

## THE SPATIAL DILEMMAS OF EVOLUTION

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Evolutionary game theory can be extended to include spatial dimensions. The individual players are placed in a two-dimensional spatial array. In each round every individual “plays the game” with its immediate neighbours. After this, each site is occupied by its original owner or by one of the neighbours, depending on who scored the highest payoff. These rules specify a deterministic cellular automaton.

We find that spatial effects can change the outcome of frequency dependent selection. Strategies may coexist that would not coexist in homogeneous populations. Spatial games have interesting mathematical properties. There are static or chaotically changing patterns. For symmetrical starting conditions we find “dynamical fractals” and “evolutionary kaleidoscopes.” There is a new world to be explored.

### 1. Introduction

Cooperation is essential for evolution. Molecules cooperate to form a cell, cells cooperate to form plants or animals. Animals cooperate in families to raise their young or in foraging groups to prey or to reduce the risk of predation. Altruistic acts are commonly observed in the animal world. Even scientists sometimes cooperate.

Cooperation may be difficult to achieve in a classic Darwinian framework. Cooperators have to succeed in the struggle for survival with defectors, who by definition have a certain fitness advantage. Three main theories have been put forward to explain the evolution of cooperation:

- (i) Cooperation may be a promising option among relatives. Here an altruistic act may pay off because it favours the survival of one’s own genes. This is Hamilton’s [1964] kin selection theory.
- (ii) Cooperation between nonrelatives can be explained by reciprocal altruism [Trivers, 1971; Axelrod & Hamilton, 1981]. This works if two individuals are likely to meet more than once and if there is some chance that a cooperative move may be reciprocated in the next round.

The famous metaphor for this reciprocal altruism is the Prisoner’s Dilemma [Axelrod & Hamilton, 1981; Axelrod, 1984; Wilkinson, 1984; Lombardo, 1985; Molander, 1985; May, 1987; Milinski, 1987; Axelrod & Dion, 1988; Nowak & Sigmund, 1992].

- (iii) Cooperation may also evolve if selection works on the level of groups rather than individuals [Williams, 1966; Wilson, 1980]. Thus groups with more cooperators are more likely to survive. This explanation requires a mechanism to assure that whole groups are indeed the unit of selection and that individuals cannot easily jump between groups. This kind of explanation usually requires that populations are genetically structured in particular ways and that such structuring of sub-populations is maintained.

There are often no clear border lines among these three mechanisms. They are approaches to the same phenomena. If individuals live in groups then it is likely that relatedness within a group is larger than between groups. In the same way reciprocal altruism may occur more often between

individuals living in the same group and/or related individuals.

In this paper we explore to what extent spatial effects may, by themselves, be sufficient for the evolution of cooperation. We develop a new mathematical framework to study evolutionary game theory in a spatial context [Nowak & May, 1992].

Classical evolutionary game theory [Maynard Smith, 1982; 1989] does not include the effect of spatial structures of populations. Different individuals (strategies) interact with each other in proportion to their relative frequency in the population. The payoff of the game is then related to the reproductive success. The resulting dynamics is typically described by the time continuous game dynamical equation [Taylor & Jonker, 1979].

$$\frac{dx_i}{dt} = x_i \left( \sum_{j=1}^n A_{ij} x_j - \sum_{i=1}^n x_i \sum_{j=1}^n A_{ij} x_j \right).$$

$$i = 1, \dots, n$$

Here  $x_i$  is the frequency of strategy  $i$  and  $A_{ij}$  is the payoff to strategy  $i$  in the game with strategy  $j$ . There are  $n$  different strategies. An extensive mathematical treatment of this and similar equations is given by Hofbauer & Sigmund [1988].

In this paper we develop the idea, first suggested by Axelrod [1984], of placing the individual "players" in a two-dimensional spatial array. In each round every individual "plays the game" with its immediate neighbours. After this, each site is occupied either by its original owner or by one of the neighbours, depending on who scores the highest total payoff in that round. This theory serves as a deterministic framework of an aspect that has been largely neglected in models of evolutionary biology: the direct effect of spatial structures upon population organisation and frequency dependent selection (i.e., "spatial evolutionary game theory").

One of the simplest and yet most interesting games of evolution is the Prisoner's Dilemma (PD). The simple PD is a game with two players, each having two options:  $C$  (to cooperate) and  $D$  (to defect). If both players cooperate, both obtain  $R$  points; if both defect, both receive  $P$  points each; if one player defects and the other cooperates, the defector gets the highest payoff,  $T$  and the cooperator the lowest payoff  $S$ . We have  $T > R > P > S$ . It is obvious that strategy  $D$  is dominant, in the sense that it is best, no matter what the other player

does. In the absence of any spatial structure the defectors will necessarily be favoured by selection and out-compete the cooperators. (Usually it is also assumed that  $2R > T + S$ , otherwise an agreement to alternate  $C$  or  $D$ , out of phase, beats cooperation, thus clouding the analysis. But this is not essential.)

Most of the recent work on the PD has dealt with the interactions between various strategies (such as tit-for-tat) when players who recognise each other meet repeatedly (see Axelrod & Dion [1988]) or with ensembles of strategies and the effects of occasional errors (Nowak & Sigmund, 1989, 1990, 1992; Nowak, 1990). In contrast to Axelrod (who considered "all  $D$ " versus "tit for tat," and other interactions among strategies played by players with memories of past encounters), our approach to games in spatial arrays neglects all strategical complexities or memories of past encounters and considers only two simple kinds of individuals: those who cooperate and those who defect. We will show that these cooperators and defectors can coexist either in static irregular patterns or in dynamic patterns with chaotic fluctuations around predictable long-term averages.

The PD is not the only evolutionary game that can be played with spatially structured interactions. Other game theoretical metaphors display equally interesting dynamics. In the Hawk-Dove game [Maynard Smith, 1982] the payoff for a hawk interacting with another hawk is less than the payoff for a dove interacting with a hawk; and similarly a dove gets less from another dove than a hawk gets from a dove. This gives rise to an equilibrium between both strategies even in the absence of spatial effects. We will show that the spatial version of the Hawk-Dove game generates intricate and mathematically interesting patterns.

We find in general that spatial chaos and dynamic fractals are typical features of spatial evolutionary game theory (i.e., evolutionary games played with neighbours on spatial lattices). For symmetric initial conditions we find "evolutionary kaleidoscopes."

Our "spatial games" are cellular automata. These are originally due to John von Neumann [1966] and have recently received a lot of interest [Wolfram, 1984; Langton, 1986; Toffoli & Margulós, 1987; Chua & Yang, 1988]. One of the most fascinating cellular automata is Conway's "Game of Life" (see Berlekamp, Conway & Guy [1982], Poundstone [1985]).

## 2. The Rules of Spatial Games

Let us imagine that populations are not completely homogeneous but have certain spatial structures. Let us imagine that animals or molecules are located at certain positions (territories, patches, pixels or cells) and are more likely to interact with their neighbours (= individuals at a closer distance). Therefore the probability that a certain phenotype,  $A$ , interacts with another phenotype,  $B$ , is no longer just the product of their relative frequencies in the population, but depends in a nontrivial way on the spatial structure of the population.

Let us consider two different strategies  $C$  (for cooperation) and  $D$  (for defection). Their interaction is described by the following payoff matrix (which is a simplification of the more general PD matrix defined earlier):

	$C$	$D$
$C$	1	0
$D$	$b$	0

If two cooperators interact both receive 1 point. If a defector "exploits" a cooperator, the defector receives the payoff  $b$  and the cooperator 0. The interaction between two defectors also leads to the zero payoff. This game is designed to keep things as simple as possible. In fact there is only one parameter,  $b$ , the advantage for defectors.

This game is now played on a two-dimensional square lattice. Each position is occupied either by a cooperator or a defector. In each generation the payoff of a certain individual is the sum over all interactions with the 8 nearest neighbours (the cells corresponding to the chess king's move) and with its own site. It seems reasonable to include this self-interaction, if one assumes that several animals (a family) or molecules may occupy a single patch. But the general properties of the game do not depend on this assumption, and we will also explore the situation without self-interaction.

Let us consider two examples. A cooperator surrounded by 8 cooperators receives the payoff 9, a defector surrounded by 8 cooperators receives the payoff  $8b$ .

In the next generation, an individual cell is occupied with the strategy that received the highest payoff among all the 8 immediate neighbours of the cell and, of course, the cell itself. Thus whatever happens to a cell depends on the state of the cell, the 8 neighbours and their neighbours. These are altogether 25 different cells. In the terminology of

the cellular automata literature, our simple game is characterised by a transition matrix with  $2^{25}$  different rules. That is, in cellular automata terms, the rules are very complex; our underlying biological "game," however, enables the rules to be stated very simply.

The rules of our game are now completely defined. The game is deterministic. The outcome depends on the initial configuration and the magnitude of the parameter  $b$ .

Figure 1 shows the time evolution of the frequency of cooperators,  $x$ , starting with the same random initial condition, but for different values of the parameter  $b$ . This simulation is performed on a  $20 \times 20$  square lattice with periodic boundary conditions. This toroidal world is chosen to get rid of any boundary effects. Later we will also consider situations with fixed boundary conditions. The initial configuration is obtained at random by assigning a cooperator to an individual cell with probability 0.9. Thus in the beginning we have  $x_0 \approx 0.9$ . The behavior is quite similar for  $b = 1.13, 1.15, 1.17$  and  $1.21$ . Initially the frequency of cooperators decreases to about  $x \approx 0.6$ , then the system oscillates with period 2 at around  $x \approx 0.9$ . For  $b = 1.26$  we obtain an equilibrium without oscillations;  $b = 1.30$  and  $b = 1.35$  both settle to a period 2 oscillator after about 20 to 25 generations;  $b = 1.45$  goes to a period 3 oscillator;  $b = 1.55$  needs some 120 generations to settle finally to a period 24 oscillator;  $b = 1.65$  also oscillates with period 24;  $b = 1.79$  goes to a 6 generation oscillator with very low amplitude;  $b = 1.85$  looks completely irregular and chaotic (with a time average of around  $\bar{x} \approx 0.31$ ).

Is it possible to understand this behaviour?

### 2.1. The different parameter regions

The dynamical behaviour of the system depends on the magnitude of the parameter  $b$ . The discrete nature of the possible payoff totals means that there are only discrete transition points for  $b$  that influence the dynamics. For  $1 < b < 3$  these transitions occur at  $9/8, 8/7, 7/6, 6/5, 5/4, 9/7, 8/6, 7/5, 6/4, 8/5, 5/3, 7/4, 9/5, 2, 9/4, 7/3, 5/2, 8/3$ .

#### 2.1.1. The growth of $D$ structures

At first we study the fate of a single isolated defector surrounded by cooperators. If  $b < 1$  such a defector will vanish. If  $1 < b < 9/8$  the defector will neither grow nor disappear. If  $9/8 < b < 7/5$  the defector will grow to form a  $3 \times 3$  cluster of defectors, which will return to a single defector in

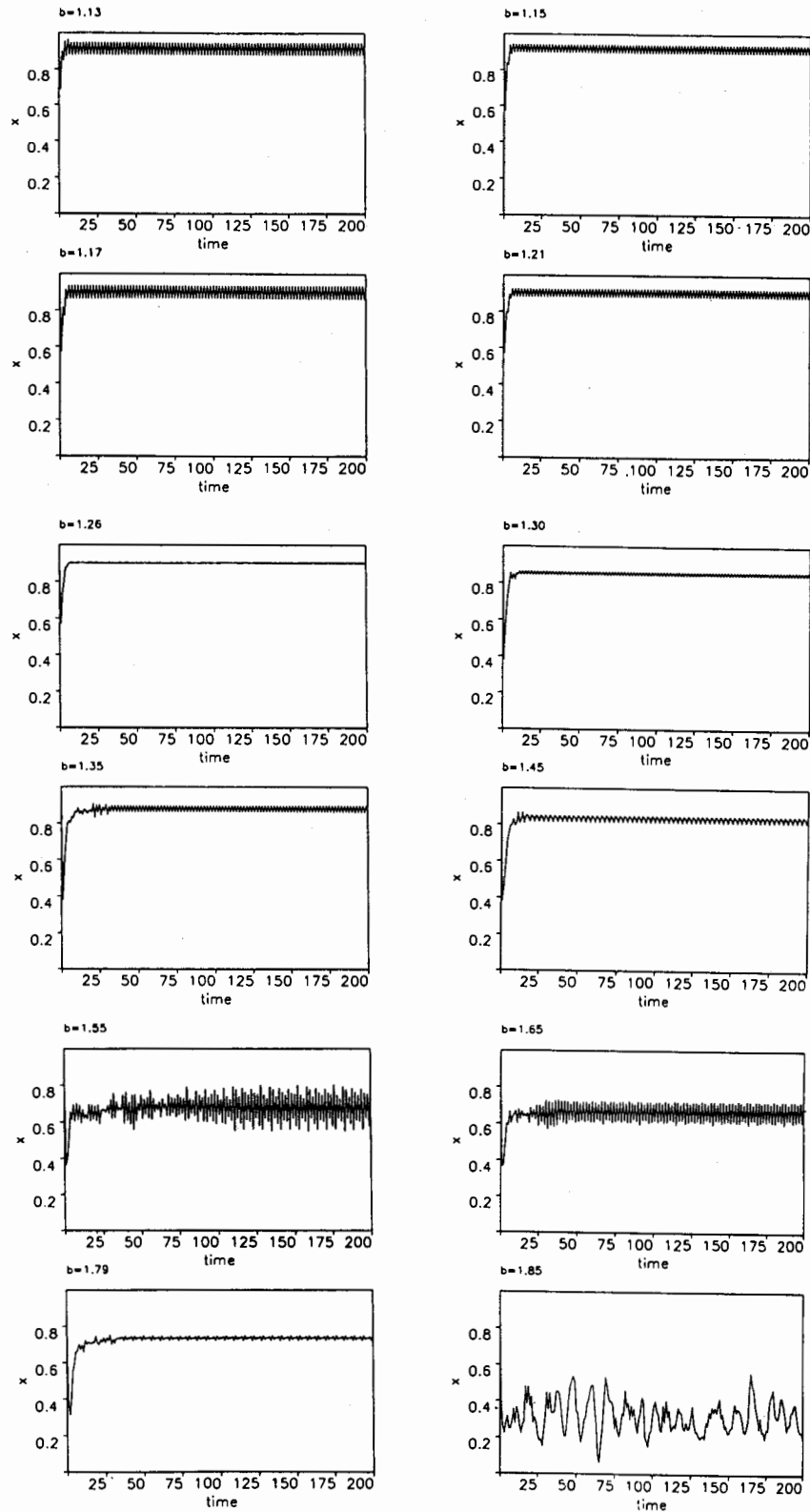


Fig. 1. The frequency of cooperators in a spatial Prisoner's Dilemma (PD) over 200 generations for different values of  $b$ , the advantage for defectors. Each simulation is performed on a  $20 \times 20$  square lattice with periodic boundary conditions. (The sides of the square fold over to form a torus.) All the simulations start with the same random initial configuration (with the initial frequency of cooperators  $x_0 = 0.9$ ). For  $b = 1.13, 1.15, 1.17, 1.21, 1.30, 1.35$  the system settles to a period 2 oscillator;  $b = 1.26$  leads to an equilibrium without oscillations; for  $b = 1.45$  we find a period 3 oscillator;  $b = 1.55$  and  $1.65$  converge to different period 24 oscillators;  $b = 1.79$  oscillates with period 6 and  $b = 1.85$  looks completely chaotic. For  $b = 2.01$  we find an equilibrium at a very low concentration of cooperators.

