

# Evolutionary dynamics of spatial games

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## Abstract

A lattice model of coevolution of strategies for a two-person  $2 \times 2$  matrix game is introduced. We explore the region of parameter space corresponding to the Prisoner's dilemma, and classify the types of dynamical and evolutionary behavior that appear.

The fact that the world is not a well-stirred reaction vessel but has spatial extension is likely to affect evolutionary processes in many ways. It has for example been argued by Mayr (Mayr, 1954, 1976) that the most significant mechanism of speciation is so called peripatric speciation, where a small founder population capable of rapid evolution is separated off beyond the periphery of the range of a species. Similar ideas can be found in the original paper on punctuated equilibria by Eldredge and Gould (Eldredge and Gould, 1972). In this case, the heterogeneity of the physical world is important; geographical barriers of various kinds may allow enough isolation for different evolutionary paths to be explored in different regions.

But spatial effects could be important for evolutionary processes even in a homogeneous environment, since spatial structure could emerge from the dynamics of the system. Spatial effects could for example be of importance to prebiotic evolution — Boerlijst and Hogeweg (Boerlijst and Hogeweg, 1991) studied a cellular automaton model of the hypercycle model of Eigen and Schuster (Eigen and Schuster, 1979) and found spiral wave dynamics which greatly increased the stability against parasites. Spatial dynamics could also be relevant to the stability of ecological systems, and thus influence evolutionary processes; as an example, locally unstable systems may persist through space-time chaos (e.g., (Hassell, Comins and May, 1991)).

In this paper we introduce a simple evolutionary model where the world is a two-dimensional lattice, and the evolving entities are strategies in a game. The game used is the Prisoner's dilemma, a two-person non-zero-sum game which provides a model for studying the evolution of cooperation, as pioneered by Axelrod (Axelrod, 1984). We consider an infinitely repeated game, where in every round each player can choose between the two moves C (for cooperate), and D (for defect), and the pay-off matrix  $M$  has the following form:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \left( \begin{array}{cc} (R, R) & (S, T) \\ (T, S) & (P, P) \end{array} \right) \end{array}$$

where  $T > R > P > S$  and  $2R > T + S$ . These constraints imply that in a single game it is rational for both players to defect, but also that it would be to the players' mutual advantage to establish cooperation in the long run. In the model, the moves of the players are influenced by noise, so that in each round an intended move is replaced by its opposite with probability  $p_{err}$ .

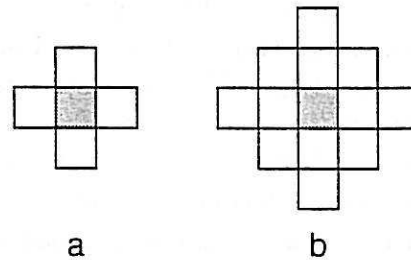


Figure 1: a. The neighborhood against which the game is played. b. The neighborhood affecting the central site at time  $t + 1$ .

In (Lindgren, 1991), a model of coevolution of strategies for the Prisoner's dilemma was studied (see also (Lindgren and Nordahl, 1993) for related work, where the result of the game determined the distribution of resources). The population dynamics of that model was based on ordinary differential equations, where in each generation each individual in the population played against all others. In the present model, an individual only interacts with its neighbors in some neighborhood  $N_1$  on a regular lattice (in this paper the four nearest neighbors on a 2-d quadratic lattice, see Fig 1a). The details of the genetic representation and mutations are identical to those of (Lindgren, 1991) — the model considered there could be viewed as a mean-field approximation to the present model.

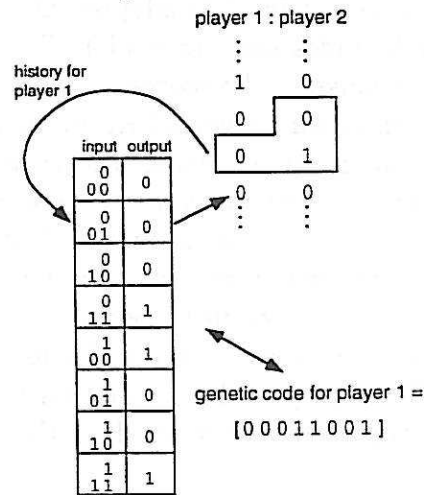


Figure 2: The representation of strategies as binary strings is illustrated for the memory 3 strategy 00011001.

