

LET US NOW STUDY the deterministic evolutionary dynamics of spatial games. The members of a population are arranged on a two (or higher)-dimensional array. In each round, every individual plays the game with its immediate neighbors. After this, each site is occupied by its original owner or by one of the neighbors, depending on who scored the highest payoff in that round. These rules specify a deterministic cellular automaton. John von Neumann stood at the beginning of both game theory and cellular automata. In the theory of spatial games, these two approaches meet for the first time.

We will see that spatial effects can dramatically change the outcome of frequency-dependent selection. In space, strategies can coexist that exclude each other in a homogeneous setting. Moreover, spatial games have fascinating mathematical properties and a rich dynamical behavior. We will encounter spatial chaos, dynamic fractals, and evolutionary kaleidoscopes. Our goal is to formulate the simplest possible theory for deterministic spatial evolutionary game dynamics.

9.1 SPACED OUT

Consider an evolutionary game between two (or more) strategies. Each player occupies a position on a spatial grid and interacts with all of its neighbors. The payoffs from these interactions are added up. In the next generation, depending on the payoff, each player retains its current strategy or adopts the strategy of a neighbor.

We want to design a completely deterministic spatial game. This can be achieved with the following two rules: (i) each player adopts the strategy with the highest payoff in its neighborhood and (ii) all players are updated in synchrony.

Figure 9.1 illustrates the rules of the game for a square lattice and the Moore neighborhood; each cell has 8 nearest neighbors defined by a king's move on a chessboard. A player will retain its current strategy if it has a higher payoff than all of its neighbors. Otherwise the player will adopt the strategy of that neighbor that has the highest payoff. Note that the fate of a cell depends on its own strategy, the strategies of the 8 neighbors, and the strategies of their neighbors. Thus 25 cells in total determine what will happen to a cell. In the terminology of cellular automata, the transition rules are complex, but in terms of an evolutionary game they can be stated simply and naturally.

We are studying deterministic evolutionary game dynamics (without mutation) in a population with spatial structure. The transition rules are entirely deterministic. The outcome of the game depends only on the initial configuration of the population and the payoff matrix.

9.2 SPATIAL COOPERATION

As a specific example, we will explore the most interesting evolutionary game, the struggle between cooperators, C , and defectors, D . We will find that spatial games lead to a fascinating new mechanism for the evolution of cooperation, called “spatial reciprocity.”

Consider the following Prisoner's Dilemma payoff matrix

Spatial games

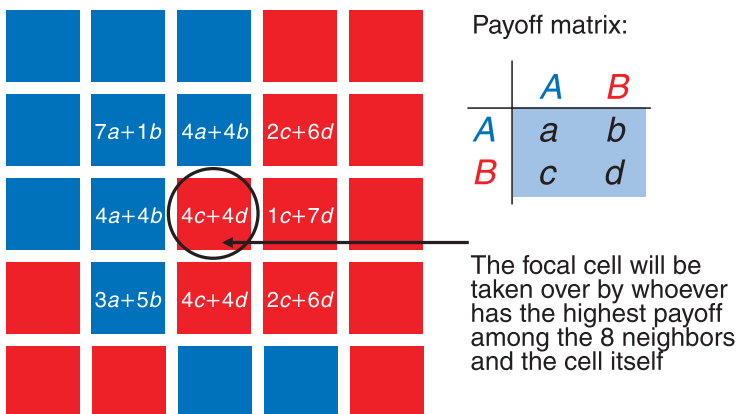


Figure 9.1 The rules of spatial games. Each cell plays the game with all of its neighbors. In this example, we use a square lattice and the Moore neighborhood, where each cell has 8 neighbors. The payoff for each player is evaluated. Subsequently each player compares its own payoff with that of its neighbors and adopts the strategy of whoever has the highest score. The fate of each cell depends on the state of all 25 cells in the 5×5 square that is centered around the cell.

$$\begin{array}{c} C \\ D \end{array} \begin{array}{cc} C & D \\ \left(\begin{array}{cc} 1 & 0 \\ b & \epsilon \end{array} \right) \end{array} \quad (9.1)$$

If two cooperators interact, both receive one point. If a defector meets a cooperator, the defector gets payoff $b > 1$, while the cooperator gets payoff zero. The interaction between two defectors leads to the very small positive payoff ϵ . This payoff matrix is designed to keep things as simple as possible. For exploring different evolutionary dynamics, we vary the single parameter, b , and we choose to set $\epsilon \rightarrow 0$.

On the square lattice with the Moore neighborhood, each individual has 8 neighbors. Therefore, the possible payoffs for a cooperator are given by the set $\{1, 2, 3, \dots, 8\}$. The possible payoffs for a defector are given by the set $\{b, 2b, 3b, \dots, 8b\}$. The discrete nature of the possible payoff values means that there are only discrete transition points for b that can influence the dynamics. For $1 < b < 2$, these transitions occur at

$$8/7 = 1.1428 \dots$$

$$7/6 = 1.166 \dots$$

$$6/5 = 1.2$$

$$5/4 = 1.25$$

$$8/6 = 1.333 \dots$$

$$7/5 = 1.4$$

$$3/2 = 1.5$$

$$8/5 = 1.6$$

$$5/3 = 1.666 \dots$$

$$7/4 = 1.75$$

$$9/5 = 1.8$$

Figure 9.2 shows typical distributions of cooperators and defectors for different values of the parameter b . All simulations are performed on a 100×100 square lattice. There are periodic boundaries, which means that the edges of the square are wrapped around to generate a torus. This geometry has the advantage that all positions on the grid are equivalent. There are no boundary effects. The initial configuration is obtained at random with half of the cells being cooperators, the other half defectors.

