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Spatial suppression of error catastrophe in a growing pattern

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Abstract

Error catastrophe is studied in a growing pattern with cellular automata. It is found that, although the critical error threshold P_c for error catastrophe decreases monotonically with decreasing diffusion coefficient D, P_c remains at a finite value in the limit that D goes to 0 because particles with higher growth rate repress the growth of those with lower growth rate spatially. The possibility that the spatial structure accelerates the evolution is also discussed.

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1. Introduction

Although evolution often entails physical space, roles played by space in evolution remain incompletely understood. Situations we assumed in this paper include bacterial colonies [1,2], viral propagations [3–5], diffusion of cultures, customs, or languages [6], and especially prebiotic replication of molecules at the surface of minerals [7–11] or in the porous media [12,13], that is, systems in which informational elements self-replicate in physical space accompanied by mutations.

Eigen's quasispecies theory [14,15] has been providing fruitful ways to treat the evolution of biological information. The theory states that the true target of the selection is, instead of a single genotype, an ensemble of related genotypes localized around a few genotypes with the highest fitness. Stability of the quasispecies depends on the balance between the mutation rate and the strength of the selection pressure, and the quasispecies collapses above the critical mutation rate, namely, the so-called *error catastrophe* occurs. Quasispecies theory has been investigated in many contexts [16–20]; especially, Altmeyer and McCaskill [21] examined the error catastrophe in a spatially resolved open system with constant population size, and found that the critical error threshold P_c for the error catastrophe decreases monotonically with decreasing diffusion

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coefficient D and converges to 0 as D tends to 0. This led them to conclude that the effect of spatial correlations or compartmentation is universally negative for the sustention of quasispecies, so that physical interactions between sequences are necessary in order for spatial effects to enhance the stabilization of biological information. However, the effect of the fluctuations from the small population size due to the decreasing effective space size was the only matter of their concern, and spatial structures which often emerge in the spatially resolved system was not cared. In this work, we studied the error catastrophe in a growing pattern with cellular automata. In such a system, spatial structure, or pattern, gives restraint conditions to the selection of elements and the selected elements form spatial structure. In this sense, it is natural to suppose that the selection of a higher order, which exceeds the Darwinian principle of the survival of fittest, emerges even if there is no explicit interaction between elements (see [22] for an example of such a phenomenon).

2. Model

We constructed two models. The difference of two models is whether diffusion is implemented or not.

2.1. CD model: diffusion, replication, and mutation

In this model, the diffusion algorithm proposed by Chopard and Droz [23,24] was adopted, in which we consider particles, or replicators, moving on two-dimensional square lattice with spacing λ under periodic boundary condition. Every particle has a velocity which can face to the four possible directions (north, east, south, west). Although each lattice site can contain four particles in maximum, the exclusion principle, which inhibits particles from facing to the same direction with each other in a site, is imposed. At each time step, particles move towards one of their nearest neighbours according to their directions of motion, and these directions are rotated after moves. To ensure the exclusion principle, all the particles entering a site are rotated by the same angle. The angle to be rotated is chosen randomly from the four possible angles: 0, $\pi/2$, π, and $3\pi/2$ with probabilities p_0, p_1, p_2, and p_3, respectively, where $\sum_i p_i = 1$. The values of $\{p_i\}$ determines the diffusion coefficient; for example, particles are rarely deflected if p_0 is large, so that the diffusion coefficient D becomes large. On the other hand, particles flip frequently between two opposing directions if p_2 is large, so that D becomes small. Remember that particles do not remain in a single site even if $D = 0$, instead oscillate between two adjacent sites.

A particle self-replicates with probability p_k if there is an extra space for the new particle in the nearest neighbour site (von Neumann neighbourhood is adopted). The velocity direction of the new particle is determined at random.

The cellular automata rules described above read:

$$n_i(\vec{r} + \lambda\vec{c}_i, t + \tau) = \sum_{l=0}^{3} \mu_l \left[n_{i+l} + k(1 - n_{i+l}) \times \sum_{m=0}^{3} \nu_m n_m(\vec{r} + \lambda\vec{c}_m, t) \right], \quad (1)$$

where we introduced the occupation number $n_i(\mathbf{r}, t)$, which takes 1 if there is a particle entering the site $\vec{r}$ with the velocity pointing in direction $\vec{c}_i$ at time t, and otherwise 0. $\{\vec{c}_i\}$ are defined as the unit vectors pointing to the four main directions in the square lattice (east, north, west, south). $\{\mu_i\}$ are the random Boolean variables, such that only one of the four μ_i takes 1 with probability p_i and others take 0. $\{\nu_i\}$ are also random Boolean variables, such that only one of the four ν_i takes 1 with probability 1/4 and others take 0. $k = 1$ with probability p_k and 0 with $1 - p_k$. The subscripts of $n_i, \vec{c}_i, \mu_i, \nu_i$ are defined modulo 4. For isotropy reasons, we shall impose $p_1 = p_3 \equiv p$.

Eq. (1) can be transformed to the corresponding partial differential equation (Fisher–Kolmogorov equation) by Chapman–Enskog method [23,24]. Up to first order of τ, we get:

$$\frac{\partial\rho}{\partial t} = K\rho\left(1 - \frac{\rho}{4}\right) + D\nabla^2\rho,$$

$$K \equiv \frac{p_k}{\tau}, \quad D \equiv \frac{\lambda^2}{4\tau}\frac{p + p_0}{1 - (p + p_0)}, \quad (2)$$

where ρ is the population density of particles ($0 \le \rho \le 4$).

Consider the actual lives, each individual has a specific genotype, which sometimes mutates into the other