC becomes rapidly high for $d \to 0$. Endangered species thus forms clumps. Similar clumping formation is observed for AD patches: In Fig. 5, $R_{AD,AD}$ is depicted against $r - r_0$, where we use $r_0 = 0$ for PA and $r_0 = 0.17$ for LLVM. We find from Fig. 5 that

$$R_{AD,AD} \propto (r - r_0)^{-\beta}, \quad \beta \sim 1. \tag{9}$$

This result is also proven by the pair approximation (PA: Appendix). Clumping behavior (9) well explains the abrupt increase in AC population: If r approaches r_0 from above, AD patches are strongly clumped, so that they cannot easily catch AC. Thus, the PA model qualitatively account for the increase of P_{AC}. However, the phase transition (extinction of AD) observed in the simulation result (Fig. 4) cannot be explained by this approximation.

5. Concluding Remarks

All Cooperate (AC) is the evolutionarily maintainable strategy (EMS) which gains the highest score in a population of a single strategy, so that AC may become the strongest strategy in a certain environment. In the present article, I present island and lattice models to study metapopulation dynamics. These models are essentially equivalent to the prey-predator (host-parasite) system The conclusion in the present article is, however, different from the previous works. It is found that both island and lattice models exhibit the phase transition between a phase where both AC and AD survive, and a phase where AD is extinct. The latter phase means that AC beats AD completely.

In the case of island model, the phase transition (extinction of AD) occurs, only when the extinction rate (d) of the AD habitat exceeds a critical value ($d > d_0$: $d_0 = 2$). Such a transition is possible to occur, since the AD population gains the least fitness. For the lattice model, the same cause of phase transition is confirmed (Fig. 2); the critical value takes a smaller value than LVE ($d_0 \sim 0.9$). Moreover, in lattice model, we observe another cause of phase transition: AD disappears, when the colonization rate (r) of AC becomes below a critical value ($r \leq r_0$: $r_0 \sim 0.17$) (see Fig. 3). The latter phase transition is related to the cluster formation of PD patches (Fig. 5).

Our patch dynamics belongs in the class of group selection. Actually, AC (or AD) minimizes (or maximizes) the extinction rate of its habitat. Nevertheless, our theory has distinct properties never seen in the previous theories of group selection (Eshel, 1972; Aoki, 1982):

1) I point out the role of minimum viable population (MVP), and account for the reason why the extinction rate of AD habitat takes a high value.

2) I demonstrate that AC can beat AD completely. Similarly, I can show that the former beats any other strategy; the extinction (colonization) rate of AC population takes the highest (lowest) value among all strategies. It may be impossible to prove this by usual theories of individual selection (Maynard Smith, 1989).

3) Since EMS is defined by the strategy which gains the highest fitness in a single strategy, it is never contrary to an essence of the individual selection.

In the present paper, I demonstrate that AC is superior to any other strategy. This result has psychological and biological meanings: Golden Rule in human society may become the best strategy in a certain condition. I assume that individuals (people) live in a patchy environment; the residence (community) of AD is separated from that of AC. This assumption may be plausible in a human society: when a person (A) is defected by another person (B), then A will avoid to make a friend with B in most cases. The strategies of AC and AD often form patch-like communities. Hence, the evolution of Golden Rule is possible to occur in human societies.

Finally, we discuss other assumptions contained in this paper:

1) The interaction (migration) between different patches is assumed to occur rarely. If migration frequently occurs, all patches are effectively connected. In this case, AD beats AC completely.

2) In the system (1), we neglect the colonization process of AD. If the MVP size of the target species takes a small value, then we cannot neglect the colonization process. Even in this case, AC can win the game.