The color code is as follows:

Blue represents a C that was a C in the previous generation.

Red represents a D that was a D in the previous generation.

Green represents a C that was a D in the previous generation.

Yellow represents a D that was a C in the previous generation.

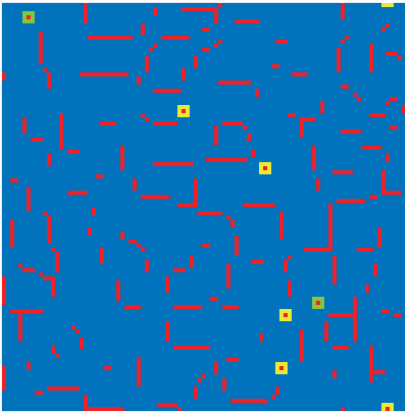
Therefore blue and red indicate static cells, while green and yellow show changing cells. If a picture contains only red and blue, then it is a fixed point of the evolutionary dynamics: nothing has changed from the last generation, and nothing will change anymore. The more green and yellow cells, the more changes are occurring.

For $b = 1.10$, we observe a rather static pattern. Most cells are cooperators. There are isolated lines of defectors, which do not change. There are a few isolated single defectors, which generate squares of 9 defectors only to oscillate back to a single defector in the next generation. For $b = 1.15$, the lines of defectors oscillate at the end. There are many oscillating positions including isolated defectors. For $b = 1.24$, the lines of defectors start to be connected. There are a few oscillating positions. There are single defectors that oscillate to squares of 9 defectors, then to crosses of 5 defectors and back to single defectors. For $b = 1.35$, there is a pulsating network of defectors. Lines oscillate between thickness one and three. For $b = 1.55$, there is an irregular but static network of defectors permeating a world which is still dominated by cooperators.

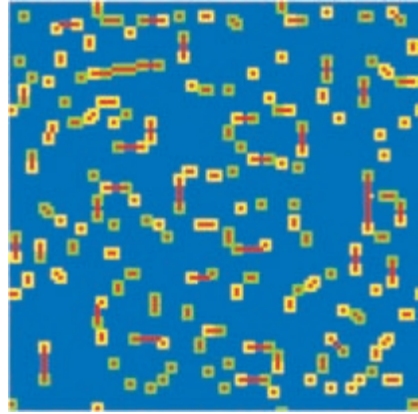
For $b = 1.65$, the tide has turned. Defectors have won the majority. Cooperators survive in clusters. The picture is neither static, nor oscillatory, but highly dynamic. The clusters of cooperators always try to expand. They collide, break into pieces, and disappear. New clusters are being formed all the time. The system will certainly run into a cycle eventually (there are only finitely many states), but the transient can be longer than the lifetime of the universe. For $b = 1.70$, the pattern is again very static. There are mostly defectors. Cooperators survive in a few clusters.

Is it possible to understand these observations?

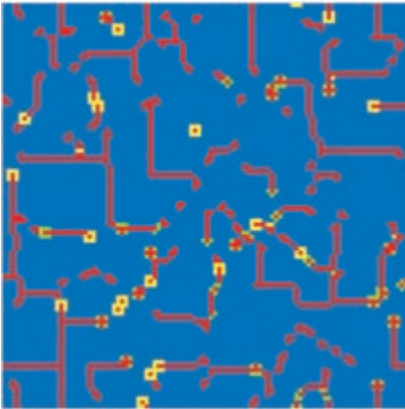
$b = 1.10$



$b = 1.15$



$b = 1.24$



$b = 1.35$

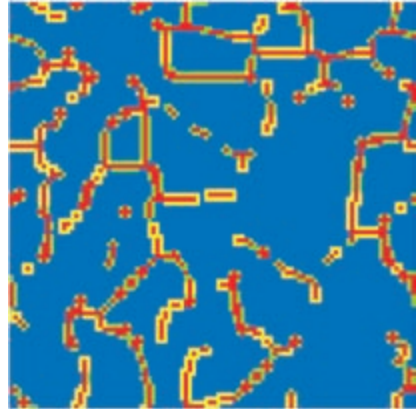
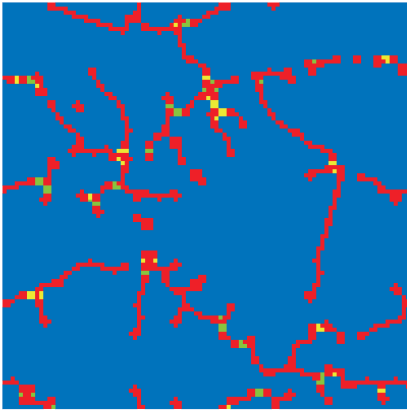
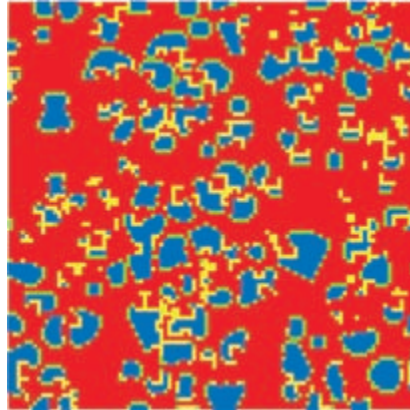


