

ON A SPATIAL ROCK-PAPER-SCISSORS GAME

ROBERT D. MACMARTIN AND JAN RYCHTÁŘ

ABSTRACT. We extend the spatial rock-paper-scissors game to include both short and long range interactions. We study a model of three strains of *E. coli* bacteria in a competitive loop. Using a Monte Carlo simulation, we study the resulting spatiotemporal patterns and long term behaviors of the dynamical system. We found that the coexistence of all three competing species is possible only in large environments; if the environment is small, the system always tends towards a monomorphic population. We found that if the system is in a balance, then slight weakening of one strain leads to its final dominations, whereas making one strain slightly stronger eventually leads to its elimination.

1. INTRODUCTION

This note deals with a cyclic system whose basic rules are similar to those of the rock-paper-scissors game. We built the model describing three competitive strains of *E. coli* bacteria: colicinogenic, colicin-sensitive, and colicin-resistant strains. The colicinogenic bacteria produce a toxin colicin that kills the sensitive strain but does no harm to the resistant one. The rate of growth of resistant bacteria exceeds that of colicinogenic bacteria, but is smaller than the growth rate of sensitive bacteria. This occurs because the resistant strains do not pay the energetic price of carrying the mechanism for producing colicin, yet they carry the mechanism that makes them resistant to the toxin; colicinogenic bacteria have to carry both ([1], [6]). Thus, a sensitive (S) strain is replacing a resistant (R) strain, a resistant strain (R) is replacing a colicinogenic (C) strain, and a colicinogenic (C) strain is replacing a sensitive (S) strain. Equivalently, the system satisfies a rock-paper-scissors relationship.

The spatial rock-paper-scissors system described above is well studied in literature (see [6], [2], [3]). It is known that a spatial structure promotes biodiversity, meaning different strains can coexist in the system if the habitat is structured in a way that only local (short range) interactions are allowed. Results of this kind were supported by Monte Carlo simulations ([6]) as well as by experiments *in vitro* ([6]) and *in vivo* ([7]).

We extend and enrich the model by allowing the toxin to diffuse in the environment. As a result, we get the short term behavior same as discussed above if only the local interactions occur. Due to the diffusion of the toxin, however, the toxin can influence the habitat far away from its origin. It means that there are

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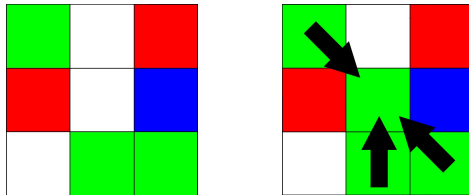


FIGURE 1. Updating an empty cell (white = empty cell, red=C, green=R, blue=S). On the left: the middle cell is selected for updating. Out of 8 neighboring cells, 6 are occupied - 1 by blue, 2 by red, 3 by green. On the right: a neighboring cell is selected for propagation. Probabilities that the selected cell will be white, red, blue and green respectively are $2/8$, $2/8$, $1/8$ and $3/8$ respectively. A random number between 0 and 1 is generated and the cell will be updated to white, red, green, or blue if the number falls in $[0, 2/8]$, $(2/8, 4/8]$, $(4/8, 5/8]$, $(5/8, 8/8]$. In this example, one of the green neighbors was selected and its offspring filled the empty middle cell.

long range interactions in the system as well. Thus, the long term behavior of the system is different and resembles more the situation of an unstructured habitat.

2. THE MONTE CARLO SIMULATION

The simulation was programmed using Matlab. The environment was represented as a square lattice with dimensions 250×250 , 100×100 , and 50×50 respectively. Each site in the lattice is either empty or occupied by one of the strains. The time of the system is measured in *generations*, where one generation is represented by updating the same number of sites as is in the lattice (i.e. based on dimensions, 250×250 , 100×100 or 50×50 sites). The core of the simulation lies in updating the sites.

- The site for updating is selected randomly in the lattice (each site has the equal probability of being updated).
- When the selected site is empty, it may become occupied by a new “born” bacteria. The type of the bacteria is directly influenced by the neighborhood sites. If more of a certain strain of bacteria are present in the neighborhood, then it is more likely that a bacteria of same type will be born into the empty cell. See Figure 1 for illustration and explanation.
- When the selected site is occupied by a colicinogenic (resistant, sensitive, resp.) bacteria, it will become an empty cell with probability Δ_C (Δ_R , Δ_S , resp.) or it will remain unchanged with the probability $1 - \Delta_C$ ($1 - \Delta_R$, $1 - \Delta_S$, resp.).