The genomes in the model represent strategies in the game. A strategy is a rule for determining the next move of a player given the history  $h = ((x_0, y_0), \dots, (x_t, y_t))$  of the game, where the pair  $(x_t, y_t)$  consists of the moves of the player and the opponent, respectively, at time  $t$ . We consider only deterministic strategies of finite memory  $m \geq 1$ . For  $m$  even, the strategy depends on the last  $m/2$  moves of both players; for  $m$  odd on the last  $\lceil \frac{m+1}{2} \rceil$  moves of the opponent and the last  $\lceil \frac{m-1}{2} \rceil$  moves of the player himself. Writing 1 for the action C, and 0 for the action D, a strategy

of memory  $m$  can be represented as a binary string  $s$  of length  $2^m$ , see Fig. 2. The symbol at position  $i = (b_1, b_2, \dots, b_m)_2$  in  $s$  represents the action when the  $m$  last moves are given by  $\bar{h} = ((b_1, b_2), \dots, (b_{m-1}, b_m))$  for  $m$  even, while for  $m$  odd, the history taken into account is  $\bar{h} = (b_1, (b_2, b_3), \dots, (b_{m-1}, b_m))$ , so that only the move of the opponent affects the strategy at time  $t - \lfloor \frac{m+1}{2} \rfloor$ .

In the reproduction of a strategy, three types of mutations may occur: point mutations, gene duplications, and split mutations. Point mutations flip single bits in the genome with frequency  $p_{mut}$ . The gene duplication operator increases the memory of a strategy from  $m$  to  $m + 1$  (with frequency  $p_{dupl}$ ) while leaving the actual strategy unchanged. This corresponds to duplicating the genome: 1011  $\rightarrow$  10111011, for example. Gene duplication is a neutral mutation, which increases the size of the evolutionary search space without immediately affecting the phenotype. Additional point mutations can then give rise to new strategies without shorter memory equivalents. In this way, we may consider evolution in an unbounded space of strategies (though in a computer implementation the maximal memory allowed is of course bounded). Finally, the split mutation splits a genome into two parts of equal size with frequency  $p_{split}$ ; one of these is chosen at random and kept in the population.

Each lattice site is occupied by a single strategy; empty lattice sites are not allowed. All lattice sites are updated simultaneously in the following manner: first the score of a site  $(i, j)$  is calculated as the sum of the average scores obtained when the strategy  $s_{(i,j)}$  at the site plays the infinitely iterated game against the strategies in the neighborhood  $N_1$  (the four nearest neighbors in the case studied here). The score of a site is then compared to the scores in a neighborhood  $N_2$  (taken as the von Neumann neighborhood consisting of the site itself and its four nearest neighbors), and the highest scoring strategy in  $N_2$  is adopted at  $(i, j)$  at the next time step (note that the neighborhood includes the site itself). Ties are broken by adding a very small amount of random noise to the scores.

Since the scores of the nearest neighbors in turn depend on the strategies of their neighbors, the strategy at a certain site is actually updated depending on the strategies in a neighborhood of radius 2 (see Figure 1b). This means that if we were to restrict ourselves to a finite set of strategies, the model would be a cellular automaton. Similar CA models (but with a fixed set of strategies and without evolution) were introduced in (Axelrod, 1984); in (Nowak and May, 1992) the dynamics of the memoryless strategies C and D on a lattice was studied in more detail. For a different approach to a spatial Prisoner's dilemma based on an  $n$ -person game where strategies may depend on the actions in some neighborhood, see (Matsuo, 1985).

The interaction between two individuals is *a priori* described by five parameters:  $R, S, T, P$ , and the error rate  $p_{err}$ . However, the dynamics described above can be shown to be invariant under affine transformations of the pay-off matrix of the form  $M \rightarrow aM + bM_1$ , where  $M_1 = \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}$  and  $a > 0$ . This means that we can choose a normal form for the pay-off matrix where  $(R, S, T, P) = (1, 0, p, q)$ , with  $1 < p < 2$  and  $0 < q < 1$  for the Prisoner's dilemma. The boundary of this region will sometimes be included in the investigation. This leaves three parameters; in the simulations below we study the effects of varying the error rate with a fixed pay-off matrix given by  $(R, S, T, P) = (1, 0, 5/3, 1/3)$  (equivalent to the commonly used  $(3, 0, 5, 1)$ ), and of varying the pay-off matrix with the error rate fixed at  $p_{err} = 0.01$ .