Figure 9.2 The spatial Prisoner's Dilemma displays an amazing variety of patterns where unconditional cooperators coexist with defectors. The figure shows configurations of 100×100 square lattices for seven different parameter regions. There are periodic boundary conditions, which means the edges are wrapped around to generate a toroidal universe. The color code is as follows: blue is a cooperator that was a cooperator in the previous round; red is a defector that was a defector in the previous round; green is a cooperator that was a defector in the previous round; yellow is a defector that was a cooperator in the previous round. The more yellow and green in a picture, the more changes are occurring. An entirely blue and red pattern is completely static. The payoff matrix is given by equation (9.1). The parameter b denotes the advantage for

$b=1.55$



$b=1.65$



$b=1.70$



defectors. Cooperators dominate the scene for $b = 1.10, 1.15, 1.24, 1.35,$ and 1.55 . For these parameter values, there are various (static or pulsating) network structures of defectors in a mostly cooperative world. For $b = 1.65$ there is a dynamic coexistence between cooperators and defectors. Cooperators form clusters that grow, collide, disappear, and fragment to form new clusters. The pattern is always changing, but the average frequency of cooperators is always very close to 0.30. For $b = 1.70$ there are static clusters of cooperators in a frozen world. The initial condition is a random configuration with 10% cooperators; except for $b = 1.70$ when the simulation started with 50% cooperators.

Defectors invading Cooperators

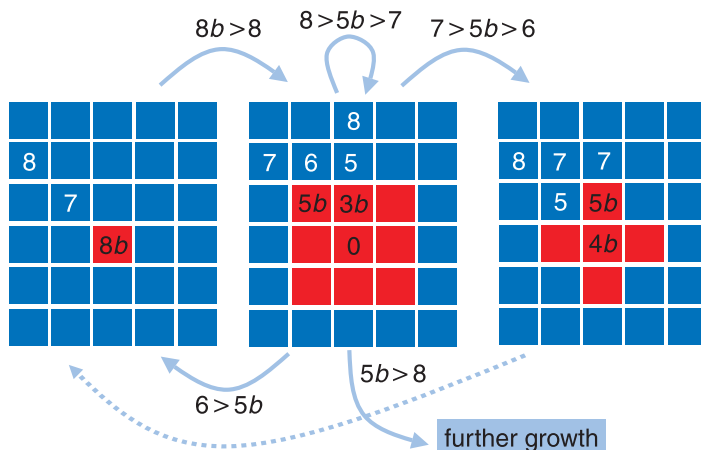


Figure 9.3 Invasion conditions for defectors. If $b > 1$ then a single defector gives rise to a square of 9 defectors, 9D. If $b < 6/5$, this square returns to a single defector. We have a period two oscillator. If $6/5 < b < 7/5$, then the 9D square turns into a 5D cross, which turns into a single defector. We have a period three oscillator. If $7/5 < b < 8/5$, the 9D square is stable. If $8/5 < b$, the 9D square can expand.

9.3 INVASION

The standard procedure for analyzing evolutionary games is to explore the conditions for invasion. When does natural selection favor the spread of a new mutant? Let us start with defectors invading cooperators.

9.3.1 Defectors Invading Cooperators

Figure 9.3 illustrates the conditions for a single defector to invade a population of cooperators. The defector has payoff $8b$. All of its immediate neighbors are cooperators and have payoff 7. All of their neighbors have payoff 8. Therefore, if $8b > 8$, which means $b > 1$, then the defector will take over all its neighbors.

In the square cluster of 9 defectors, 9D, the central defector has payoff 0, the four defectors at the corners have payoff $5b$, the four remaining defectors have

Cooperators invading Defectors

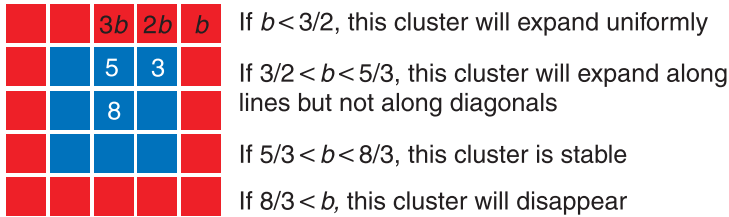


Figure 9.4 Cooperators can invade defectors when starting from a small cluster. Here we analyze a cluster of 9 cooperators, 9C. If $b < 3/2$, this cluster will expand uniformly. If $3/2 < b < 5/3$, the cluster can grow along the lines but not along the diagonals. In the next generation, there will be 12 new cooperators; all cells in a 5×5 square except the 4 corner cells will be cooperators.

payoff $3b$. The cluster is surrounded by cooperators with payoffs 5, 6 and 7. The second row of cooperators all have payoff 8. There are four possibilities:

- (i) If $b < 6/5$, then the 9D square will return to a single defector.
- (ii) If $6/5 < b < 7/5$, then the 9D square will turn into a cross consisting of 5 defectors which will subsequently turn into a single defector. There is a period three oscillator: 1D to 9D to 5D and back to 1D.
- (iii) If $7/5 < b < 8/5$, then the 9D square will not change.
- (iv) If $8/5 < b$, then the 9D square will grow into a square consisting of 25 defectors, which will continue to expand.