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APPENDIX: PAIR APPROXIMATION (PA)

In the case of lattice model, the evolution equations for the two-body densities are

$$\dot{P}_{AC,AC} = rP_{AC,O} + 3[rP^{O}_{AC,AC} - P^{AC}_{AC,AD}], \quad (A1a)$$

$$\dot{P}_{AD,AD} = P_{AC,AD} - 2dP_{AD,AD} + 3P^{C}_{AD,AD}, \quad (A1b)$$

$$\dot{P}_{O,O} = 2dP_{AD,O} - r3P^{O}_{AC,O}, \quad (A1c)$$

$$2\dot{P}_{AC,AD} = -2dP_{AC,AD} - P_{AC,AD} + 3[P^{AC}_{AC,AD} + rP^{O}_{AC,AD} - P^{AC}_{AD,AD}], \quad (A1d)$$

$$2\dot{P}_{AD,O} = 2d(P_{AD,AD} - P_{AD,O}) + 3[P^{C}_{AD,O} - rP^{O}_{AC,AD}], \quad (A1e)$$

$$2\dot{P}_{AC,O} = 2dP_{AC,AD} - rP_{AC,O} + 3[rP^{O}_{AC,O} - rP^{O}_{AC,AC} - P^{AC}_{AD,O}], \quad (A1f)$$

where $P^{i}_{j,k}$ denotes three-body probability finding a strategy i at a site and strategy j and k at nearest neighbours of that site. Similarly to (7), the following relations hold:

$$P^{i}_{j,k} = P^{i}_{k,j}, \quad \Sigma_k P^{i}_{j,k} = P_{ij}.$$

The pair approximation (PA) is defined by:

$$P^{i}_{j,k} = P_{i,j}P_{i,k}/P_i. \quad (A2)$$

Setting all the time derivatives in (A1) to be zero, we have $(d \to 0)$

$$R_{AC,AC} \propto d^{-\alpha}; \ \alpha = 1. \quad (A3)$$

Similarly, we prove (9): the critical point is given by $r_0 = 0$, so that we get

$$R_{AD,AD} \propto (r - r_0)^{-\beta}, \quad \beta = 1. \quad (A4)$$

According to the PA model, the critical exponents α and β take the same value.

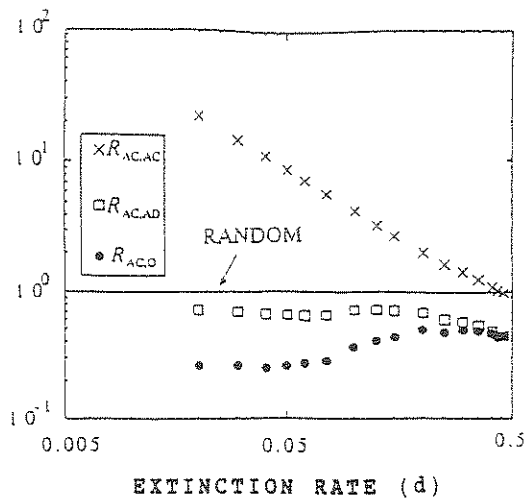

FIG. 4 The ratios of joint probabilities $R_{AC,AC}$, $R_{AC,AD}$ and $R_{AC,O}$ are shown against d, where the plots represent the simulation result of lattice model (LLVM). These quantities are defined by eqn (8); in particular, $R_{AC,AC}$ represents the degree of clumping of AC. If the distribution of AC and AD patches is random, then $R_{i,j}$ takes the value of unity for any pair of i and j ($i, j =$AC, AD, O).

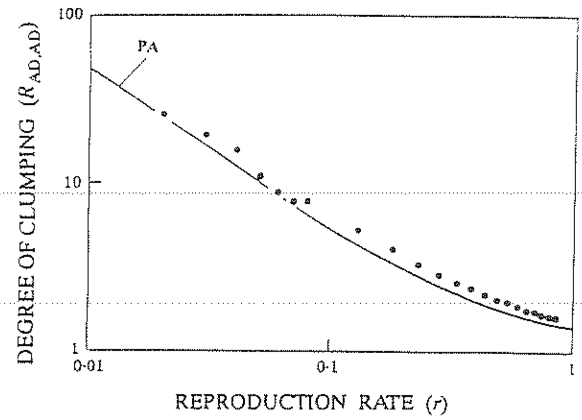

FIG. 5 For the lattice model (LLVM), the relation between $R_{AD,AD}$ and $r - r_0$ is displayed. The ratio $R_{AD,AD}$ represents the degree of clumping of AD. The solid curve is the theoretical prediction of PA. I use $r_0 = 0$ for PA, and $r_0 = 0.17$ for LLVM.