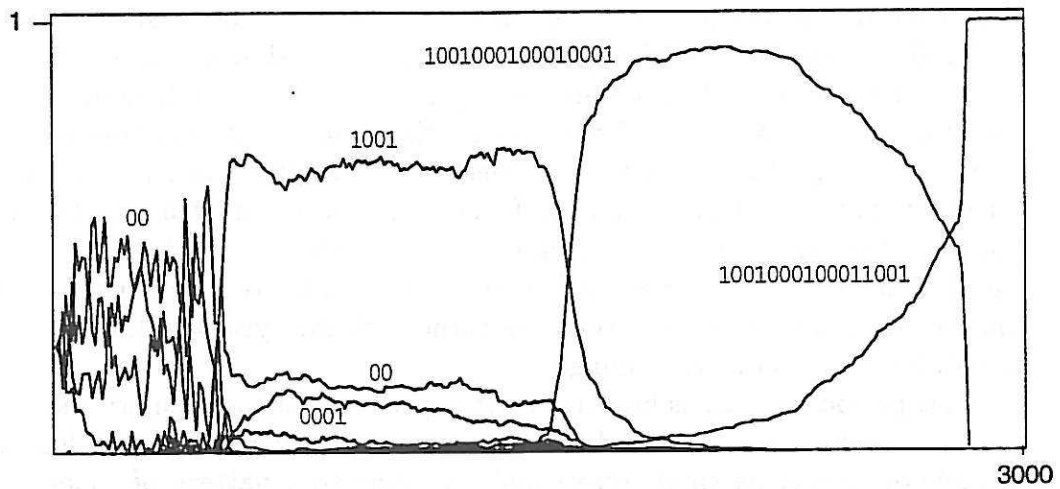


Figure 3: Population densities as function of time for the parameter values  $(p, q) = (5/3, 1/3)$ ,  $p_{err} = 0.01$ . The first 3000 generations of the simulation are shown.

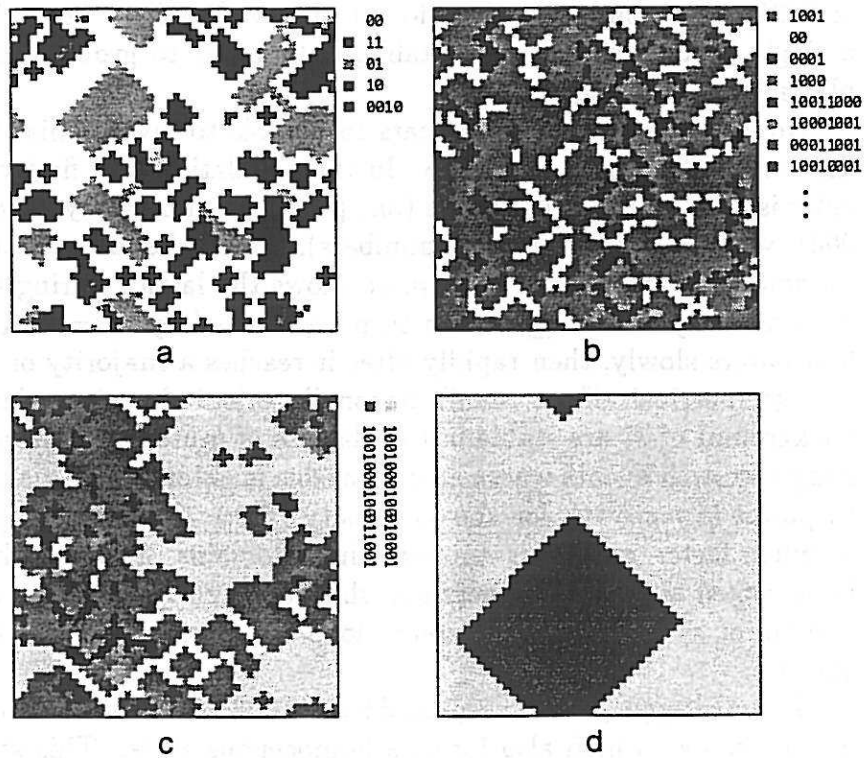


Figure 4: Examples of lattice configurations during the simulation of Figure 3: a.  $t = 200$ : Frozen domains of 00 and 11; waves of 01; b.  $t = 1000$ : 1001 dominates, 00 and 0001 at low levels; c.  $t = 1600$ : The previous state is invaded by  $s_1 = 1001000100010001$ ; d.  $t = 2400$ : Domains of  $s_2 = 1001000100011001$  grow in a sea of  $s_1$ .



A first example of the behavior of the model is obtained by letting  $(R, S, T, P) = (1, 0, 5/3, 1/3)$ ,  $p_{err} = 0.01$ ,  $p_{mut} = 0.002$ , and  $p_{dbl} = p_{split} = 0.001$ . In the initial state each site is randomly assigned one of the four memory 1 strategies with equal probability. The results of a typical simulation are shown in Fig. 3. After some initial oscillations, a state dominated by 00, 11, and 01 with essentially constant densities is reached. A snapshot of the spatial structure during this period of stasis is shown in Fig. 4a. The always cooperating strategy 11 forms stable islands in a sea of 00 defectors; 01, alias Tit-for-Tat, can invade a homogenous 00 configuration, but is in turn invaded by 11. Mutations where 00 goes to 01 generate spreading waves of activity. In this way, 01 is maintained at a fairly high density, and some 10 mutants also appear. If mutations are turned off, the system will freeze with only a few stable 01 domains remaining.