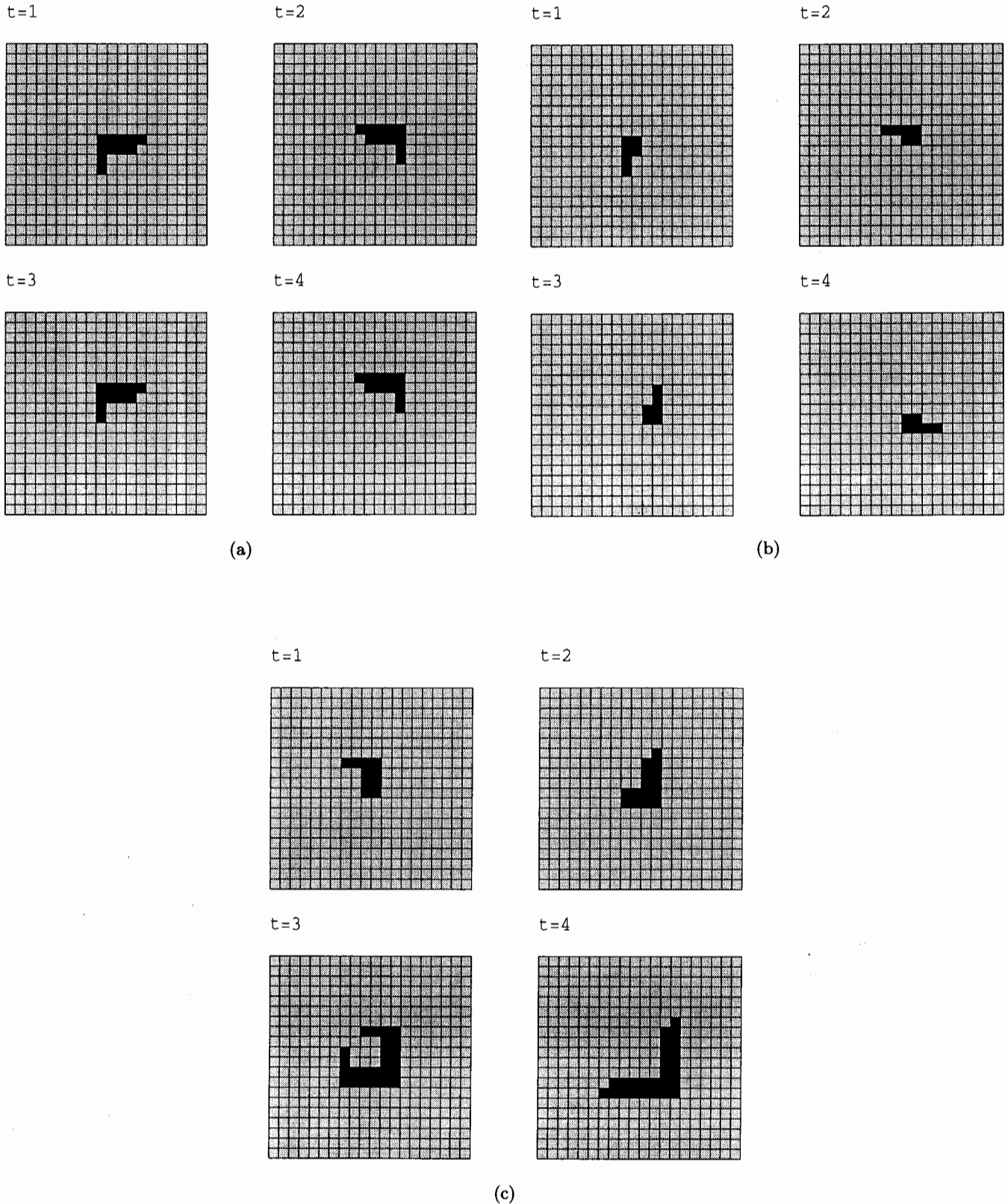
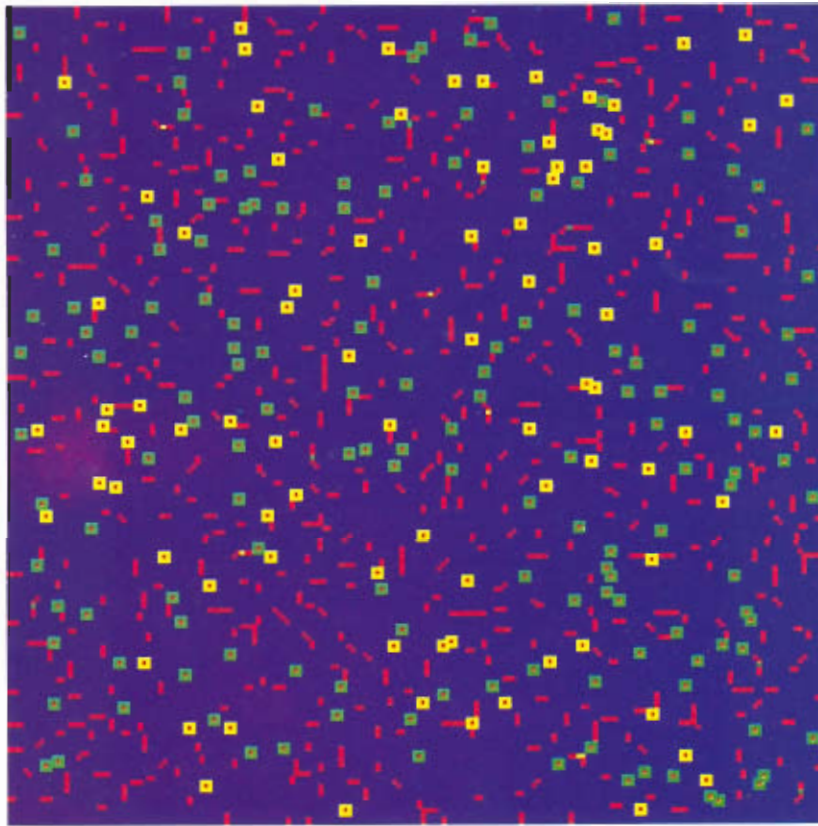


Fig. 2. (a) The “glider” is a structure that consists of 11 cooperators that moves in a world of defectors. The speed of the glider is one step per generation (4 times faster than Conway’s glider in his Life). The tail is rotating. Glider collisions can lead to amusing outcomes (like in real ‘Life’). The glider exists for  $1.4 < b < 2$ . (b) A ‘rotator’ is a structure of 6 cooperators entirely surrounded by defectors. It rotates 90 degree per generation (either to the left or to the right). A rotator exists for  $1.25 < b < 2$ . Both gliders and rotators are frequently formed out of random initial configurations. (c) A ‘grower’ is a cluster of 10 cooperators. Its fate is shown in Fig. 7. Here  $b = 1.79$ . Colour code: cooperators black, defectors white.

But whenever two such clusters come too close, the defectors between them get high payoffs and start to grow. The cooperators win along straight lines, the defectors win along irregular boundaries. The result is a dynamic equilibrium. It is an always changing, but dynamically stable dimorphism. For  $b = 2.01$  another static pattern is observed.

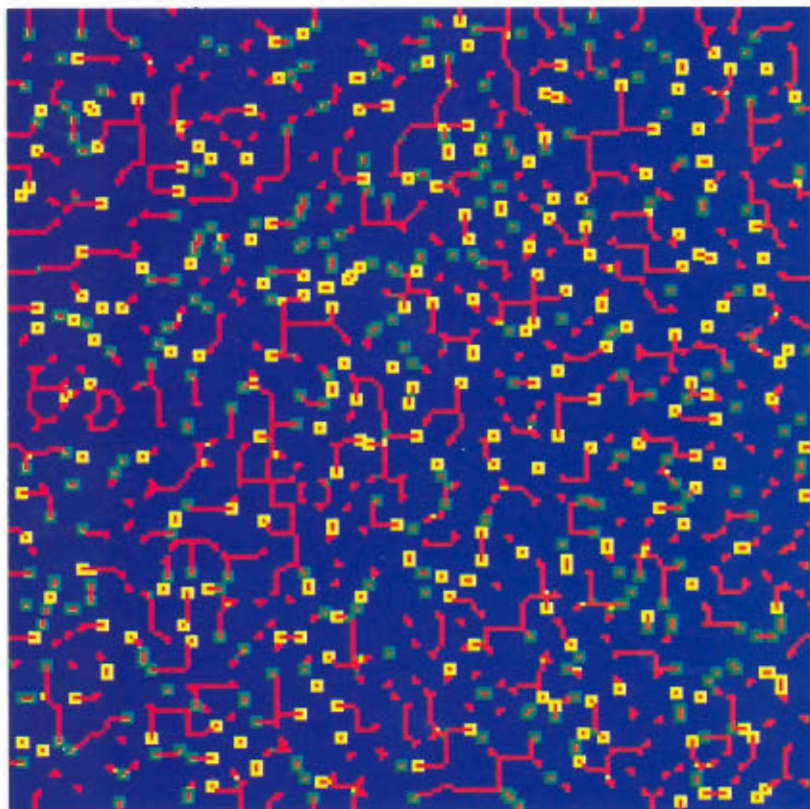
### 2.1.3. The frequency of cooperators

For very low initial frequencies of defectors, it is straightforward to calculate the approximate equilibrium frequencies (as long as  $b < 1.8$ ). This can be done by assuming that most of the defectors will occur in single isolated cells. In this case we know

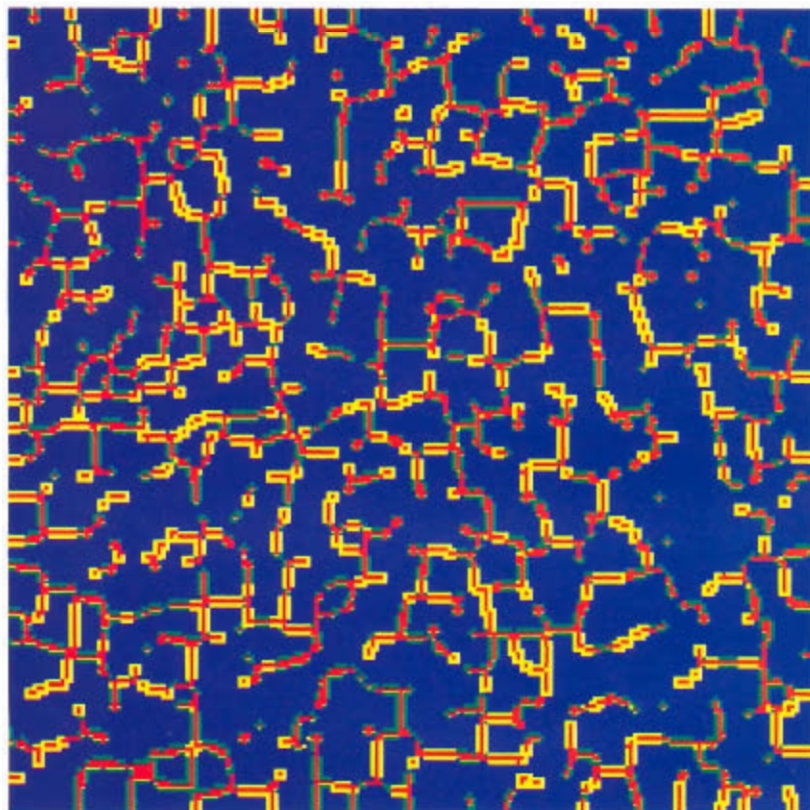


(a)  $b = 1.15$

Fig. 3. The spatial Prisoner's Dilemma can generate a large variety of qualitatively different patterns, depending on the magnitude of the parameter,  $b$ , which represents the advantage for defectors. This figure shows some examples. All simulations are performed on a  $200 \times 200$  square lattice with fixed boundary conditions. All simulations start with the same random initial configuration with 10% defectors (and 90% cooperators). The figure shows the asymptotic pattern after 100 generations. The colour-coding is as follows: blue represents a cooperator ( $C$ ) that was already a  $C$  in the preceding generation; red is a defector ( $D$ ) following a  $D$ ; yellow a  $D$  following a  $C$ ; and green a  $C$  following a  $D$ . The amount of green and yellow indicates how many cells are changing from one generation to the next. A purely red and blue pattern is static. (a) For  $b = 1.15$  there are isolated points of defectors, which oscillate with period 2 (the  $1D \rightarrow 9D \rightarrow 1D$  oscillator). There are also isolated lines of defectors, which do not oscillate. Most of the cells are cooperators. (b) The lines of defectors are more connected for  $b = 1.35$ . The end of lines oscillate with period 2. (c) For  $b = 1.55$  lines of defectors are connected and oscillate. There are large connected structures of defectors, which form high period oscillators. (d) An irregular, but static pattern emerges if  $1.75 < b < 1.8$ . The equilibrium frequency of  $C$  depends on the initial conditions, but is usually between 0.7 and 0.95. (e) Spatial chaos characterises the region  $1.8 < b < 2$ . The large proportion of yellow and green indicates many changes from one generation to the next. Both  $C$ -clusters can invade  $D$ -regions and vice versa. This leads to an always changing, dynamically stable coexistence between  $C$  and  $D$ . The frequency of  $C$  is (almost) completely independent of the initial conditions and is around 0.32. (f) Another static pattern is generated for  $b = 2.01$ . Here most of the cells are occupied with defectors. Cooperators form stable clusters. Conditions:  $200 \times 200$  square lattice, fixed boundaries, 8 neighbours plus self-interaction, random initial configurations, initial frequency of cooperators  $x_0 = 0.9$ .