9.3.2 Cooperators Invading Defectors

Let us now analyze the conditions for cooperators to invade defectors (Figure 9.4). First, we note that a single cooperator can never survive or expand, but is always doomed to become eliminated in one step. In this deterministic game, cooperators only have a chance if they arise in clusters.

If $b < 3/2$, then a square of 4 cooperators will expand to a square of 16 cooperators, then to 36 cooperators, and so on. There will be ever-increasing

squares of cooperators. If $b > 3/2$, then a square of 4 cooperators will be eliminated.

A square of 9 cooperators will also grow into bigger and bigger squares if $b < 3/2$. If $3/2 < b < 5/3$, then the 9C square can expand along the side lines, but not diagonally. It will give rise to a cross-like structure of 21 cooperators. This structure will continue to grow. If $5/3 < b < 8/3$, then the 9C square is stable; it will neither expand nor decline. If $b > 8/3$, the 9C square will be eliminated in two steps.

9.3.3 Three Classes of Parameter Regions

In summary, the above analysis suggests the existence of three classes of parameter regions.

- (i) If $b < 8/5$, then only *C* clusters can keep growing.
- (ii) If $b > 5/3$, then only *D* clusters can keep growing.
- (iii) If $8/5 < b < 5/3$, then both *C* and *D* clusters can keep growing.

The various dynamical behaviors observed in Figure 9.2 fall into these three broad classes. As long as $b < 8/5$, the world is dominated by cooperators. If $b > 5/3$, defectors take over. If $8/5 < b < 5/3$, there is a dynamic balance between cooperators and defectors.

In parameter regions (i) and (ii), the final abundance of cooperators strongly depends on the starting condition. In parameter region (iii), however, most initial conditions converge to the same mixture of the two strategies with roughly 30% cooperators. While the actual pattern of cooperators and defectors is changing all the time, the frequency of cooperators, in a sufficiently large array, is almost constant. We call this behavior a “dynamic equilibrium.”

9.4 DYNAMIC FRACTALS AND EVOLUTIONARY KALEIDOSCOPIES

An interesting sequence of patterns emerges if a single defector invades a world of cooperators in the parameter region $8/5 < b < 5/3$. The defector grows to form a 3×3 and then a 5×5 square of defectors. The payoff for defectors at the corners of this square is $5b$, which is larger than 9. The payoffs for defectors

The corner-and-line condition

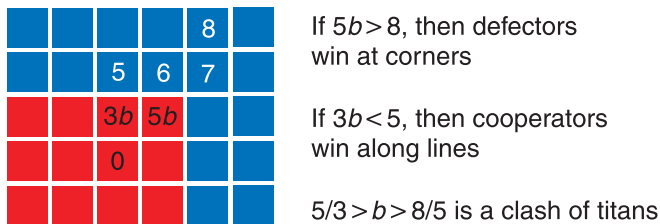
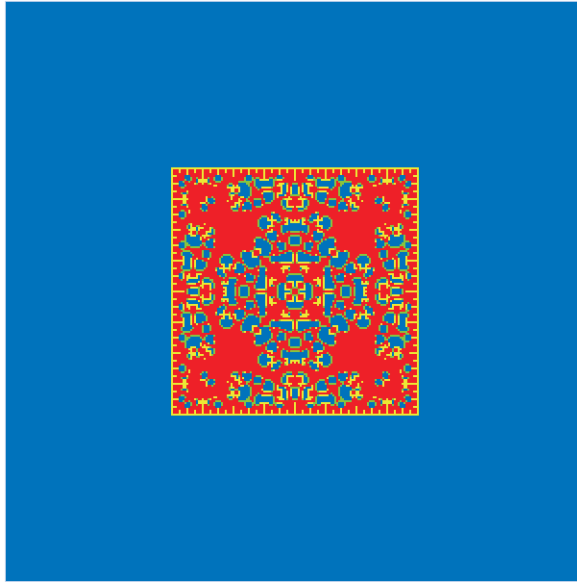


Figure 9.5 The corner-and-line condition is responsible for spatial chaos, dynamic fractals, and kaleidoscopes. A large square-shaped cluster of defectors can expand on the corners if $8/5 < b$, but shrink along the lines if $b < 5/3$. Hence in the parameter region $8/5 < b < 5/3$, cooperators win along straight lines, but lose along irregular boundaries.