This period of stasis is broken by the appearance of the memory 2 strategy 1001, which spreads rapidly and takes over almost the entire lattice. This strategy is capable of correcting single errors and returning to a pattern of cooperation when playing against itself (Lindgren, 1991). Fig 4b shows a typical state during this second period of stasis. We can see that 00 and 0001 are able to coexist with 1001 at low densities. These strategies tend to form a network of mostly diagonal lines where each mutant plays against two 1001 individuals, but many other stable shapes are also possible. Some other mutants (such as 1000) may also enter in small quantities. These can be strategies which exploit 1001, but less efficiently than 00 or 0001, and at the same time do not play well against themselves. This means that a single mutant site may be stable, but unable to grow, since that would involve playing its own kind.

No memory 3 strategy appears to be able to invade this state, but at least two memory 4 strategies can do so. In the simulation, the first memory 4 strategy to enter is  $s_1 = 1001000100010001$  (one point mutation away from the quadruplicate of 0001, which is present in small numbers), which takes over most of the lattice, except for small islands of 1001 (Figure 4c shows the lattice during the invasion process). This memory 4 strategy can in turn be invaded by  $s_2 = 1001000100011001$ , which first enters slowly, then rapidly after it reaches a majority of the population. This is a geometrical effect: small diagonally oriented rectangular domains of  $s_2$  in a background of  $s_1$  are stable in the absence of mutations; mutations along the edges trigger growth events where an entire edge is extended by a site. This initially leads to power law growth for the  $s_2$  density. Once  $s_2$  reaches significant size, a phase of much faster growth is entered, since domains of  $s_1$  in a background of  $s_2$  will be attacked at convex corners and shrink away rapidly. Figure 4d shows a growing domain of  $s_2$  in a sea of  $s_1$ ; steps along the edges propagate to extend the side by one site.

The strategy  $s_2$  is then replaced by 10010000000010011001000100011001, a memory 5 strategy which also forms a homogenous state. This strategy appears to be very stable against memory 5 mutants (at least on a time scale of  $10^5$  generations). We have not yet explored longer memory.

These parameters were chosen for comparison with (Lindgren, 1991). At memory 1, the behavior of the spatial model is entirely different from the mean-field model, where a stable state with coexistence of 01 and 10 is found. The strategy 1001 which dominates at memory 2 usually shows up in the mean-field model as well, but there it is more efficiently exploited by 0001, which has a slight advantage over

1001 and dominates at memory 2. In the lattice model, the exploitation is less efficient due to the geometry, which allows cooperative strategies to cluster, and limits non-cooperative strategies to exploiting their nearest neighbors, and in this case the cooperative strategy 1001 has an advantage.

No analogue of the symbiotic pair of memory 3 strategies found in (Lindgren, 1991) appears to exist in the spatial model. The memory 4 strategies that appear on the lattice both belong to a group of strategies often encountered as a very stable final state of the mean-field model (in fact evolutionarily stable against single mutants). In that model, a group of similar, nearly degenerate strategies will coexist as a quasispecies at large times; in the lattice model a single strategy  $s_2$  among these is singled out even in the presence of mutations. This higher degree of discrimination is due to the fact that the highest scoring strategy in the neighborhood  $N_2$  is always reproduced, instead of making a stochastic choice according to the scores. In this way only the ordering of the scores matter, not the score differences. This is also the reason why a slightly refined memory 5 strategy is able to completely eliminate  $s_2$ .

For all parameter values studied, a first period of stasis with a population consisting almost exclusively of memory 1 strategies with approximately constant densities is found. The dynamical nature of this state does however vary with the choice of parameters. If we fix the pay-off matrix to  $(R, S, T, P) = (1, 0, 5/3, 1/3)$  and vary the error rate between 0 and 0.5, we find the following behavior:

- $0.0 < p_{err} \leq 0.148$ . Frozen state of 00 and 11; waves of 01 maintained by mutations as described above for the case  $p_{err} = 0.01$ .
- $0.148 \leq p_{err} \leq 0.226$ . Space-time chaos involving 01 and 11, see Figure 5.
- $0.226 \leq p_{err} \leq 0.244$ . Transition region with slowly shifting domains of 11 in a background of 01, together with frozen 00/11 domains.
- $0.244 \leq p_{err} \leq 0.269$ . Single 00 sites in a 01 background.
- $0.269 \leq p_{err} \leq 0.341$ . Network of lines of 00 in a background of 01.
- $0.341 \leq p_{err} \leq 0.419$ . Small islands of 01 in a sea of 00.
- $0.419 \leq p_{err} < 0.5$ . Small islands of 01 or 10 in a sea of 00.
- $p_{err} = 0.5$  Completely random play, i.e., all strategies are equivalent. Domains are formed because of the finite neighborhood used in the reproduction step; domain walls move randomly.