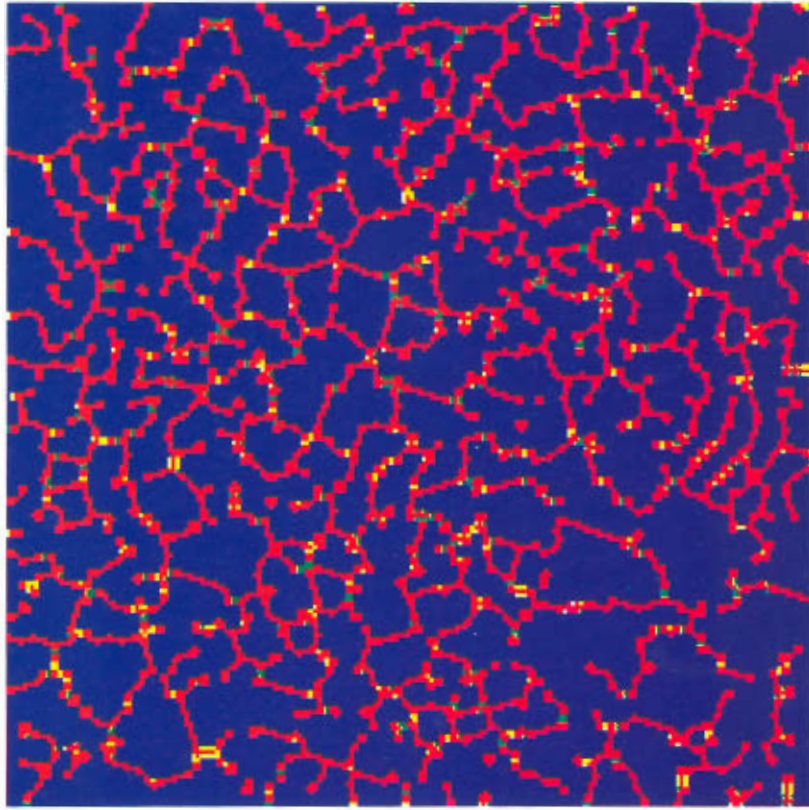


(b)  $b = 1.35$

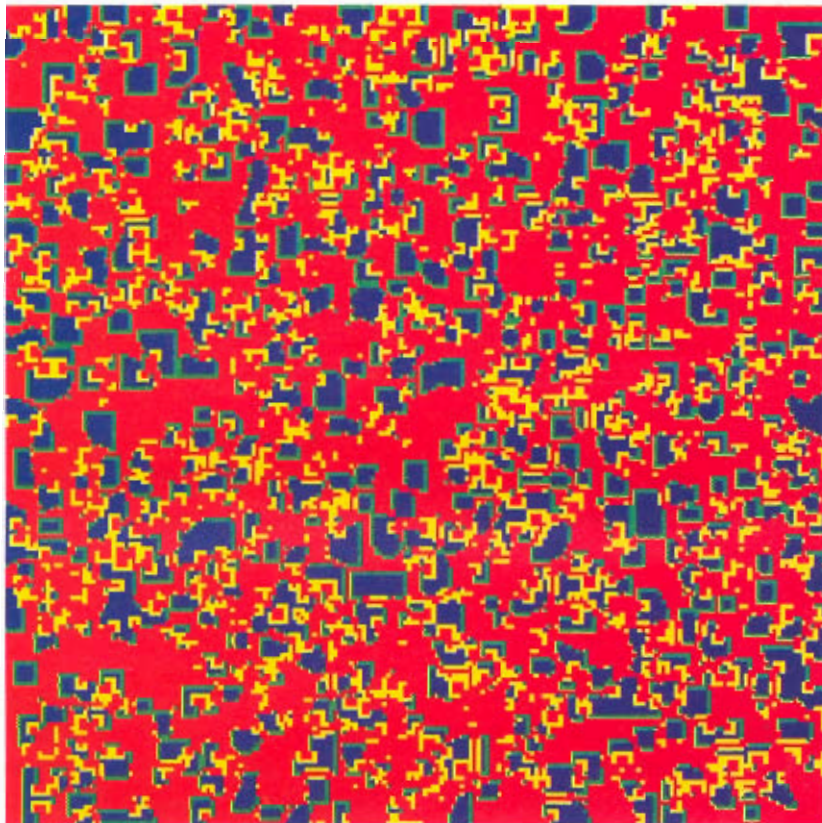


(c)  $b = 1.55$

Fig. 3. (*Continued*)



(d)  $1.75 < b < 1.8$



(e)  $1.8 < b < 2$

Fig. 3. (Continued)

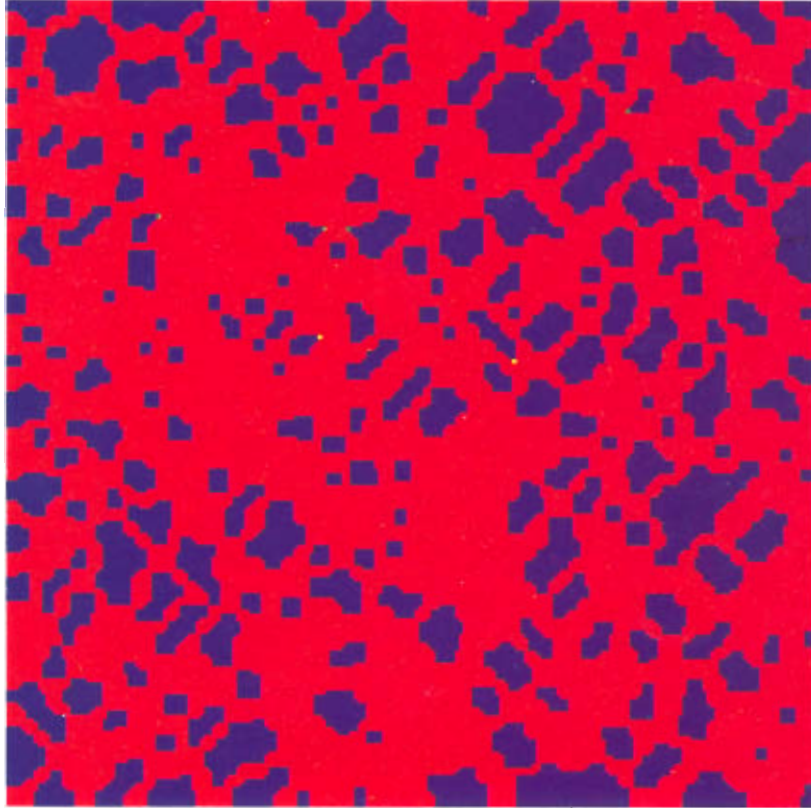
(f)  $b = 2.01$ 

Fig. 3. (Continued)

exactly the fate of each individual  $D$ . Let  $y_0$  denote the initial frequency of defectors, and  $\bar{y}$  the equilibrium frequency (or time average) of defectors. For  $b < 1$  we have  $\bar{y} = 0$ . The following results hold for very small values of  $y_0$ . For  $1 < b < 9/8$  we have  $\bar{y} = y_0$ . If  $9/8 < b < 7/5$  we have  $\bar{y} = 5y_0$ . This is the time average of the  $1D \rightarrow 9D \rightarrow 1D$  oscillator. If  $7/5 < b < 8/5$  we find again that  $\bar{y} = 5y_0$ . This is the time average of the  $1D \rightarrow 9D \rightarrow 5D \rightarrow 1D$  oscillator. If  $8/5 < b < 9/5$  we have  $\bar{y} = 9y_0$ , because all single defectors turn into stable  $3 \times 3$  squares. If  $9/5 < b$  a single defector gives rise to growing structures, and the calculation of the equilibrium frequency of cooperators becomes nontrivial (and will be discussed in Sec. 4).

We do not attempt to calculate the equilibrium frequencies of cooperators in the simulations that start with a larger fractions of defectors. For a random initial configuration the defectors are always at an advantage, because they find themselves in the neighbourhood of many cooperators. Many cooperators disappear in the first two generations. Connected structures of defectors arise and the situation

becomes difficult. Random fluctuations may leave us with a few  $C$ -clusters that cannot grow, like gliders or rotators or with a simple  $C$ -square that grows to win the whole world. For  $1 < b < 1.8$  most initial conditions lead to cooperator frequencies somewhere between 0.7 and 0.95. For  $1.8 < b < 2$  most initial conditions lead to cooperator frequencies around 0.3.

### 3. The Invasion of Defectors: An Evolutionary Kaleidoscope

An interesting sequence of patterns emerges if a single defector invades a world of cooperators in the parameter region  $1.8 < b < 2$ . In generation  $t = 0$  we start with one defector. This defector first grows to form a  $3 \times 3$  and then a  $5 \times 5$  square of defectors. The payoff for the defectors at the 4 corners of this square is  $5b$  (which is larger than 9). The payoffs for the defectors 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. The result is an interesting and beautiful growth pattern. We can study these patterns in a finite

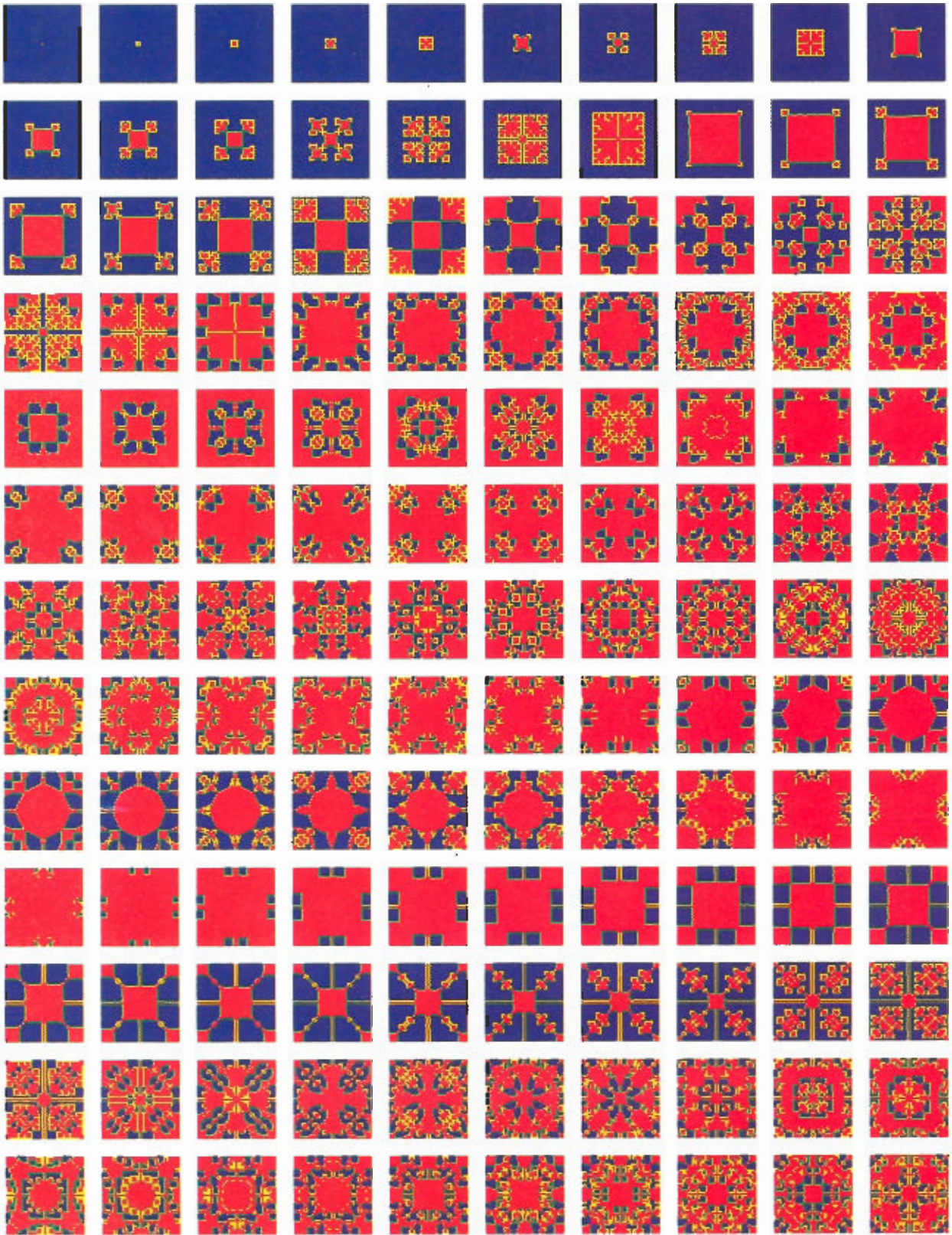


Fig. 4. Spatial games can generate “kaleidoscopes.” These are long (but finite) sequences of different patterns (on a finite array). The initial symmetry is always maintained, because the transition rules of our games are symmetric. The frequency of individual strategies in subsequent generations oscillates in a chaotic way. The final state of such a kaleidoscope is also quite “unpredictable” (see Table 1). This picture shows generations  $t = 0 - 179$ , starting with a single defector invading a  $49 \times 49$  array of cooperators. There are fixed boundary conditions and  $b = 1.85$ . The colour code is the same as in Fig. 3 (and throughout the paper). These “evolutionary kaleidoscopes” combine chaos (unpredictability) and symmetry.

world (with fixed or cyclic boundary conditions) or in an — effectively — infinite world.

Figure 4 shows the “evolutionary kaleidoscope” that is generated by a single defector invading a finite array of  $49 \times 49$  cooperators with fixed 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 cannot continue forever. What is the eventual fate of such a kaleidoscope? The total number of possible states is only finite (although very large: for an  $n \times n$  array we have approximately  $2^{n^2}/8$  different configurations). The kaleidoscope must eventually converge to some oscillator with finite period (this can also be a fixed point). Smaller kaleidoscopes eventually go to a state where all cells are occupied with defectors. This “all- $D$ ” state is an absorbing state, which means, once you are there you will remain there. Table 1 shows the number of generations required to go to an all- $D$  state for kaleidoscopes with different sizes. This sequence is quite fun. Would you expect that a  $49 \times 49$  kaleidoscope takes 1140 generations to go to an all- $D$  state, but a  $59 \times 59$  only 33 generations? And what happens if a single defector invades a  $57 \times 57$  world? It never goes to an all- $D$  state. Quite contrary, it goes to almost an all- $C$  state. After 4770 generations there is a single cross of 113 defectors left over. This oscillates with period 2. All other cells are cooperators. A  $61 \times 61$  kaleidoscope takes 3900 generations to generate a pattern consisting of 48 cooperators in a world of defectors.

Another absorbing state is the all- $C$  state. But this state can never be reached by a kaleidoscope that starts with a defector in the center, because this defector can never be replaced by a cooperator. This follows from symmetry arguments. If this central defector is to be replaced by a cooperator, then it must have cooperators in its neighbourhood. It can either have 8 or 4 cooperators as immediate neighbours. In the first case its payoff would be  $8b$ , which is larger than anything a cooperator can achieve. In the second case its payoff is only  $4b$ , but the cooperators can only get payoff 6, which is less. Hence the defector in the center will persist indefinitely. Thus the all- $C$  state can never be reached.

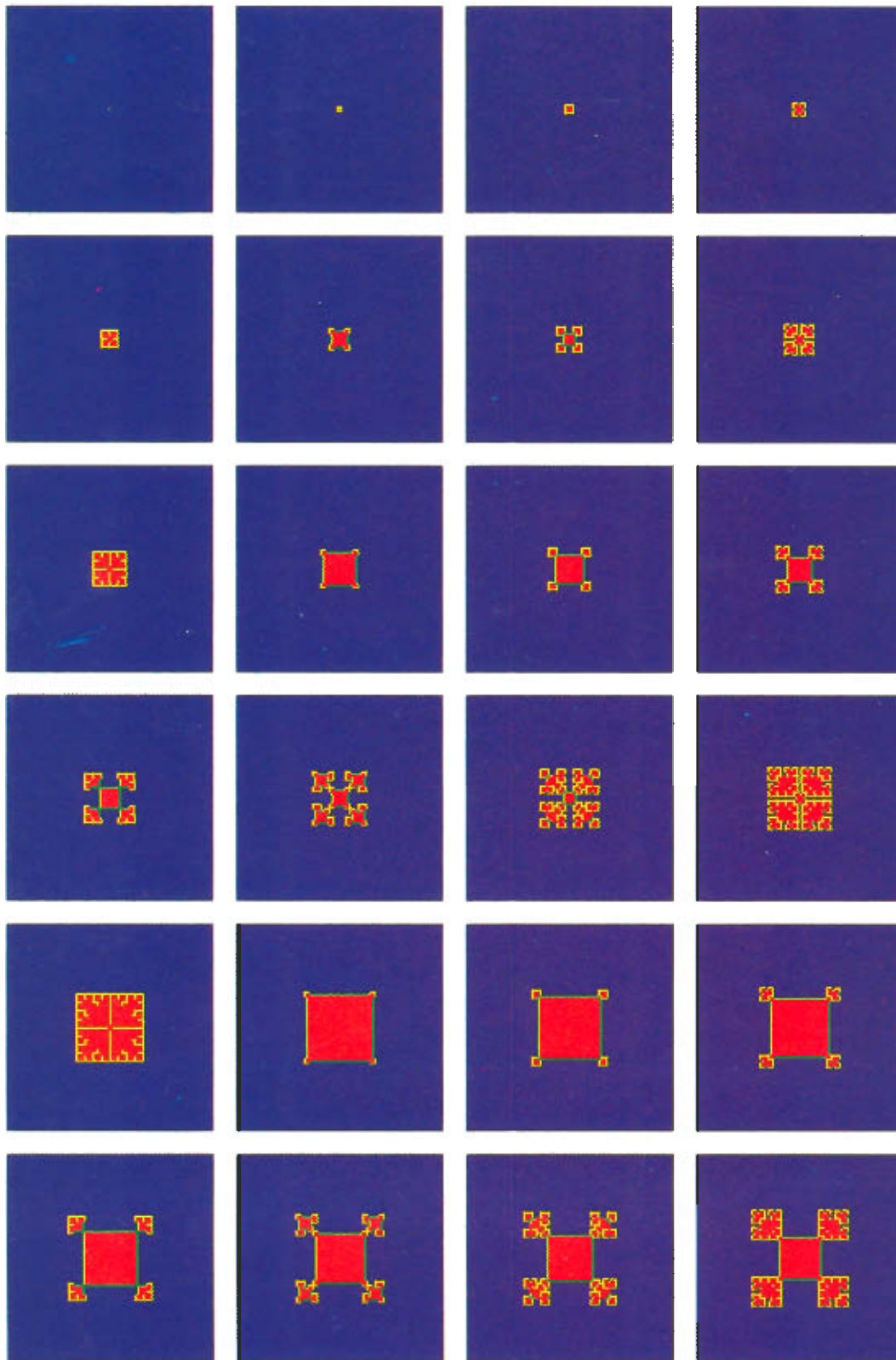
The interesting mathematical features of these kaleidoscopes arise from a combination of simplicity (the rules), deterministic unpredictability (the eventual fate), transient chaos (the frequency of

Table 1. What happens to kaleidoscopes in the long run?