The behavior of a rock-paper-scissors game is introduced to the model through the probabilities Δ_C , Δ_R and Δ_S . While Δ_C and Δ_R are absolute constants satisfying

$$\Delta_R < \Delta_C$$

to ensure that R outgrows C, Δ_S depends (in our simulation linearly) on the amount of colicin in the given place (and thus it changes in space and in time). If there is

no toxin present in the given site of the lattice, then

$$\Delta_S = \Delta_S^0 < \Delta_R$$

(this ensures that S outperforms R). If the amount of colicin exceeds a certain threshold value, then

$$\Delta_S > \Delta_C$$

which in turn means that C outperforms S.

The colicin is released to the environment at the time of the death of a colicinogenic bacteria (see e.g. [2]). The concentration of the colicin is represented by a matrix U with the same dimensions as the living environment. The (x, y) entry of the matrix corresponds to the concentration of the colicin at (x, y) lattice site.

The standard equation for the diffusion in two-dimensional continuous space and continuous time is

$$\frac{\partial}{\partial t} C(x, y, t) = c \left(\frac{\partial^2}{\partial x^2} C(x, y, t) + \frac{\partial^2}{\partial y^2} C(x, y, t) \right)$$

where $C(x, y, t)$ is a concentration of a substance at place (x, y) in time t , c is a diffusion constant, (see [8]). To avoid the concentration of a colicin increasing above any bounds, we assume that the toxin decays exponentially, i.e. we add a decay term $-kC(x, y, t)$ (where k is the decay constant) to get

$$\begin{aligned} \frac{\partial}{\partial t} C(x, y, t) &= \text{diffusion} + \text{decay} \\ &= c \left(\frac{\partial^2}{\partial x^2} C(x, y, t) + \frac{\partial^2}{\partial y^2} C(x, y, t) \right) - kC(x, y, t). \end{aligned}$$

In the simulation, we implement the discrete version of the equation in two steps:

$$\begin{aligned} U(x, y) &:= U(x, y) + c \cdot dt \cdot \frac{1}{dh^2} \left(U(x + dh, y) + U(x - dh, y) + \right. \\ &\quad \left. U(x, y + dh) + U(x, y - dh) - 4U(x, y) \right) \\ U(x, y) &:= U(x, y) - k \cdot dt \cdot U(x, y) \end{aligned}$$

where dh represents the distance between places in our lattice, and dt is the time step.

There are 5 parameters of the simulations: $\Delta_C, \Delta_R, \Delta_S, k$ and dimensions of the lattice. After initial trials, we set the colicin decay constant to be $k = 0.01$, which proved to be small enough to see a diffusion yet large enough to prevent accumulation of a colicin in an environment. We then studied the behavior of the system depending on the remaining 4 parameter values.

3. RESULTS

3.1. Clustering behavior. In all simulations we observed a clustering behavior. This means that clusters of like-strains form relatively fast (within 10 generations) and continue to move and grow. The clustering behavior was observed and discussed earlier using a one-dimensional model of the rock-paper-scissors game (see [4]). In agreement with the findings in [4], we found our strains of bacteria organized in domains that act like the cells themselves and organize in further clusters (see Figure 2). The clustering behavior was observed independently of parameter values.

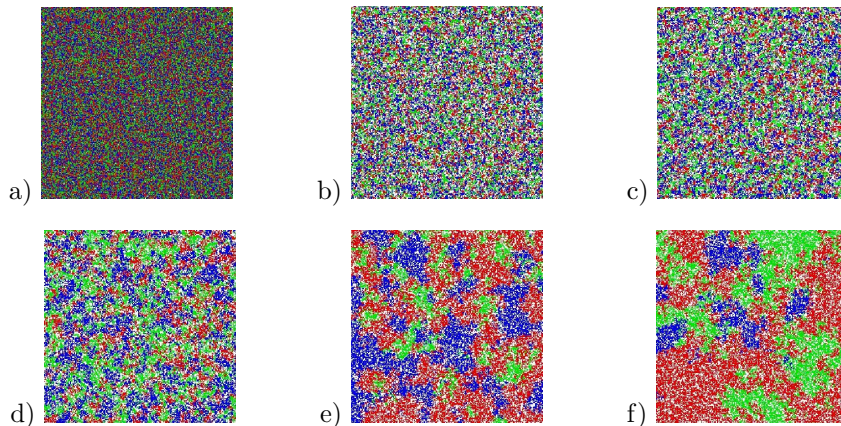


FIGURE 2. Clustering behavior. Snapshots of population: a) randomly generated initial population, b) after 10 generations, c) after 20 generations, d) after 100 generations, e) after 1000 generations, f) after 2000 generations.