The behavior at memory 1 when the error rate is fixed at  $p_{err} = 0.01$ , and the pay-off matrix is given by  $(R, S, T, P) = (1, 0, p, q)$ , with  $1 \leq p \leq 2$  and  $0 \leq q \leq 1$  is illustrated in Figures 6, 7 and 8. Figures 7a–7d show the steady state densities of the strategies 00, 01, 10, and 11, in a system where only point mutations are allowed ( $p_{mut} = 0.002$ ). Each point in these diagrams is based on an average over 5 runs on a  $100 \times 100$  lattice, where densities were time averaged from  $t = 1000$  to  $t = 1500$ . The phase diagram in Figure 6 summarizes the different types of behavior that appear. Eight principal regions of this diagram can be identified (see Figure 6):

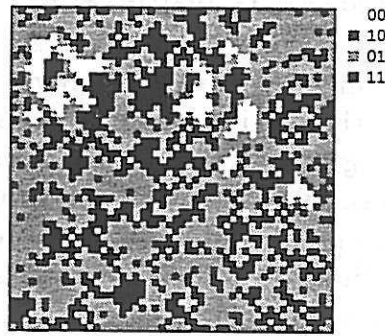


Figure 5: A configuration from a simulation with  $p_{err} = 0.15$ .

1. Homogenous state of 11.
2. Space-time chaos involving 00, 01, and 11 (see Figure 8a).
3. Frozen state of 00 and 11; waves of 01 (see Fig 4a). The point  $(p, q) = (5/3, 1/3)$  discussed above is located inside this region close to the boundary.
4. Homogenous state of 00.
5. Spiral waves of 00, 01, and 11 (see Figure 8b).
6. Irregular wave fronts and patches (see Figure 8c).
7. Space-time chaos involving 01 and 11, similar to Figure 5.
8. Homogenous state of 01.

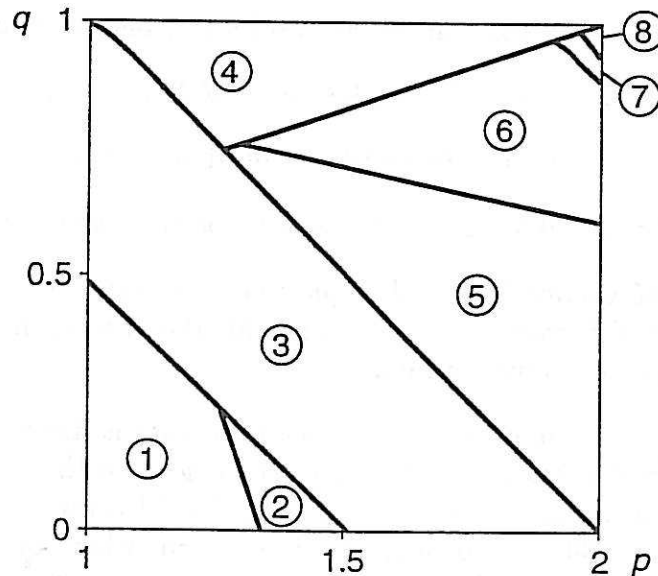


Figure 6: Phase diagram for memory 1 when the pay-off matrix is varied ( $p_{err} = 0.01$ ,  $p_{mut} = 0.002$ ).

In most of these cases, additional strategies may be present at low densities because of mutations. Most of the transitions are clearly indicated in the density