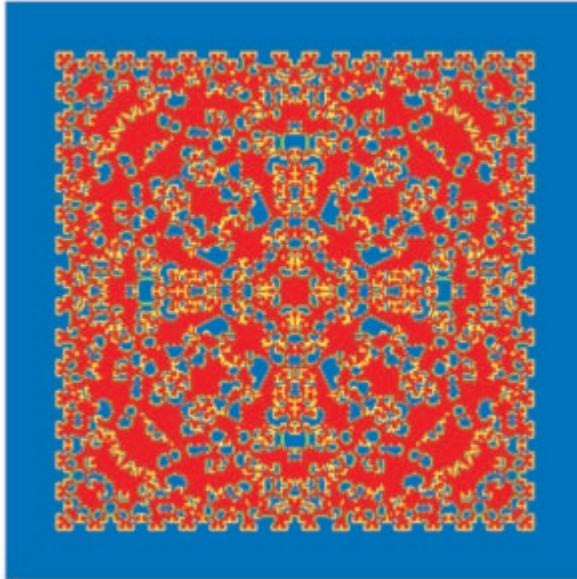
along the edges of the square is $3b$, which is smaller than 6. Therefore the defectors gain at the corners, but lose along the lines (Figure 9.5). The result is a dynamic fractal that combines symmetry and chaos. Figure 9.6 shows the growing fractal after 64, 124, and 128 time steps before it has encountered any boundaries. There are fractal-like structures that repeat themselves. The growing fractal is square-like at generations that are the powers of 2. The fractal contains many clusters of cooperators, which move around, expand, collide, fragment, and give birth to new clusters of cooperators. The frequency of cooperators within the growing fractal converges to $x \approx 0.30$, which is the same numerical value as in the simulations with random initial conditions.

Figure 9.7 shows a sequence of the “evolutionary kaleidoscope” that is generated by a single defector invading a population of cooperators in a fixed array with periodic boundaries. Each generation shows a new picture. There is an amazing variety. The initial symmetry is never broken, because the rules are symmetrical. The frequency of cooperators oscillates chaotically. These oscillations, however, cannot continue forever, because the total number of possible states is finite. The kaleidoscope must eventually converge to some oscillator with a finite period or a static configuration. Note that this convergence to a periodic orbit also holds, of course, for asymmetric initial conditions.

$t=64$



$t=124$



$t = 128$

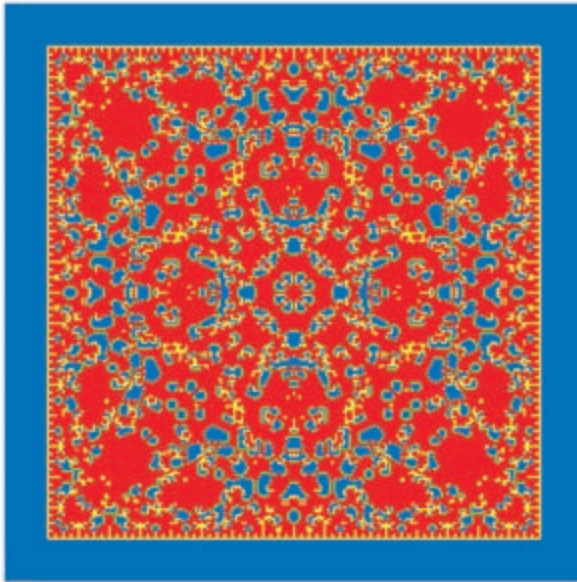
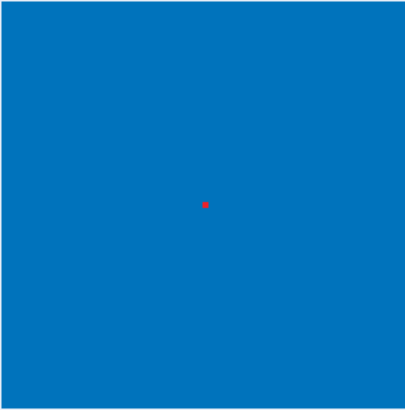
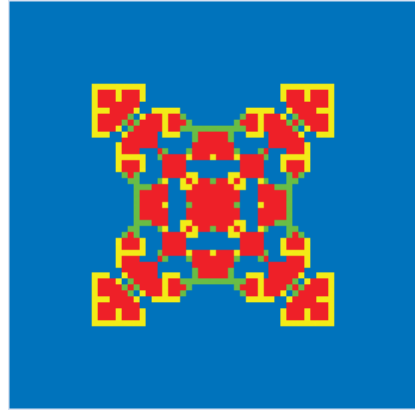


Figure 9.6 Starting with a single defector in a world of cooperators, there is an amazing sequence of ever-growing “Persian carpets.” The structure is square-like with straight boundaries at every generation that is a power of 2. Here we show generations 64, 124, and 128. Parameter region $8/5 < b < 5/3$.