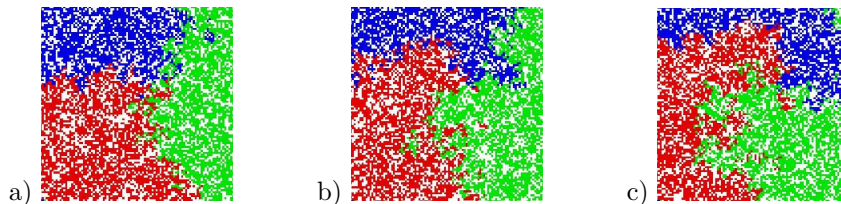


FIGURE 3. Chasing behavior. Snapshots of population that started originally as colonies: a) after 250 generations, b) after 480 generations, c) after 780 generations. Lattice has dimension 100x100.

3.2. Chasing behavior. As one would expect, the C chases S , R chases C , S chases R . If we set up the initial situation as colonies, we can see the spinning motion as in Figure 3. This behavior was observed for all reasonable parameter values.

3.3. Cycling behavior. We kept a running count of how many of each bacteria existed in the population and observed a sinusoidal pattern. See figure 4.

This behavior is typical of a rock-paper-scissors game. In an ideal case the following happens: the equilibrium of the system is attained exactly when all three types are equally represented. As soon as there are slightly less C , S lacks its only enemy and thus has an advantage and starts to grow faster. Hence, it gradually replaces R . When the amount of R decreases, C gets an advantage and starts to replace S . Once S is almost out of the picture, R lacks its competitor and increases in numbers, which in turn yields the decrease of C and the whole cycle repeats again.

This behavior was observed only for certain parameter values. For 250x250 lattices, the values had to be near $\Delta_C = 0.3233$, $\Delta_R = 0.3175$, $\Delta_S^0 = 0.2687$ which more or less corresponds to findings of authors in [6] ($\Delta_C = 1/3$, $\Delta_R = 10/32$, $\Delta_S^0 = 10/35$). One could change those parameters in any direction by up to 0.01 and the

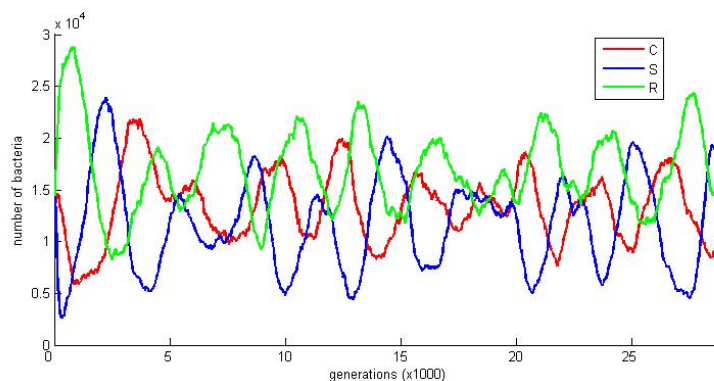


FIGURE 4. Cycling behavior, lattice of dimensions 250×250 , $\Delta_C = 0.3233$, $\Delta_R = 0.3175$, $\Delta_S^0 = 0.2687$.

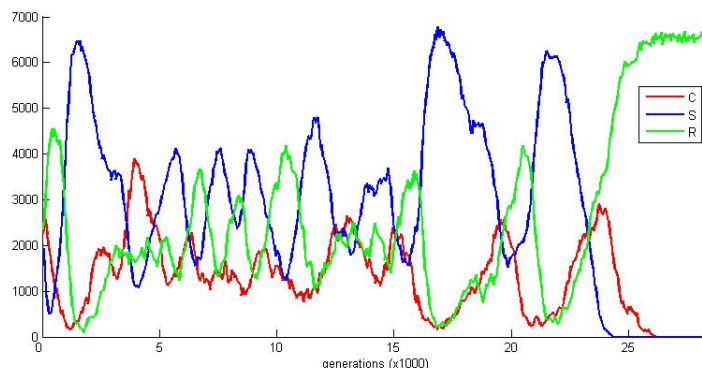


FIGURE 5. Cycling behavior, lattice of dimensions 100×100 , $\Delta_C = 0.3253$, $\Delta_R = 0.3175$, $\Delta_S^0 = 0.2687$.

behavior of the system would not differ significantly from Figure 4. For the above values, the system was in a balance and kept cycling for a long period of time (10^5 and more generations).

For 100×100 lattices, the values of the parameters needed for inducing the cycling behavior were near $\Delta_C = 0.3253$, $\Delta_R = 0.3175$, $\Delta_S^0 = 0.2687$. This time, there was less freedom on the parameter values (one could not change the values by more than 0.002 in order to see similar results). Moreover, we did not observe cycling behavior for more than roughly 3×10^4 generations; after such time one of the strains died out. Figure 5 depicts a typical simulation.

For 50×50 lattices we have observed cycling behavior only once and it did not last over 5000 generations. The reasons are discussed in the next section.