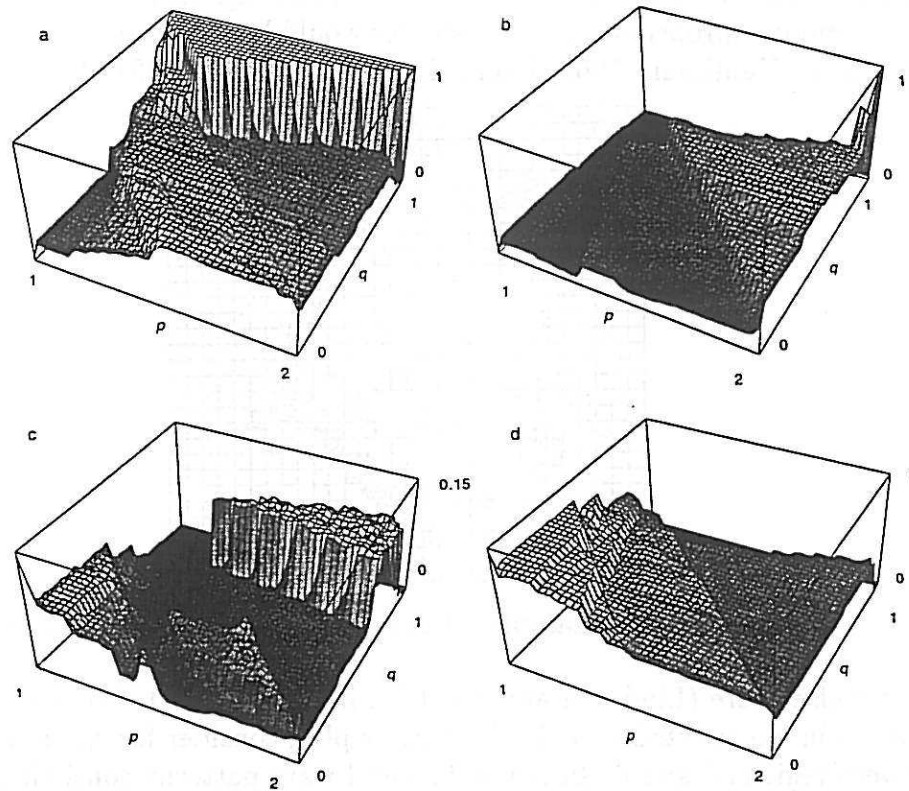


Figure 7: Invariant densities of memory 1 strategies as function of  $p$  and  $q$  when only point mutations are allowed ( $p_{err} = 0.01$ ,  $p_{mut} = 0.002$ ). a. density of 00; b. density of 01; c. density of 10; d. density of 11.

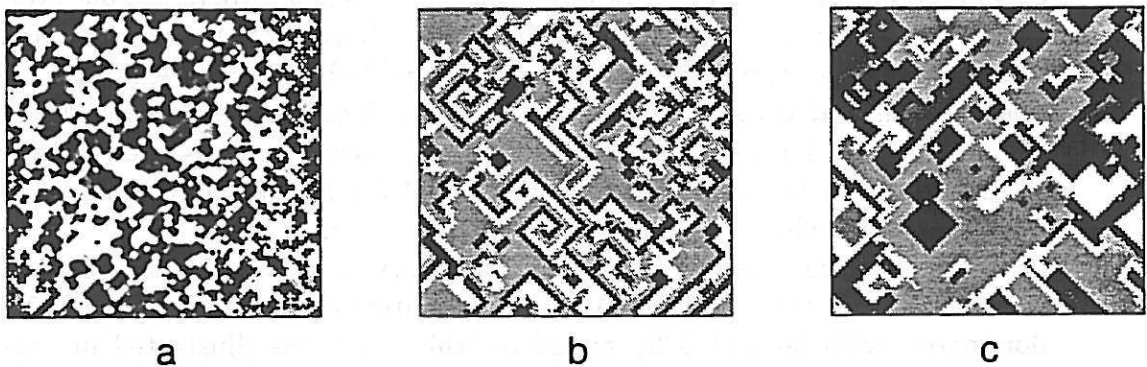


Figure 8: Examples of typical configurations from simulations with parameters from a. Region 2 of the memory 1 phase diagram,  $(p, q) = (1.4, 0.05)$ ; b. Region 5,  $(p, q) = (1.9, 0.2)$ ; c. Region 6,  $(p, q) = (1.9, 0.8)$ .



plots of Figure 7. The transitions to the chaotic regions are an exception; in those cases a more appropriate order parameter would be the spreading rate of small perturbations (Kauffman, 1969; Packard, 1985; Nordahl, 1992). We shall explore this

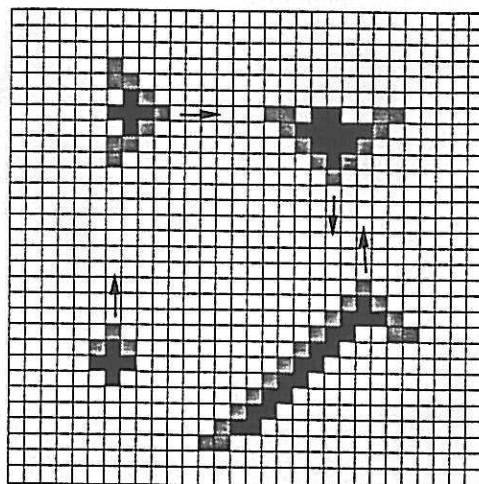


Figure 9: Some examples of gliders found at  $(p, q) = (1.2, 0.815)$ .

further elsewhere (Lindgren and Nordahl, in preparation). Some of the transitions show up in unexpected ways in the density plot, consider for example the transition between regions 5 and 6. In region 5, spiral wave patterns consisting of 00, 01, and 11 emerge (often rather irregular due to the action of mutations). Mutants of the form 10 are eliminated by the spatiotemporal dynamics (a phenomenon reminiscent of what happens in (Boerlijst and Hogeweg, 1991)). In region 6, where wave fronts and patches move in a more irregular way, 10 mutants are considerably more successful. This can clearly be seen in Figure 7c. It should also be pointed out that some of the structure of the phase diagram in Figure 6 does depend crucially on the presence of mutations. In particular, the boundary between regions 1 and 3 reflects the instability towards mutations to 00 (on the region 3 side of the border) of the essentially homogenous state of 11 reached initially by the CA dynamics. Some other phenomena essentially dependent on the spatial degrees of freedom are also observed for memory 1. Several different types of gliders (stable propagating structures) are found, in particular close to the border of the 00 region (note that this is not at the transition to chaos). Figure 9 shows some examples. Another phenomenon that involves the spatial degrees of freedom in an essential way is that of a critical size for growth of clusters of cooperative mutants. For example, close to the transition from region 8 to region 4, Tit-for-Tat can only expand in a sea of defectors once a cluster of the form  $\begin{smallmatrix} \square & \square & \square \\ \square & \square & \square \\ \square & \square & \square \end{smallmatrix}$  is formed.