Size ( $n \times n$ ) $n =$	Goes to all- $D$ after $t$ Generations $t =$
1	0
3	1
5	2
7	3
9	4
11	5
13	8
15	8
17	8
19	9
21	28
23	19
25	18
27	17
29	49
31	16
33	16
35	17
37	76
39	47
41	97
43	111
45	180
47	143
49	1140
51	never (after $t = 737$ , period 2)
53	331
55	752
57	never (after $t = 4770$ , period 2)
59	33
61	never (after $t = 3900$ , fixed point)
63	33
65	33
67	33
69	? (no period for $t < 10000$ )
71–97	? (not all- $D$ for $t < 5000$ )

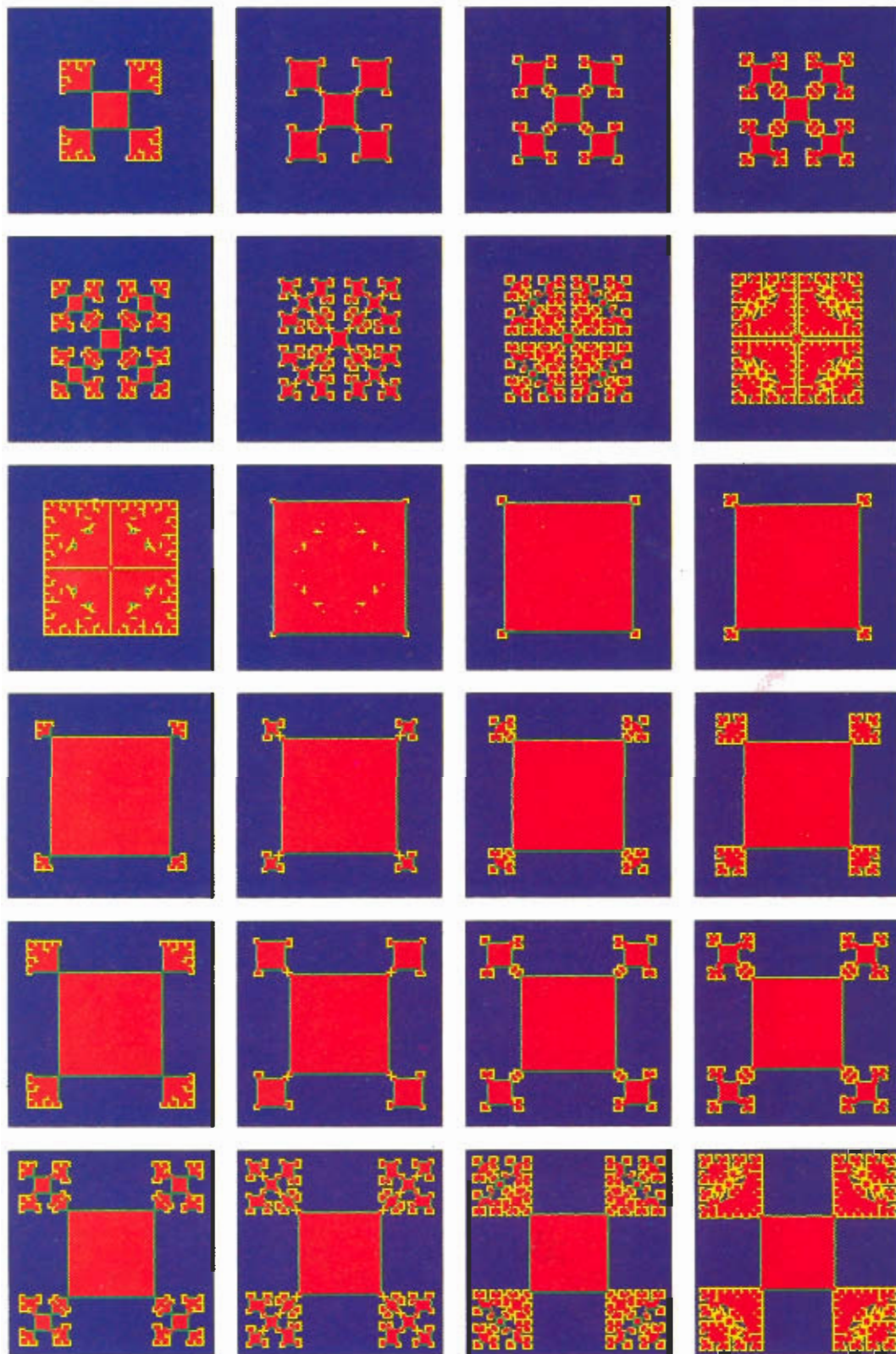
cooperators) and — for some special cases — symmetry (beauty).

Of similar interest is the case when a single defector invades an infinitely large array of cooperators (Fig. 5). There are fractal like structures that repeat themselves. The whole  $D$ -structure takes a square shaped form always at the generations which are the powers of 2. For  $t = 0, 1, 2, 4, 8$  and 16



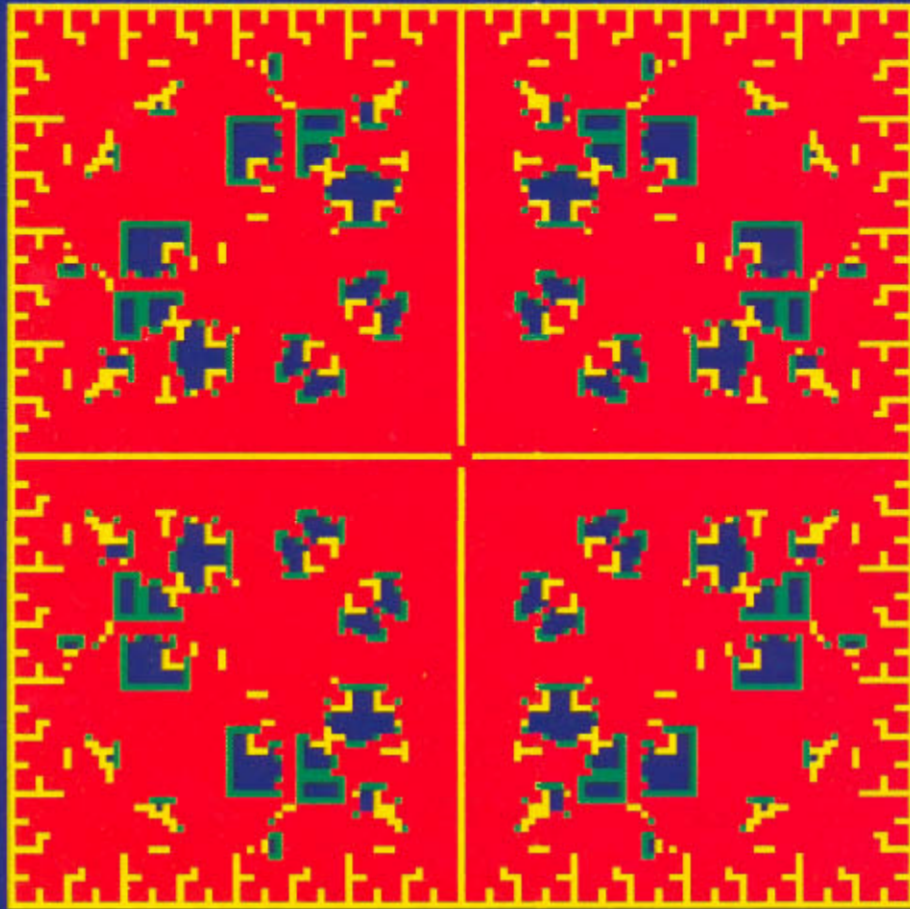
(a)

Fig. 5. A dynamic fractal is generated if a single defector invades a world of cooperators. The figure shows the generations  $t = 0 \sim 47$  and  $t = 64, 96, 128, 160, 192, 256$ . Conditions: square lattice, no boundaries, 8 neighbours plus self-interaction, parameter region  $1.8 < b < 2$ .



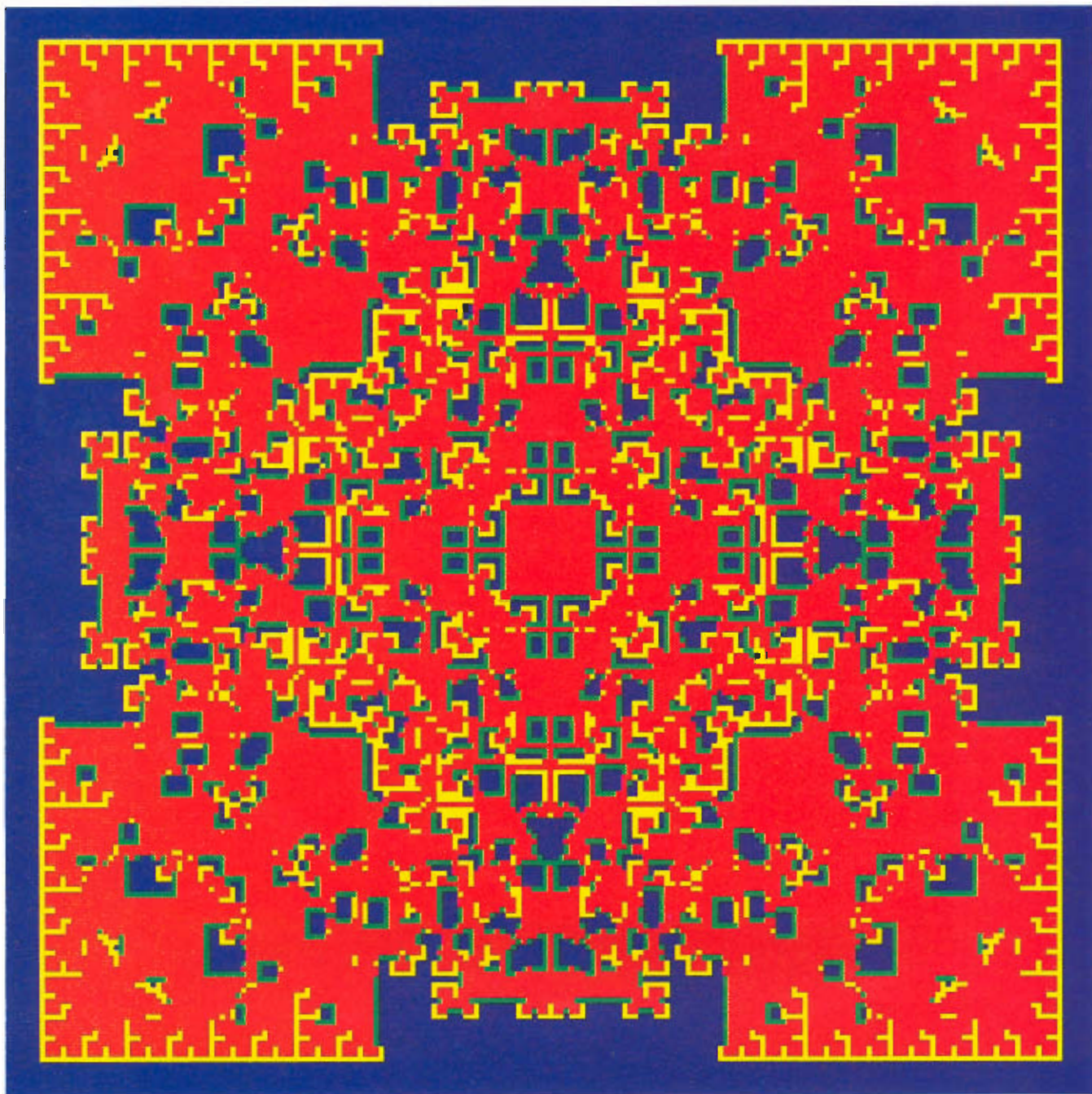
(b)

Fig. 5. (Continued)



(c)

Fig. 5. (Continued)



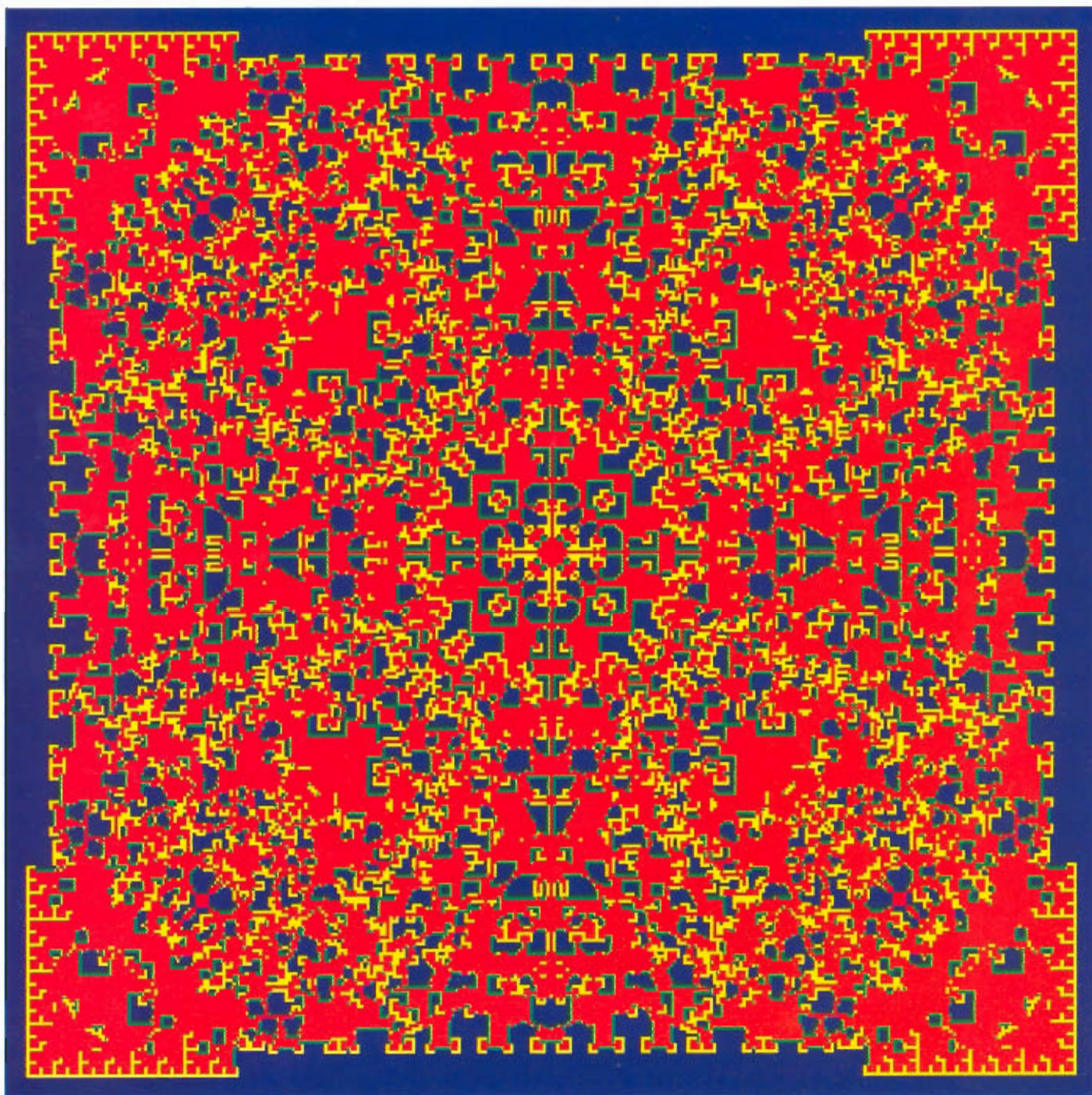
(d)