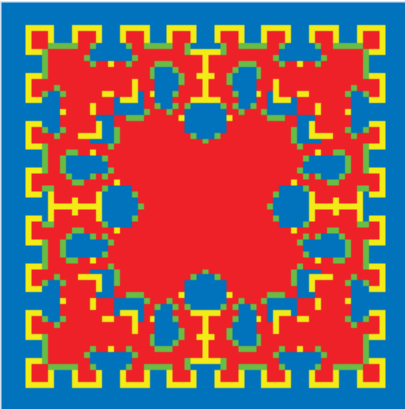
$t=0$



$t=20$



$t=30$

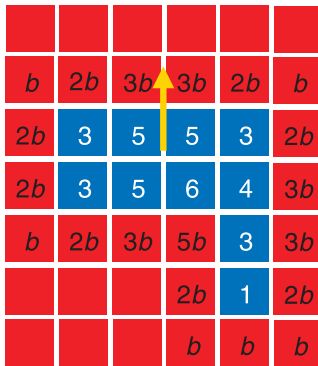


$t=2,000$



Figure 9.7 Kaleidoscopes are generated by a single defector invading a square of cooperators of fixed size. There can be an amazingly long sequence of always changing symmetric patterns. In the end (but after a very long time) the kaleidoscope must reach a fixed pattern or a cycle, because the number of all possible configurations is finite. Parameter region $8/5 < b < 5/3$. The size of the square is 69×69 with periodic boundary conditions.

A “walker”



$$8/5 < b < 5/3$$

Figure 9.8 A “walker” is a cluster of 10 cooperators. It moves into the direction indicated by the yellow arrow. The leg moves from the right to the left every other generation. When observed on a screen, it appears as if the walker is walking on two legs. Parameter region $3/2 < b < 5/3$.

The interesting mathematical features of the growing fractal and the kaleidoscopes arise from a combination of simplicity (the rules), deterministic unpredictability (the eventual fate), transient chaos (the frequency of cooperators), and symmetry (beauty).

9.5 THE BIG BANG OF COOPERATION

Although the patterns of the previous section are beautiful, there is the disconcerting aspect that they describe the invasion and partial replacement of a world of cooperators by defectors. Fortunately, the reverse invasion is also possible and even more beautiful.

A “walker” is a structure of 10 cooperators (Figure 9.8). For $3/2 < b < 5/3$, this “fellowship of cooperators” moves bravely through an adverse world of defectors. One such walker cannot change the world, but if two walkers collide they can generate a “big bang” of cooperation, exploding into a world of defectors (Figure 9.9).

Less dramatically, but no less beautiful, a big bang can also be initiated by a single square of 9 cooperators or a rectangle of 6 cooperators. Figures 9.10 and 9.11 show big bangs of cooperators for two different parameter values.

A collision of two “walkers” can lead to a “big bang” of cooperation

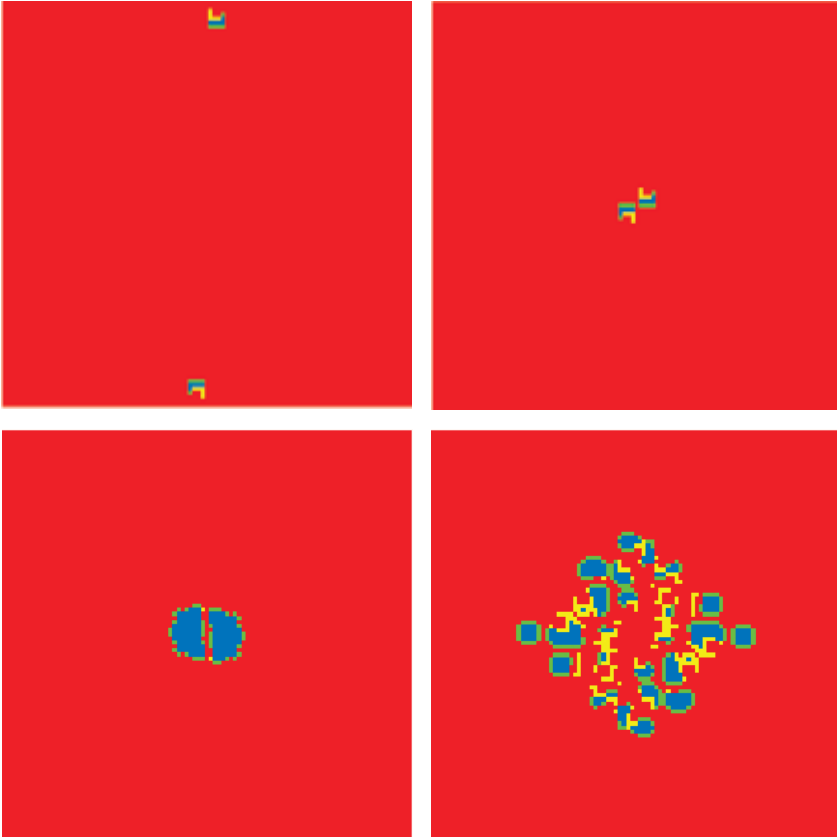


Figure 9.9 Cooperation “walks in.” A collision of two walkers in a world of defectors can generate a big bang of cooperation. Four consecutive time points are shown. Parameter region $8/5 < b < 5/3$.