3.4. Long term behavior. The long term behavior of the system differed significantly depending on the dimensions of the lattice. The coexistence of all three species (lasting longer than 5000 generations) was not observed at all for small lattices with dimensions 50×50 . Although the coexistence for more than 2×10^4 generations was observed for various parameter values in 100×100 lattices, it never

lasted longer than 3×10^4 generations. On the other hand, the coexistence was observed for 10^5 generations in 250x250 lattice (for parameters as in the Figure 4).

We believe that there are two factors responsible for such a dependence. The first one is that the balance is broken more easily in smaller grid due to random fluctuations. Indeed, a change at one site in 50x50 grid means a jump in the densities by $1/2500$ which is 25 times more than in 250x250 grid. Thus, a single death or birth in a smaller grid has much bigger impact on the population than in larger lattices. The second reason is that the diffusion of the colicin makes the interactions more global and allows colicinogenic bacteria to affect sensitive ones from relatively further distances. The distance is more important in small lattices where S cannot effectively “hide” before the toxin in the colonies of R. Since the number of S is affected (usually their number gets very low very fast), it starts the spiral of increases and decreases of numbers of all strains. Such a spiral ends by the extinction of one strain (not necessary the sensitive one). The whole process is sped up by the random fluctuations described above.

In bigger lattices, we also observed that the longer the coexistence persisted in the population, the more likely it was for S to die out as the first strain. We originally thought that it is due to the accumulation of the toxin in the environment, but we do not have enough supporting evidence to make this claim. In fact, the extinction of S occurred many times after it almost dominated the population (as in Figure 5). We explore this behavior in the next section.

3.5. Extinction of the dominant and survival of the weakest strategy. The ultimate goal of all species is to persist in the population as long as possible; in an ideal case, indefinitely. Therefore, species evolve to gain advantages over competing species. However, in our example of three competitive strains, the advantage is not always what it seems to be. We observed a coexistence for certain values of $\Delta_C, \Delta_R, \Delta_S^0$ (in lattice 250x250). One would guess that since Δ_R means the probability to die, the chances of R to survive will only get better when we decrease the value Δ_R , and that the chances get worse when we increase it. However, this is true only for drastic changes of the parameter. If we changed the value by around 0.01, we observed a different pattern. Decreasing Δ_R , i.e. increasing the competitiveness and allowing the strain to be dominant in the population, eventually resulted in the elimination of R. Whereas, increasing Δ_R , i.e. lowering the competitiveness, or in other words weakening the strain, meant an ultimate victory for R. We got similar results as above when we varied parameters Δ_C and Δ_S^0 .

Let us first discuss extinction of the dominant strategy. If Δ_R is small (smaller than it should be to assure the balance), R does not die as much as it normally would and thus has an advantage. Consequently, it will eventually dominate the population. It even may (or may not) wipe C out of the picture. But this is the worst thing that could happen to R because then there is no serious competitor for S. Consequently, S will eventually replace R and will remain the only strain in the population. It may take several peaks of domination but the cycling is eventually broken (usually no later than after the second peak, similarly to what happened to S in Figure 5).

There is a counterpart of the above situation. If Δ_R is bigger than it “should be”, then R is the weakest of all strains. As such, it will struggle to survive in small numbers because soon after the start of the simulation, almost all R will be replaced by S. But then, S is a dominant strategy and there are almost no R in

the population which allows C to wipe out all S quite fast and this is a good time for a big comeback of R. Thus, the weakest in the population can survive. Such a behavior was already observed by [5].

4. CONCLUSIONS

We built a Monte Carlo simulation to study the behavior of a system of three competitive strains of bacteria with rules similar to the rock-paper-scissors game. We conclude that size of the environments matters. The larger the environment, the more stable the situation is - there are no drastic changes in the outcomes of the simulation for reasonable changes in parameter values and the influence of random fluctuations is not very significant. The coexistence of all competing species is possible for a relatively wide range of parameter values. In smaller environments, the diffusion and random fluctuations play an important role. As a consequence, there is no long term coexistence of all three species and eventually only one strain persisted in the population. We also observed that in cyclic systems like the rock-paper-scissors game, the best strategy for dominance is to get weaker; whereas any attempt to improve the short term performance that leads to early domination often ends with extinction.

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DEPARTMENT OF MATHEMATICAL SCIENCES, UNIVERSITY OF NORTH CAROLINA AT GREENSBORO,
GREENSBORO, NC 27402, USA, PHONE: 336.334.5836
E-mail address: rdmacmar@uncg.edu

DEPARTMENT OF MATHEMATICAL SCIENCES, UNIVERSITY OF NORTH CAROLINA AT GREENSBORO,
GREENSBORO, NC 27402, USA, PHONE: 336.256.1130
E-mail address: rychtar@uncg.edu