Fig. 5. (*Continued*)



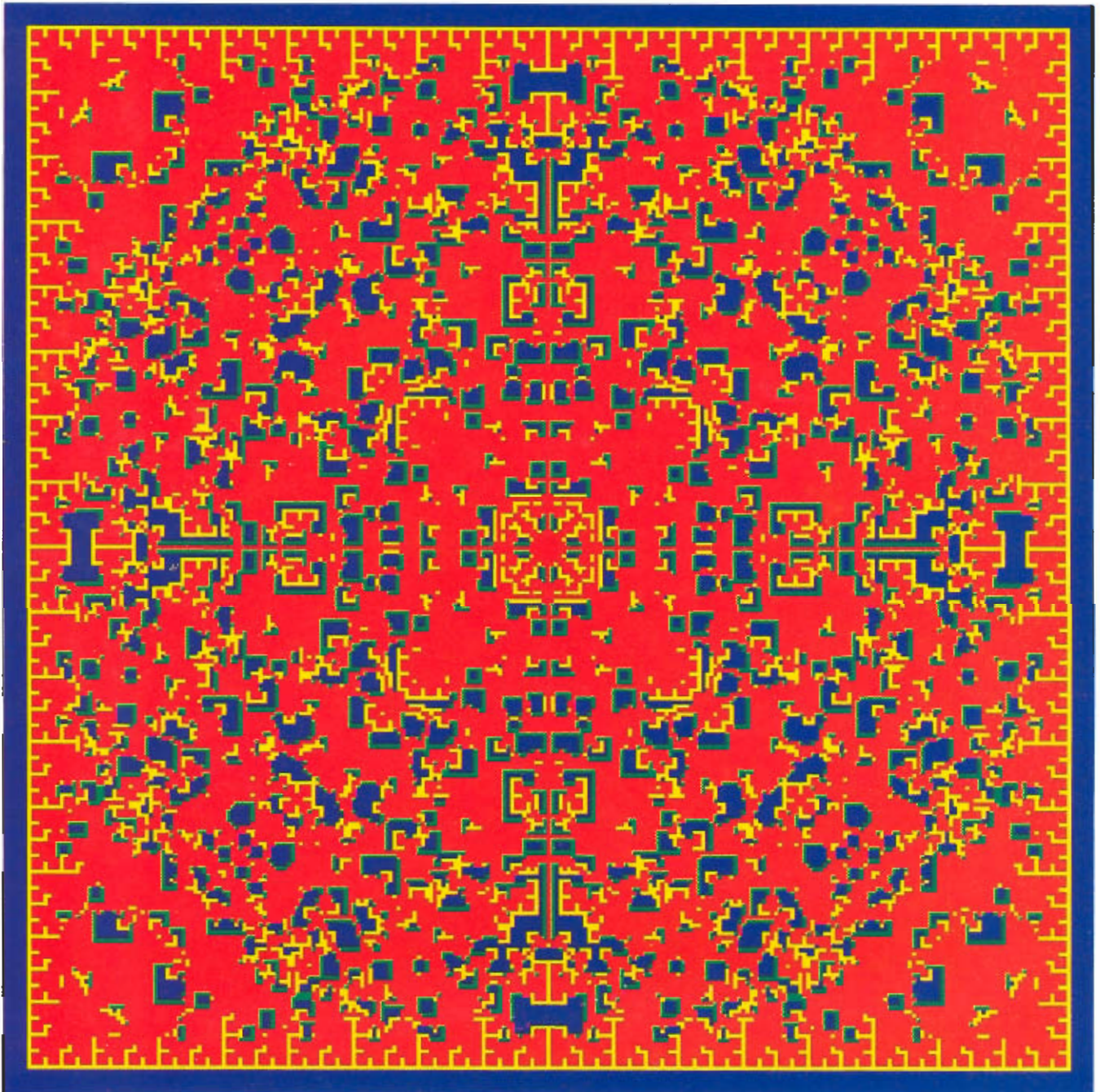
(e)

Fig. 5. (Continued)



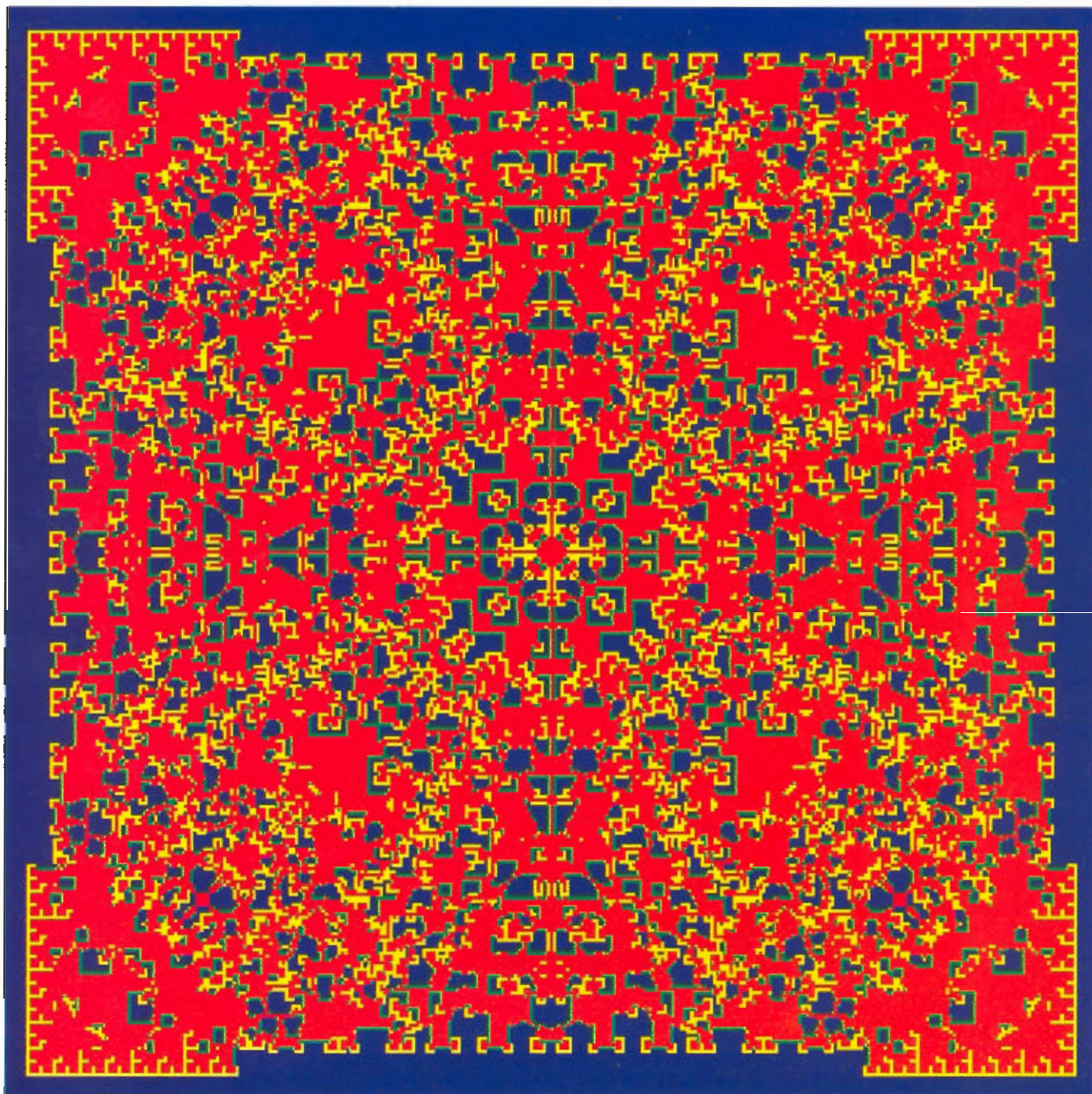
(f)

Fig. 5. (Continued)



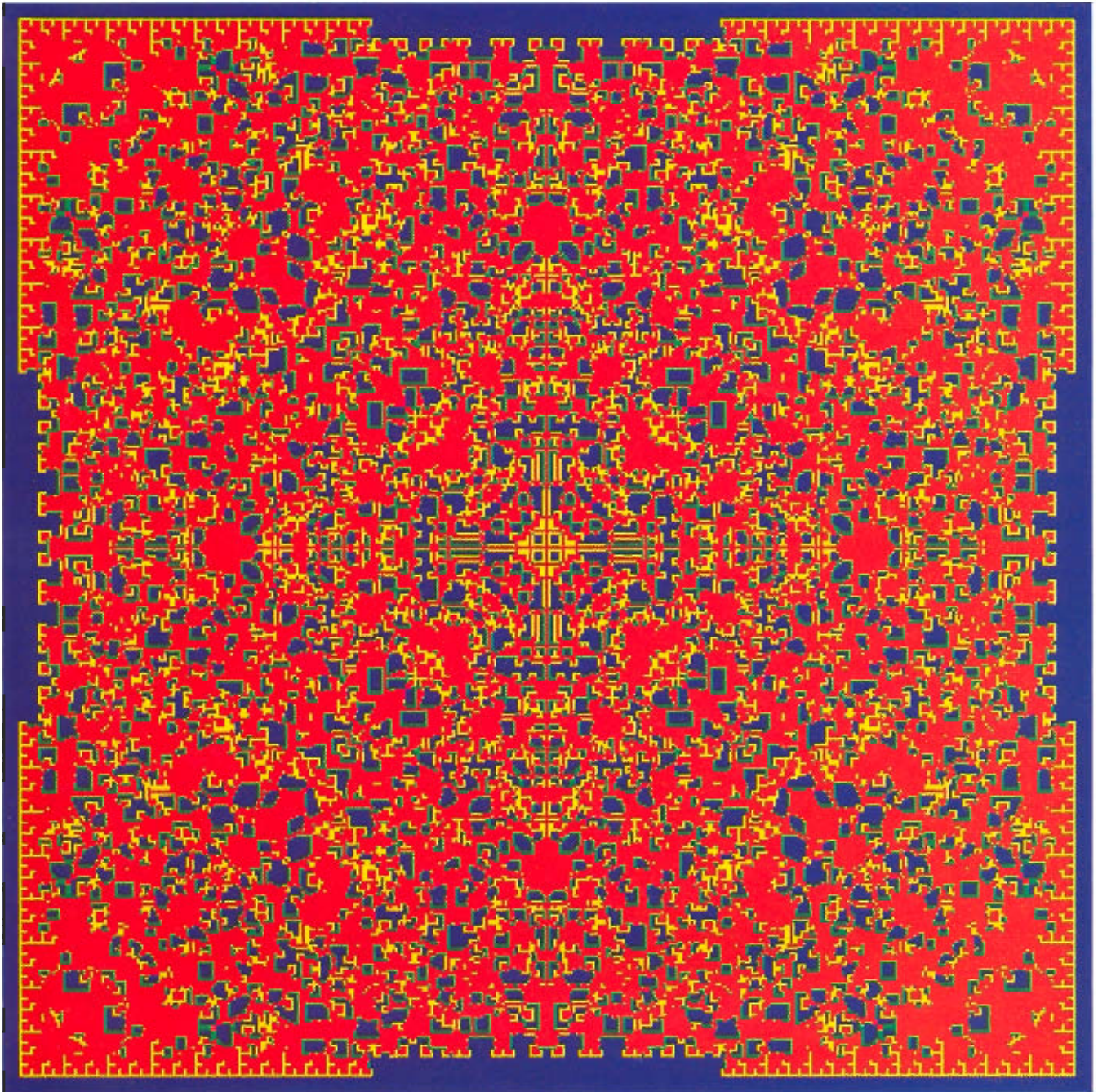
(e)

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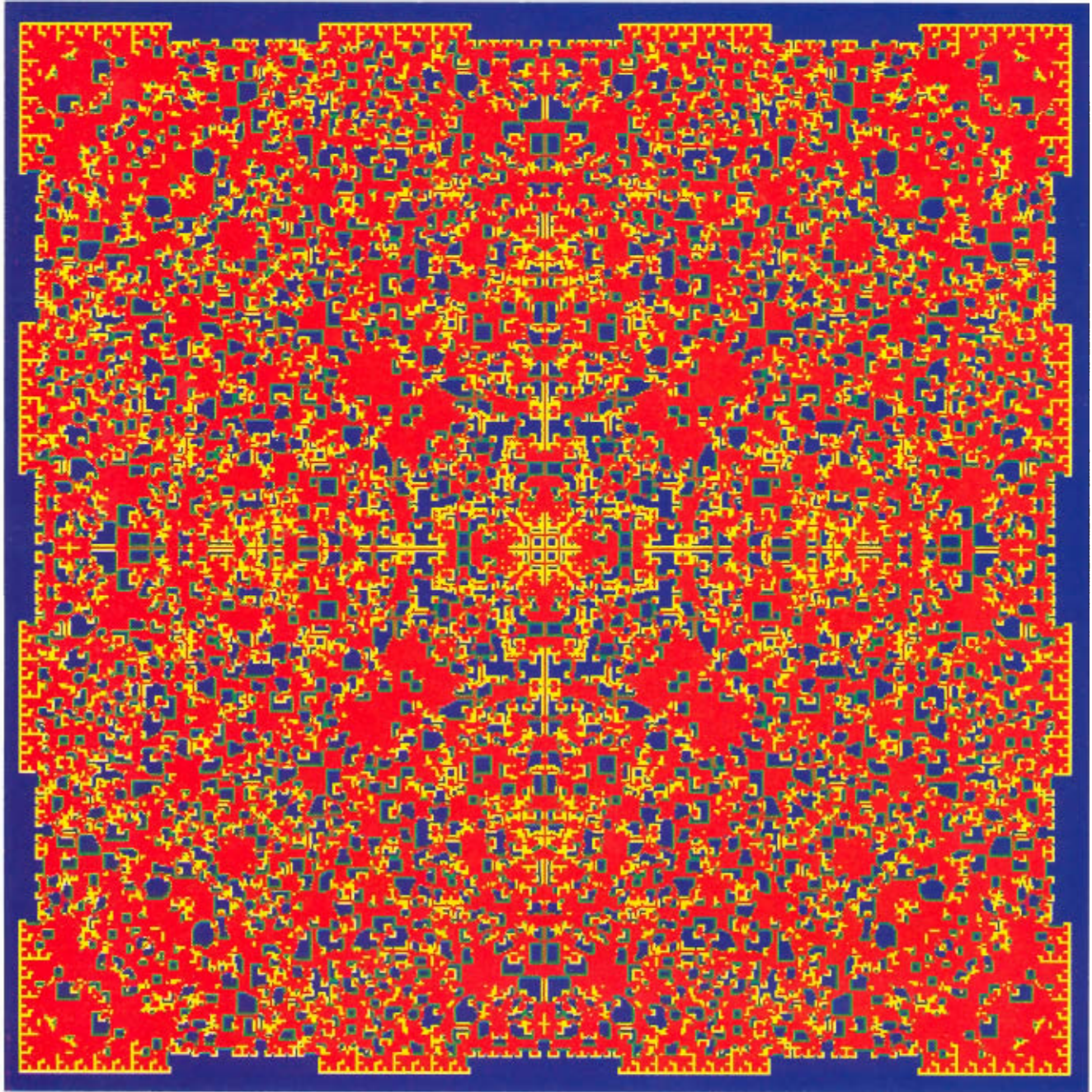
(f)