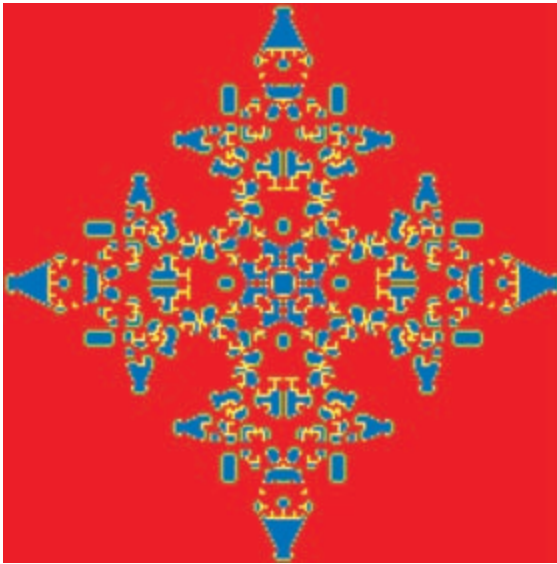


Figure 9.10 A cluster of 3×3 cooperators in the parameter region $8/5 < b < 5/3$ can invade a world of defectors and also generate a fractal-like growth pattern.

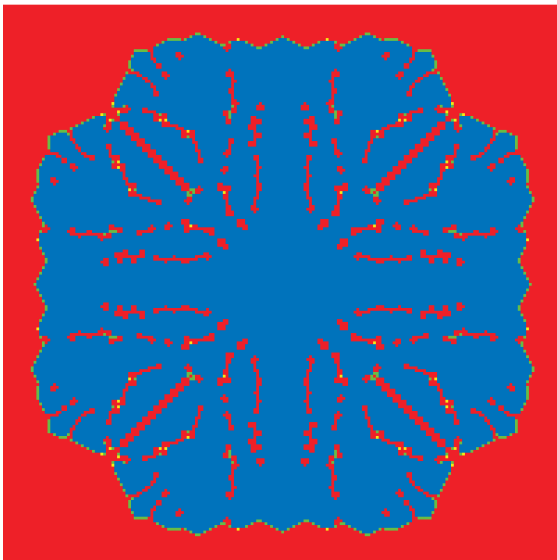


Figure 9.11 Invasion of cooperators starting from a 3×3 cluster in the parameter region $3/2 < b < 8/5$.

9.6 OTHER GEOMETRIES

Spatial games can be studied with many variations on the basic theme. Instead of the Moore neighborhood, we can investigate the “von Neumann” neighborhood, which consists of the 4 adjacent neighbors excluding the diagonals. Again there is a range of different patterns exhibiting coexistence between cooperators and defectors in the nonrepeated Prisoner’s Dilemma. For $4/3 < b < 3/2$, we encounter the dynamic equilibrium with kaleidoscopes and fractals of even greater allure (Figure 9.12). For $3/2 < b < 2$, clusters of cooperators can still expand horizontally and vertically generating a rectangular “railway” network.

In a hexagonal lattice, each cell is surrounded by six others. There again different parameter regions allow coexistence between cooperators and defectors, but there is no dynamic equilibrium. The patterns are more static. For other evolutionary games, however, it is possible to obtain a dynamic equilibrium on a hexagonal lattice.

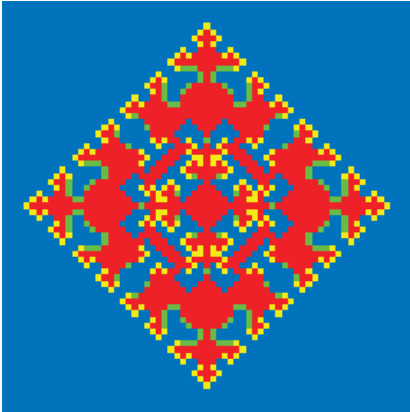
We can also distribute individual cells randomly over a two-dimensional plane. Two individuals are neighbors if their distance is less than a certain “radius of interaction,” r . Cells can differ in the number of their neighbors. The resulting random grid is, of course, closer to real-world situations than the symmetrical lattices are. The payoff of an individual is the sum over the interactions with all of its neighbors. As before, a cell is retained by its original owner or given to the most successful neighbor, whoever has the highest payoff. All cells are updated simultaneously. The evolutionary dynamics are deterministic. Cooperators survive up to certain values of r . The equilibrium frequency of cooperators depends on the initial conditions. Population dynamics on random grids are more static than on square lattices. We have not yet found games that generate spatial chaos on irregular grids. Irregularity tends to simplify dynamics.

9.7 OTHER UPDATE RULES

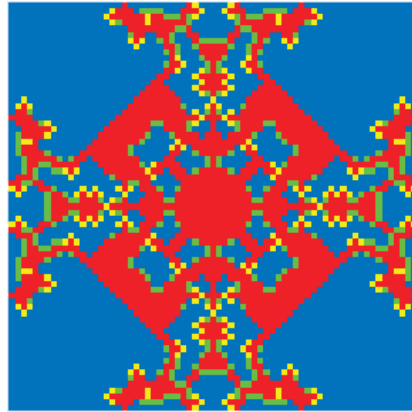
So far we have studied spatial games with entirely deterministic dynamics. Each cell is given to whoever has the highest payoff in the neighborhood, and all cells are updated in synchrony. These assumptions allowed us to study

A kaleidoscope using the
von Neumann neighborhood

$t=30$



$t=50$



$t=200$



$t=20,000$

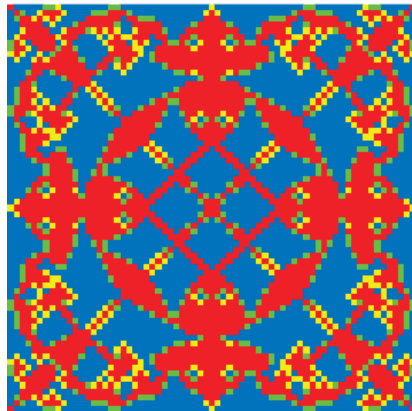


Figure 9.12 A kaleidoscope in the von Neumann neighborhood. On a square lattice, each player interacts with the four nearest neighbors. Parameter region $4/3 < b < 3/2$.

the rich mathematical properties of deterministic spatial dynamics in discrete time. We found fascinating and complicated behavior in terms of spatial chaos and dynamic fractals. Although the fate of each single cell is totally deterministic, the overall population dynamics are highly complicated.