Let us now consider the behavior at memory 2. When the error rate is varied, several different types of behavior are encountered. For  $0.0 < p_{err} \leq 0.16$ , 1001 dominates, with 00 and 0001 mixed in (this state was illustrated in Figure 4b). When the error rate exceeds 0.16, stable islands of 1101 are also possible, and a frozen state of 00, 1101, and 1001 is formed. As the error rate is further increased, quite complex communities may form, where patches of this frozen state compete with chaotic domains consisting of 01 and 1100, and where a number of other mutants may be present at significant levels. This behavior is found up to  $p_{err} = 0.3$ ; above this error level a transition to a frozen state of 01 and 00 is found. Finally, when  $0.37 \leq p_{err} < 0.5$ , no memory 2 strategy is able to invade the always defecting

strategy 00 (when the environment is very noisy, developing a sophisticated strategy is of little value).

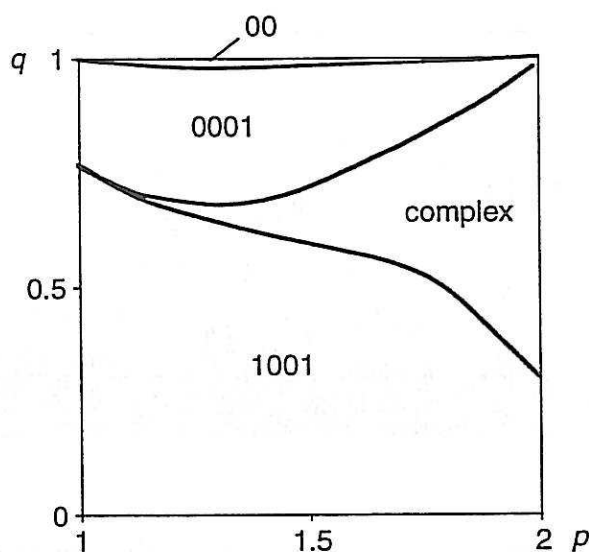


Figure 10: Approximate classification of memory 2 periods of stasis when the pay-off matrix is varied ( $p_{err} = 0.01$ ,  $p_{mut} = 0.002$ ).

The typical behavior at memory 2 when the pay-off matrix is varied with  $p_{err} = 0.01$  is indicated in the diagram in Figure 10. This diagram is slightly less well-defined than that for memory 1 (the existence of a period of stasis consisting of memory 2 strategies is not always clear; several evolutionary paths may also be possible for some parameter values). However, it is clear that 1001 is a successful strategy in a fairly large region of parameter space, and we can see that regions of non-trivial spatiotemporal dynamics exist also for memory 2.

The asymptotic behavior is also different in different regions of parameter space. It is not possible to explore this topic fully here, so we just give a few examples illustrating some of the various qualitative behaviors that may be found. The simulation of Figures 3 and 4 has already illustrated a case where asymptotically a single strategy forms a spatially homogenous state and is able to resist invasion. Examples of non-trivial spatiotemporal behavior can also be found. One may for example encounter complex communities, where the spatial extension of the system allows the coexistence of a large number of strategies in frozen patches (which may evolve slowly due to mutations).

Situations more reminiscent of Red Queen dynamics (Van Valen, 1973), with an apparently open-ended evolutionary process, are also found. Figures 11 and 12 show an example of a simulation for the parameter values  $(p, q) = (1.95, 0.95)$ ,  $p_{err} = 0.01$ , where a large number of different strategies succeed each other (this simulation was continued for 50000 generations without reaching a stationary state). There does appear to exist a certain degree of correlation between chaotic spatiotemporal dynamics and a more unstable evolutionary process in this model.