Fig. 5. (Continued)



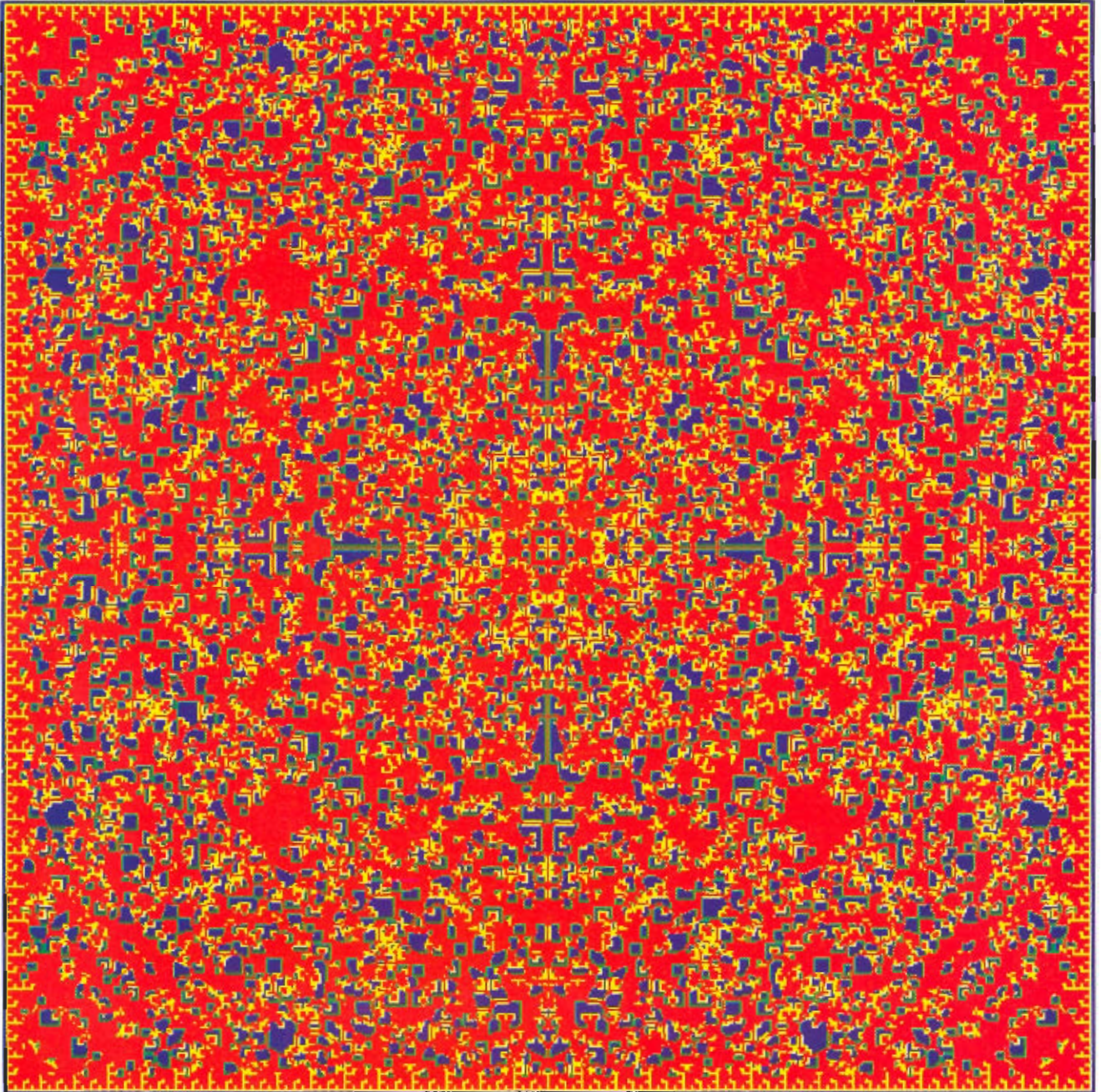
(g)

Fig. 5. (Continued)



(h)

Fig. 5. (*Continued*)



(i)

Fig. 5. (Continued)

Table 2. Total number of defectors after  $t = 0, 1, 2, 4, \dots$  generations, starting with a single defector invading an infinite world of cooperators. These generations correspond to the square-like structures of the dynamical fractal.

Time	Number of Defectors
0	1
1	9
2	25
4	81
8	289
16	1089
32	4177
64	14665
128	50389
256	189917
512	722273
1024	2889833
2048	11556509

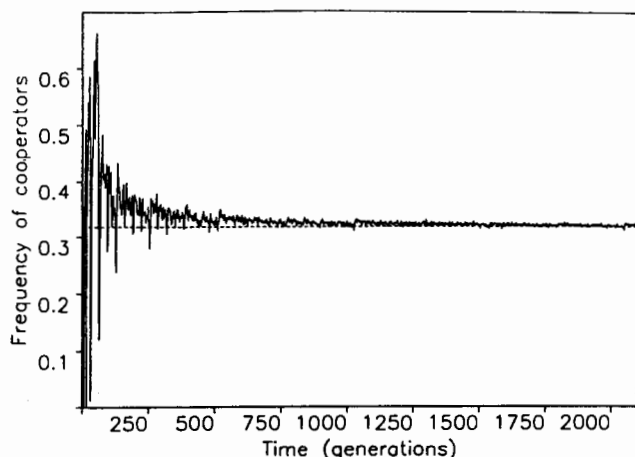
these squares only consist of defectors. For  $t = 32$  there are 8 clusters of cooperators left over, but they disappear in the next generation. For higher generations the squares contain many clusters of cooperators, which can persist. Table 2 shows the total number of defectors for the generations  $t = 0, 1, 2, 4, 8, \dots, 2048$ . Figure 6(a) shows the fraction of defectors in the growing structure for 2097 genera-

tions of growth without boundaries. (This was close to the maximum memory capacity of our computer). Note that the minima of the curve occur at powers of 2 and correspond to the square-like structures. The frequency of cooperators seems to converge to  $x \approx 0.318$  which seems to be the same value as in the simulations with random initial conditions.

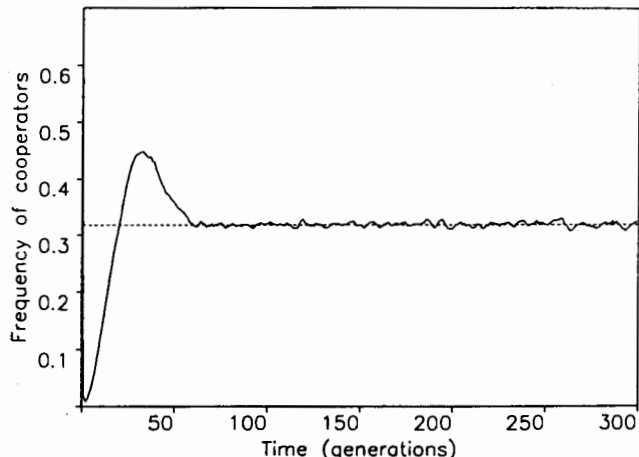
#### 4. A Dynamic Fractal: The Magic Agreement

The goal of this section is to find a model to describe the growth pattern that evolves from a single defector invading an infinite array of cooperators and to calculate the equilibrium frequency of cooperators (within the growing structure) as time goes to infinity.

We assume that at generation  $t = 2^n$  there exists a square, which consists of  $(2^{n+1} + 1)^2$  defectors. We neglect the fact that there are actually many clusters of cooperators within this square for  $t \geq 32$ . We assume that this square now grows at the corners and shrinks in the middle. This results in the formation of 4 new small squares at the corners and one large square in the center. We assume that this simplified growth pattern continues, i.e., the 4 squares at the corners get bigger and the square in the center gets smaller (Fig. 7). We neglect that the 4 squares actually only grow at the



(a)



(b)

Fig. 6. (a) The frequency of cooperators in the (infinitely) growing dynamic fractal starting from a single defector (see Fig. 5). For low generations, the minima occur at powers of 2 and correspond to the square-like structures of defectors. The broken line represents  $x = 12 \log 2 - 8 = 0.3178\dots$ , which seems to coincide with the limiting frequency of cooperators as  $t \rightarrow \infty$ . Conditions: square lattice, no boundaries, 8 neighbours plus self-interaction, parameter region  $1.8 < b < 2$ . (b) The frequency of cooperators in a simulation starting with random initial configuration. It is surprising that the time average again coincides with  $12 \log 2 - 8$ . Conditions:  $400 \times 400$  square lattice, fixed boundaries, 8 neighbours plus self-interaction, random initial conditions  $x = 0.6$ , parameter region  $1.8 < b < 2$ .

A simple approximation

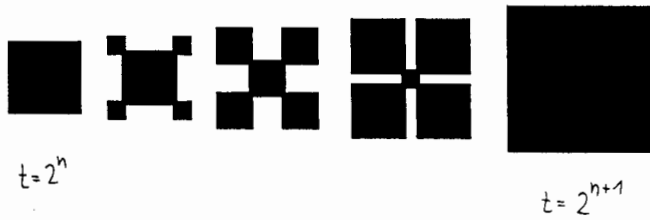


Fig. 7. A simpler model for the dynamic fractal in Fig. 5. At generation  $t = 2^n$ , there is a square of  $(2^n + 1)^2$  defectors. This square grows at the corners and shrinks along the lines. If this process continues — with 1 row of batches per generations in either direction — a new square is formed at  $t = 2^{n+1}$ . This square contains  $(2^{n+1} + 1)^2$  defectors. For large values of  $n$ , the time average of cooperators inside the structure over such a cycle from one square to the next converges to  $12 \log 2 - 8$ .

corners and loose along the side lines. Under these assumptions the number of defectors at generation  $t + i$ , with  $t = 2^n$  and  $0 \leq i < t$ , is given by

$$N_D = (2t + 2i + 1)^2 - 8i(2t - 2i - 1). \quad (1)$$

The fraction of cooperators within the square  $(2t + 2i + 1)^2$  at time  $t + i$  is given by

$$x(t + i) = \frac{8i(2t - 2i - 1)}{(2t + 2i + 1)^2}. \quad (2)$$

For very large  $t$ , this is

$$x(t + i) \approx \frac{4i(t - i)}{(t + i)^2}. \quad (3)$$

This describes oscillations with increasing period. The minima occur at  $t = 2^n$  ( $i = 0$ ) and the maxima at  $i = t/3$ . The time average of cooperators over one cycle, as  $i$  goes from 0 to  $t$ , is given by

$$\begin{aligned} \bar{x} &= \frac{1}{t} \sum_{i=0}^t \frac{4i(t - i)}{(t + i)^2} \approx 4 \int_0^1 \frac{s(1 - s)}{(1 + s)^2} ds \\ &= 12 \log 2 - 8 = 0.31776617 \dots \end{aligned} \quad (4)$$

This time average is in agreement with the numerical values of the original model. It seems to coincide both with the time limit of the fraction of cooperators in the symmetric growing patterns and with the time average in the simulations starting from asymmetric random initial conditions (Fig. 6).

## 5. The Invasion of Cooperators: Superstrings and More Fractals

Cooperators can also invade a world of defectors. Starting from a  $2 \times 2$  square of cooperators, we observe growing squares of cooperators that expand to out-compete all defectors. This happens as long as  $b < 2$ .

More interesting growth patterns occur, if we start with irregularly shaped clusters of cooperators. One such example is the grower [Fig. 2(c)]. For  $1.75 < b < 1.8$ , this grower expands to generate a peculiar geometric pattern. Eventually most cells will be occupied with cooperators. Across one diagonal there is a pulsating “superstring” of defectors left over. There are also static blocks of defectors nicely aligned in rows and columns [Fig. 8(a)]. For  $1.8 < b < 2$ , the grower also expands indefinitely, but is eaten up in the middle by fractal like defector structures — reminiscent of those we find in the symmetric kaleidoscopes [Fig. 8(b)].

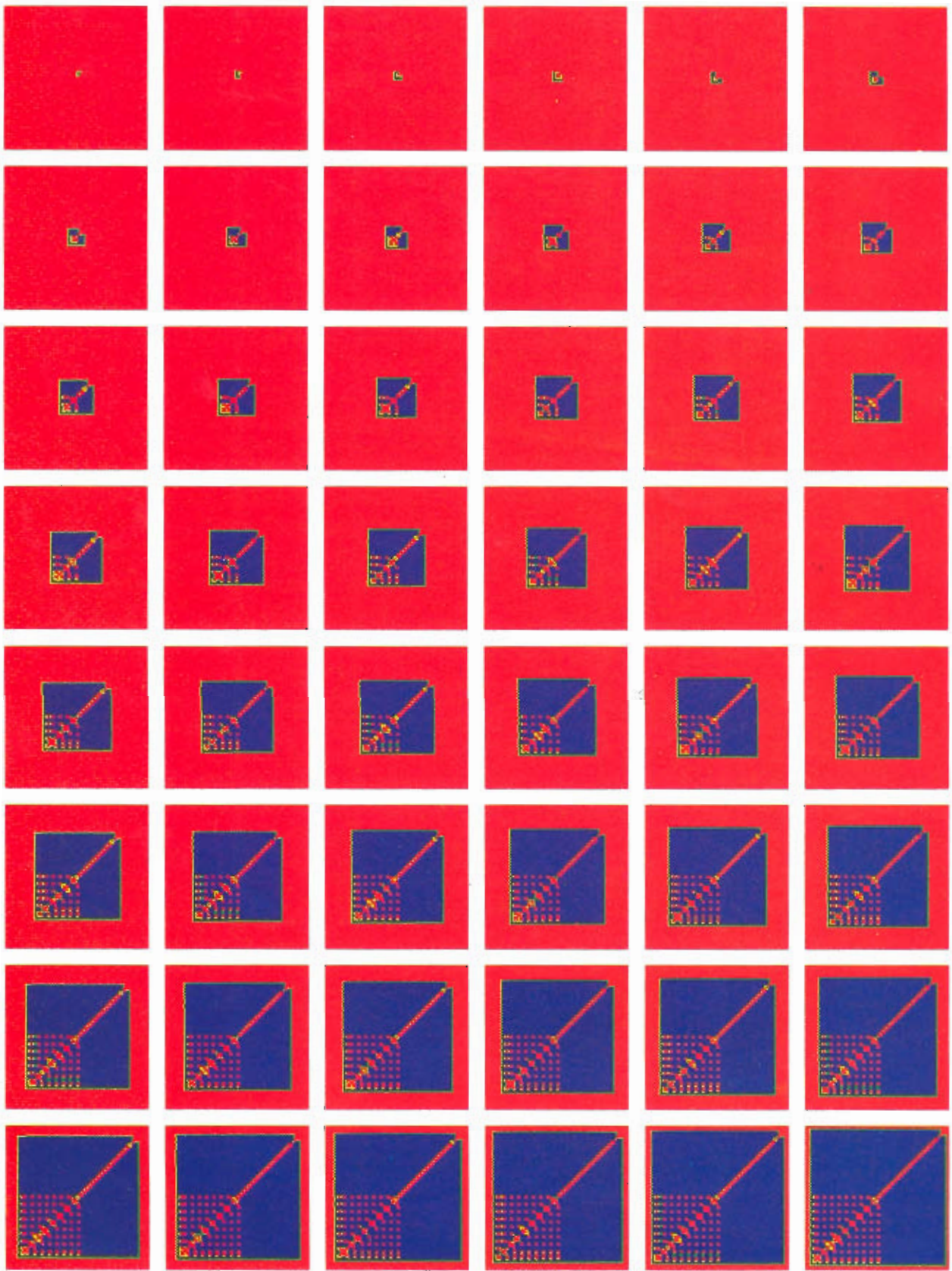
## 6. Other Geometries: Towards a Classification

This section is devoted to the exploration of the properties of spatial games with different assumptions about the geometry determining which neighbours are interacted with. In the previous sections we have seen that a dynamic equilibrium between cooperators and defectors occurs for parameter values of  $b$ , where both  $C$  and  $D$  clusters keep growing. This criterion will hold for all the other neighbourhoods we will consider.