We can also study games with stochastic transition rules. For example, a cell could become a cooperator with a probability that is given by the relative payoff of cooperators in the neighborhood.

Instead of synchronous updating, we can also investigate asynchronous updating: one player is chosen at random; its own payoff and the payoffs of all neighbors are determined. Then the player is updated. Synchronous updating means nonoverlapping generations; asynchronous updating means overlapping generations (with continuous reproduction). Asynchronous updating introduces random choice and therefore stochasticity. Figure 9.13 shows a cluster of cooperators invading a world of defectors for asynchronous updating with Moore neighborhood and $b = 1.59$.

In general, stochastic update rules display less variety in dynamical behaviors. Dynamic fractals and kaleidoscopes are not possible, because the stochastic update rules do not maintain symmetry. Stochasticity disturbs straight lines between cooperators and defectors, and irregular boundaries favor defectors.

If the spatial competition between cooperators and defectors is described by a stochastic process, then, in general, there will be only two absorbing states: all cooperators or all defectors. The system will eventually reach one of these two states, but it can take an extremely long time. In most cases, spatial games with stochastic update rules still allow the coexistence of cooperators and defectors for the lifetime of our universe.

If there are empty sites or more than two competing strategies, then spatial games can lead to spiral waves.

9.8 VIRTUALLABS

Christoph Hauert has written a beautiful programming environment that allows you to study every aspect of evolutionary games, spatial games, and games on graphs. These “VirtualLabs” can be accessed on <http://lorax.fas.harvard.edu/virtuallabs/>

Cooperators invading defectors with asynchronous updating

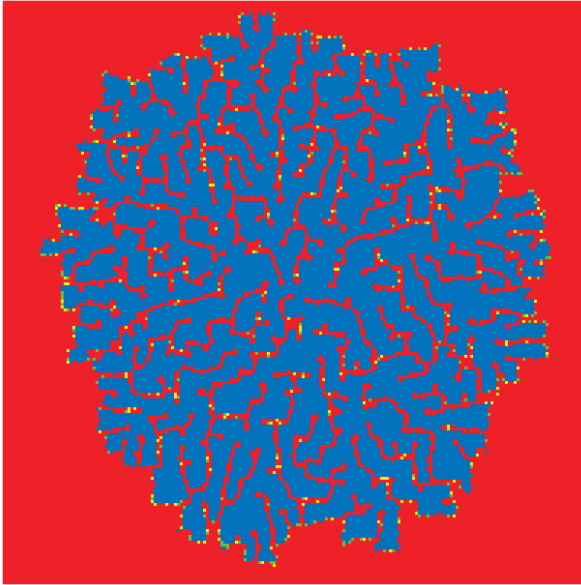


Figure 9.13 Invasion of cooperators with asynchronous updating. At each time point a random cell is chosen to be updated. Its payoff is compared with the payoff of all its neighbors. Then the cell is given to whoever has the highest payoff. This takeover rule is still deterministic, but the growth pattern is stochastic, because the cells updated in each time step are chosen randomly. The starting condition was a 3×3 cluster of cooperators in a world of defectors.

This Web page enables you to retrace the steps we have described here, but you can also make many new discoveries. VirtualLabs represent a “language” for evolutionary dynamics. Many “questions” of this language have not been asked. Many “sentences” have not been spoken. You can use the VirtualLabs to make new discoveries in many settings of evolutionary dynamics. The figures of this chapter were generated with VirtualLabs. VirtualLabs are virtually error free as they are “Swiss made.”

SUMMARY

- ◆ Evolutionary game dynamics (= frequency-dependent selection) can be studied in a spatial setting.
- ◆ In spatial games, players interact with their nearest neighbors.

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- ◆ A player keeps his current strategy or adopts one of his neighbors' strategies according to who has the highest payoff.
 - ◆ It is possible to formulate entirely deterministic spatial game dynamics.
 - ◆ In spatial games, the theory of cellular automata meets game theory.
 - ◆ In the spatial Prisoner's Dilemma, there is coexistence between cooperators and defectors.
 - ◆ Cooperators survive in clusters. This principle is called "spatial reciprocity."
 - ◆ In some parameter regions, we discover spatial chaos, dynamic fractals, and evolutionary kaleidoscopes.
 - ◆ Cooperators can invade defectors when starting from a small cluster.
 - ◆ Irregular grids tend to simplify dynamical complexity.
 - ◆ Asynchronous updating or "proportional winning" introduces stochasticity. Cooperators and defectors can nevertheless coexist for near eternity.