We have observed a number of phenomena in this spatial model that have no correspondence in a similar model based on ordinary differential equations: coexistence through space-time chaos, formation of complex communities due to coexistence in different spatial regions, transitions between different forms of spatiotemporal behavior as parameters are varied, and also more open-ended evolutionary processes

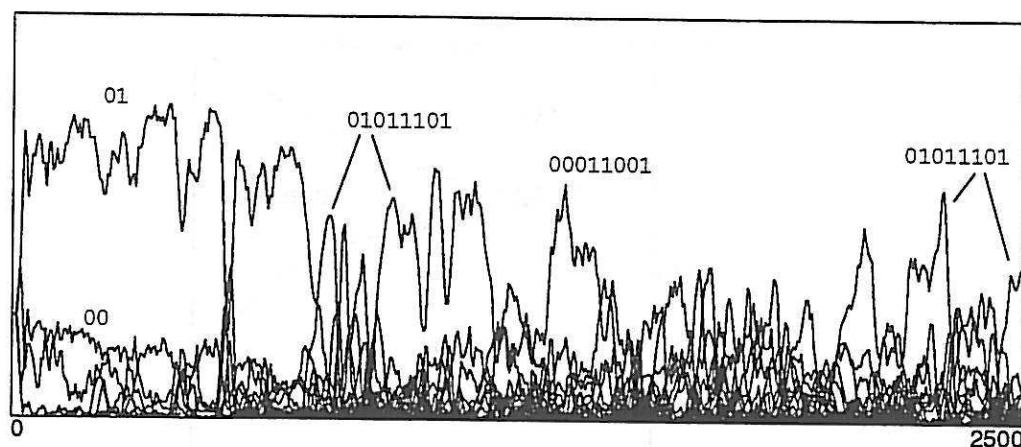


Figure 11: Population densities as function of time for the parameter values  $(p, q) = (1.95, 0.95)$ ,  $p_{err} = 0.01$ .

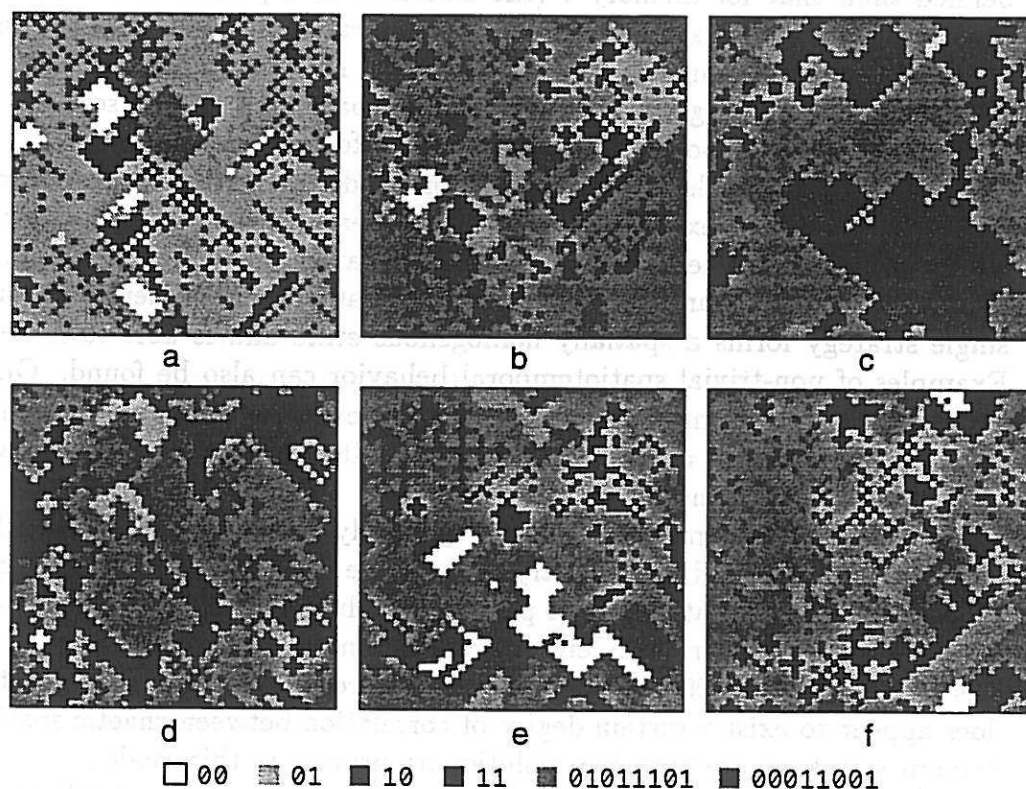


Figure 12: Examples of lattice configurations during the simulation of Figure 11: a.  $t = 545$ , b.  $t = 725$ , c.  $t = 835$ , d.  $t = 1120$ , e.  $t = 2215$ , f.  $t = 2500$ .

in some regions of the parameter space. To observe other forms of spatial behavior related to the heterogeneity of the environment, it might be necessary to introduce explicit resource flows and a non-trivial external environment, as was done in a model without spatial degrees of freedom in (Lindgren and Nordahl, 1993).

## Acknowledgements

We are grateful to Jonas Rahmn for his assistance in the exploration of some of the artificial ecologies of this paper.

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