### 6.1. Square lattices: 8 neighbours

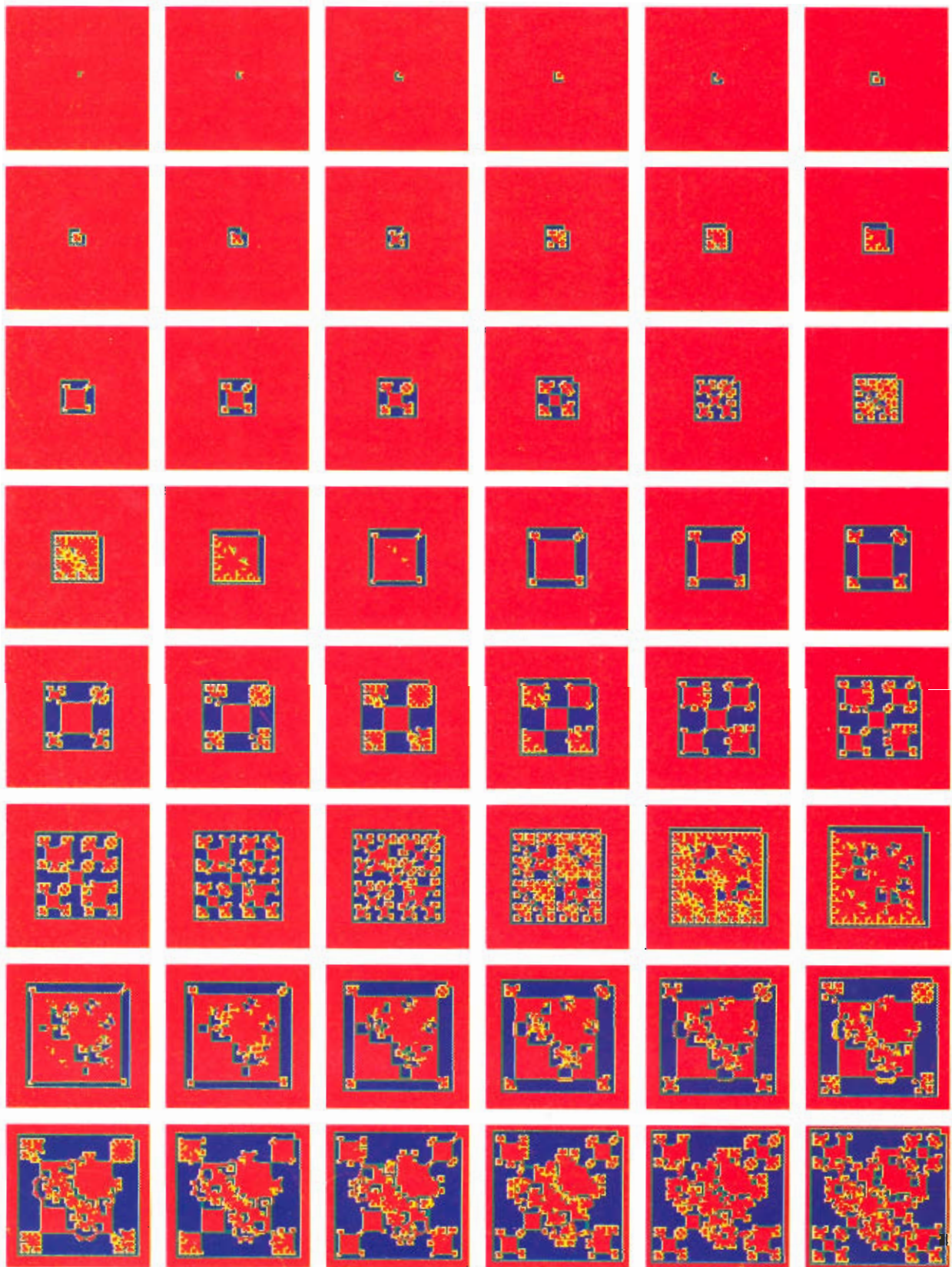
First we consider a square lattice with interaction with the 8 immediate neighbours, but without self-interaction. This case is very similar to the original one. We observe the same kind of dynamics, but for slightly different values of  $b$ . If  $b < 5/3$  then only  $C$  clusters keep growing. If  $b > 8/5$  then only  $D$  clusters keep growing. The most interesting parameter region is  $8/5 < b < 5/3$ . Here both  $C$  and  $D$  clusters keep growing. This results in a dynamic equilibrium between cooperators and defectors.

The dynamic fractal that is generated by a single invading defector is similar to Fig. 4. Figure 9(a) shows the fraction of defectors in the growing structure for 2097 generations. The frequency of cooperators seems to converge to  $x \approx 0.30$ . This value is again in agreement with the time average of



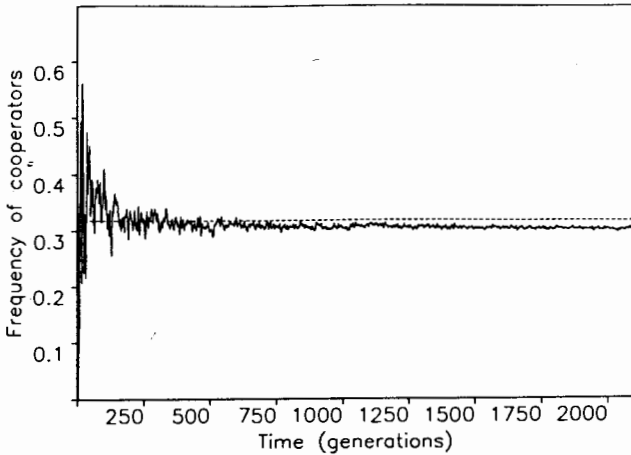
(a)

Fig. 8. Cooperators can also invade defectors and generate surprising patterns. Both simulations start with a “grower” (see Fig. 2(c)). This is a cluster of 10 cooperators. Both pictures show the first 48 generations of the grower. (a)  $b = 1.79$ . (b)  $b = 1.85$ .

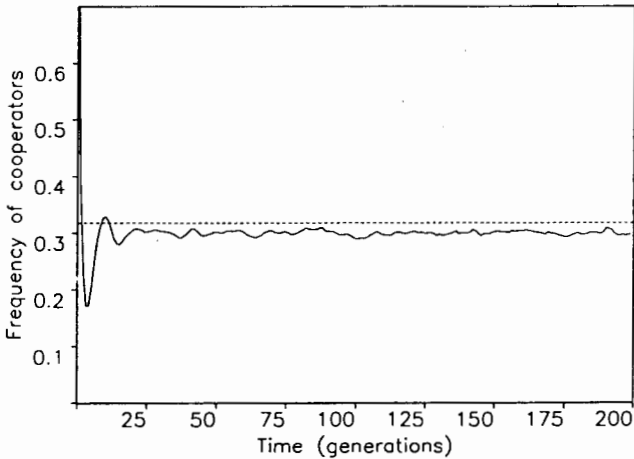


(b)

Fig. 8. (Continued)



(a)



(b)

Fig. 9. Time series of the cooperator frequency for a square with 8 neighbours, but without self-interaction. The interesting parameter region is  $8/5 < b < 5/3$ . (a) The frequency of cooperators within the dynamic fractal emerging from a single defector. (b) The frequency of cooperators for a  $400 \times 400$  square lattice, fixed boundaries, random initial conditions ( $x_0 = 0.9$ ). The straight line indicates  $12 \log 2 - 8$ .

simulations starting from random initial conditions [Fig. 9(b)] and is slightly lower than  $12 \log 2 - 8$ .

Here the invasion of cooperators in a world of defectors starting with a square of  $3 \times 3$  cooperators also gives rise to an interesting fractal-like growing pattern.

### 6.2. Square lattices: 4 neighbours

Next we consider only the interaction with the 4 immediate neighbours — excluding the diagonal neighbours. Again we can consider the two cases

with or without interaction with the own batch. The dynamic equilibrium occurs for  $4/3 < b < 1.5$  (without self-interaction) and for  $5/3 < b < 2$  (with self-interaction).

Figure 10 shows typical patterns starting from random initial conditions. Another interesting parameter region occurs for  $2 < b < 2.5$  (if  $n = 5$ ) and for  $1.5 < b < 2$  (if  $n = 4$ ). Here we find static patterns formed by crosses of cooperators that can only expand horizontally or vertically until they hit each other or a stable  $5C$  cross or a  $3C$  blinker.

Figure 11 shows the growth patterns emerging from a single defector. These patterns represent a completely different culture with royalty, crowns, crosses and lillies of France.

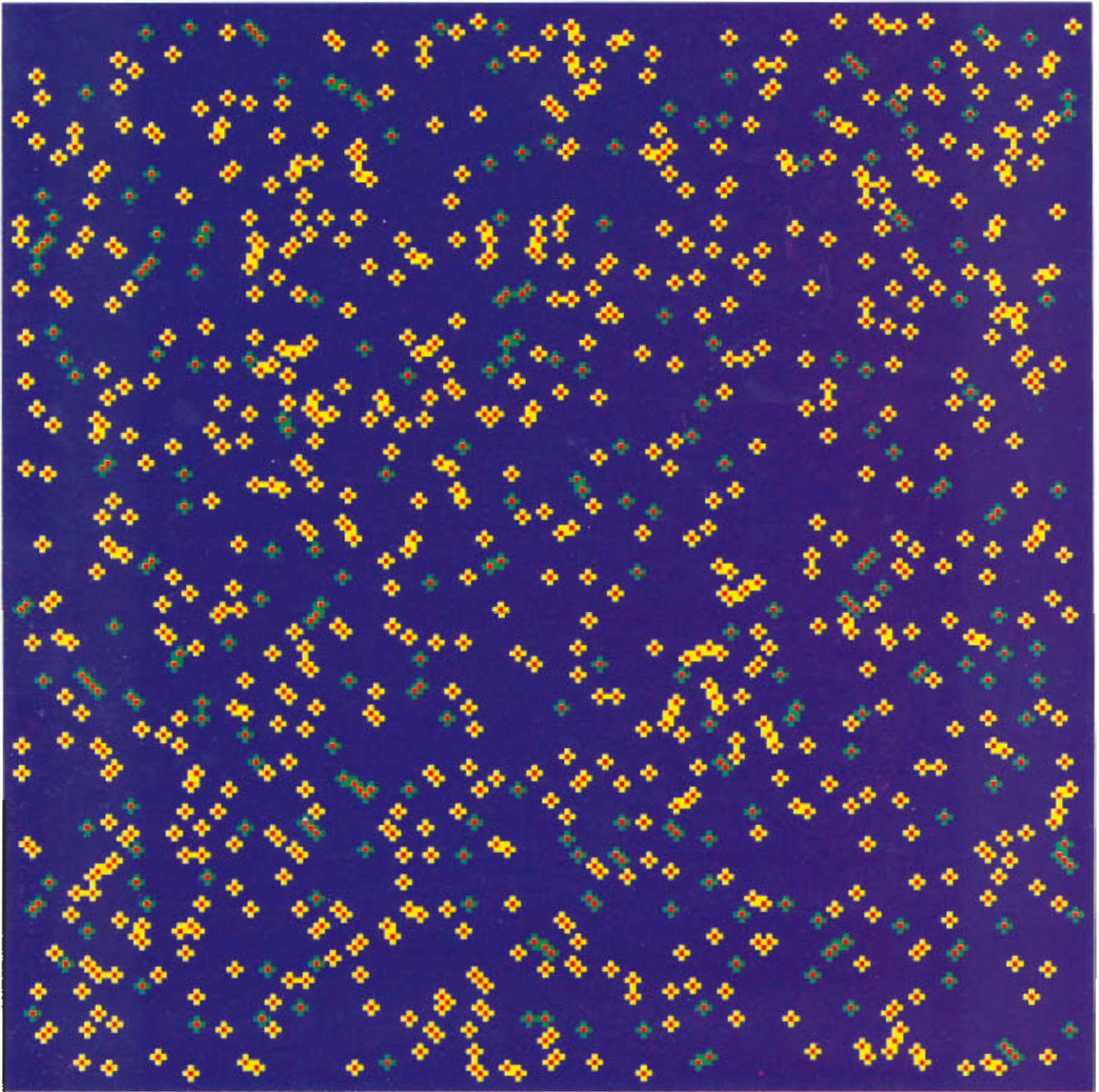
### 6.3. Hexagonal lattices: 6 neighbours

The situation is different for hexagonal lattices. Here the parameter regions where  $C$ - and  $D$ -clusters can grow do not overlap. Therefore, according to our classification, there is no dynamic equilibrium. A coexistence between cooperators and defectors can only occur in more or less static patterns. If there is no self-interaction, a generic  $D$ -cluster grows at the corners if  $b > 2$  and along the lines if  $b > 3$ . The corner and line conditions for  $C$ -clusters are obtained as  $b < 1.5$  and  $b < 2$ , respectively. Thus there is no overlap.

For hexagonal lattices a dynamic equilibrium is possible if one makes the additional assumption that individuals interact more often within their own batch. This seems biological plausible if we assume that several individuals occupy a single patch and that interactions are more frequent between individuals at a closer distance. To be specific let us assume that a cooperator receives a payoff  $k$  from interactions within its own patch (let  $k > 1$ ) and only payoff 1 from interactions with cooperators in the neighbourhood. For a defector nothing changes. Now we find that both  $C$ - and  $D$ -clusters grow (at the corners) if  $1.5 + k/2 > b > 2 + k/3$ . If this inequality is fulfilled, we obtain a dynamic equilibrium (with chaotic fluctuations) for the hexagonal lattice.

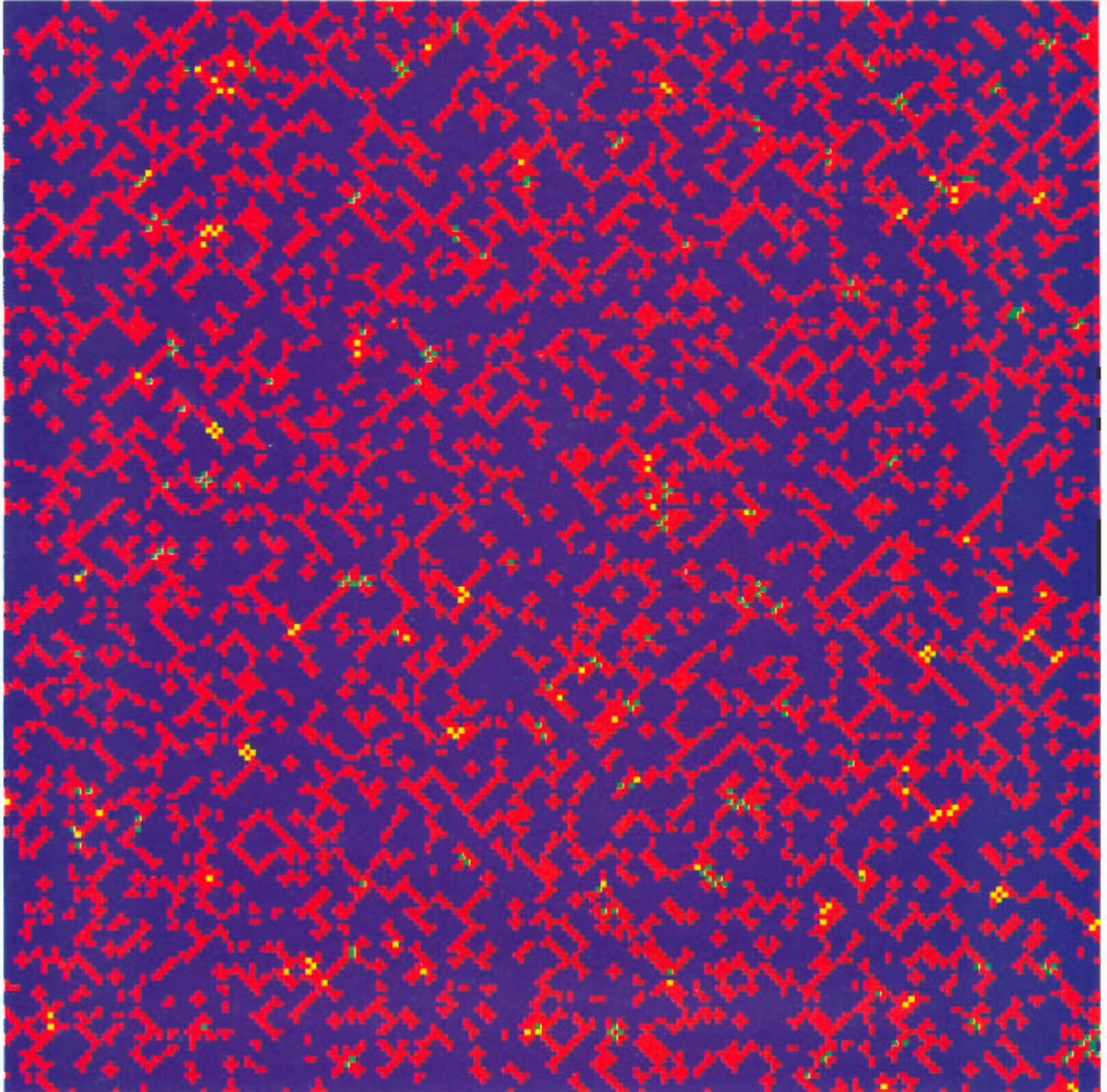
### 6.4. The radius of interaction in a more general approach

It seems to be a natural expansion of the above ideas to assume that for each individual there is a certain radius of interaction,  $r$ . The payoff is then evaluated over the area of the circle,  $r^2\pi$ . The payoff for a single defector surrounded by cooperators



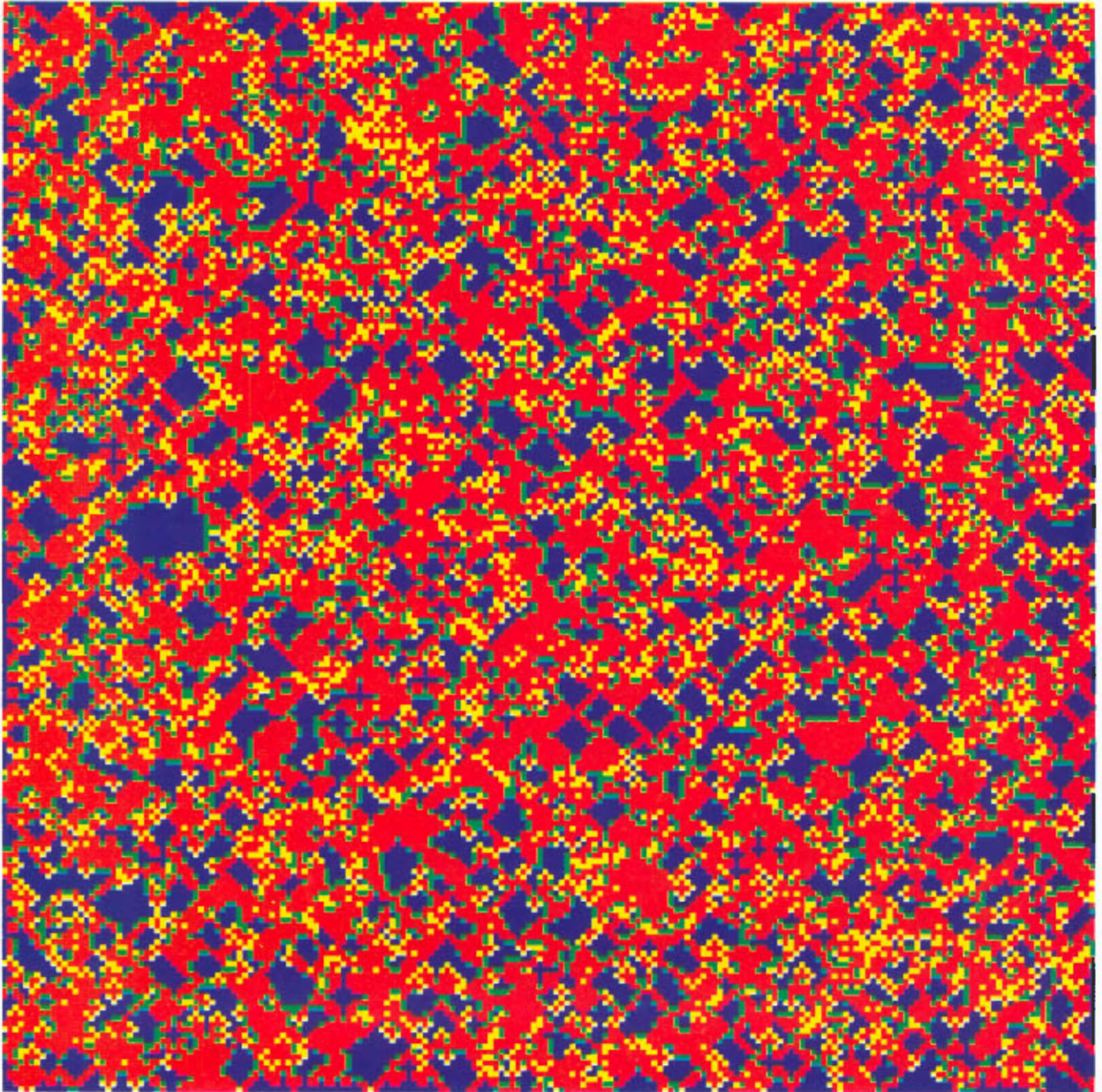
(a)

Fig. 10. Typical pictures of a square lattice with a 4 neighbours interaction. Conditions:  $200 \times 200$  square lattice, fixed boundaries, 4 neighbours plus self-interaction, random initial conditions  $x = 0.9$ . (a)  $b = 1.31$ , (b)  $b = 1.61$ , (c)  $b = 1.85$ , (d)  $b = 2.01$ .



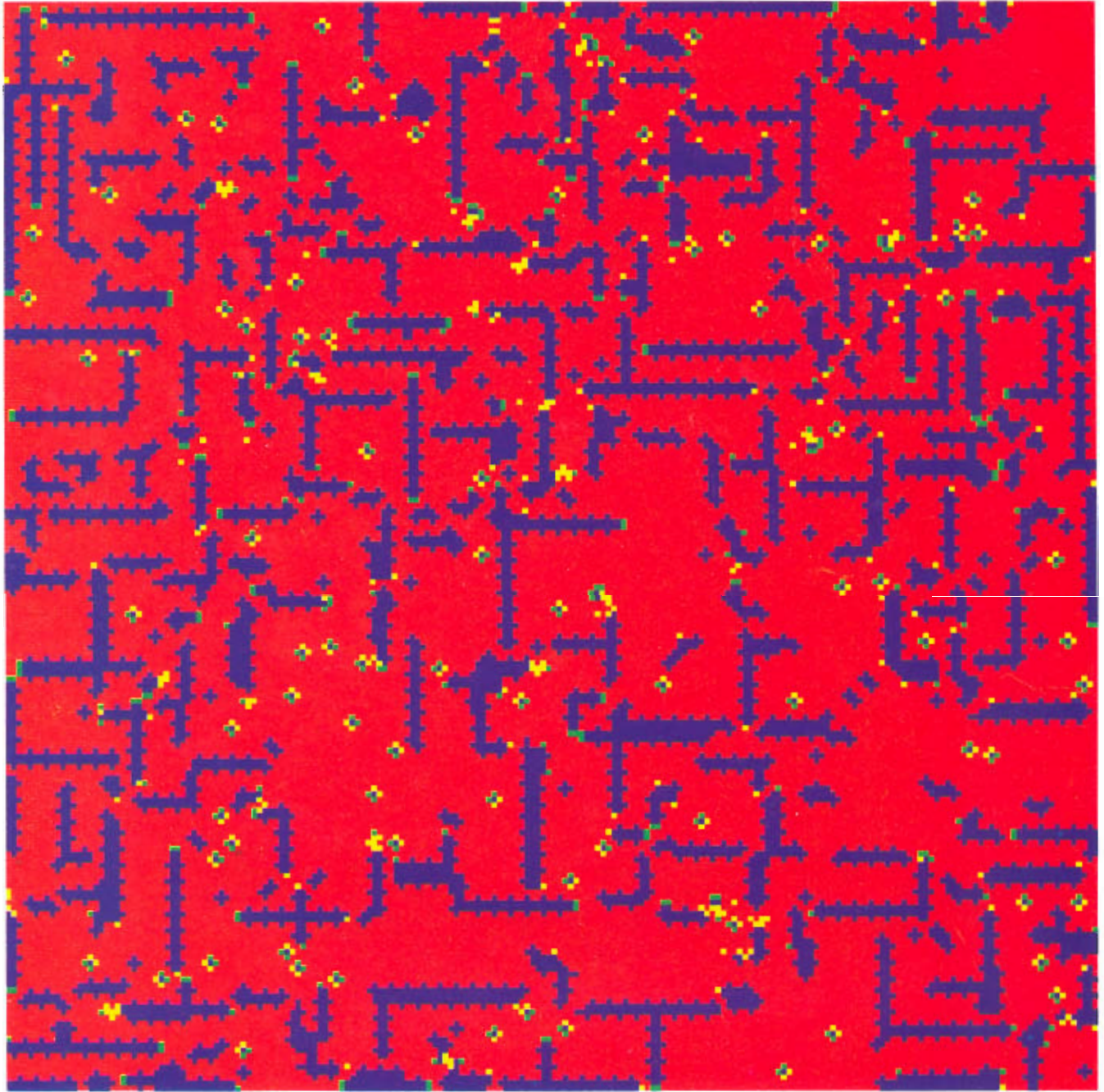
(b)

Fig. 10. (*Continued*)



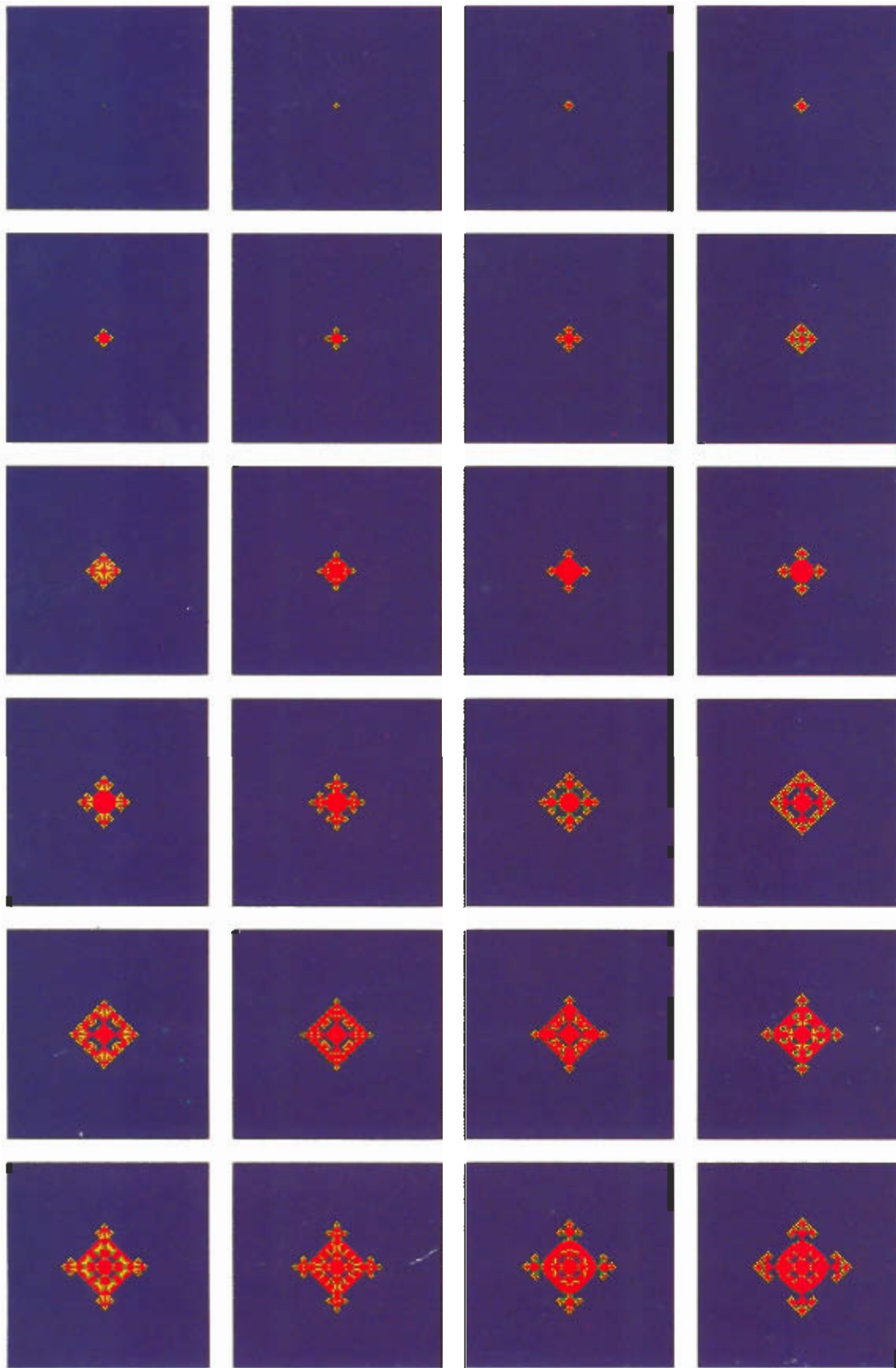
(c)

Fig. 10. (Continued)



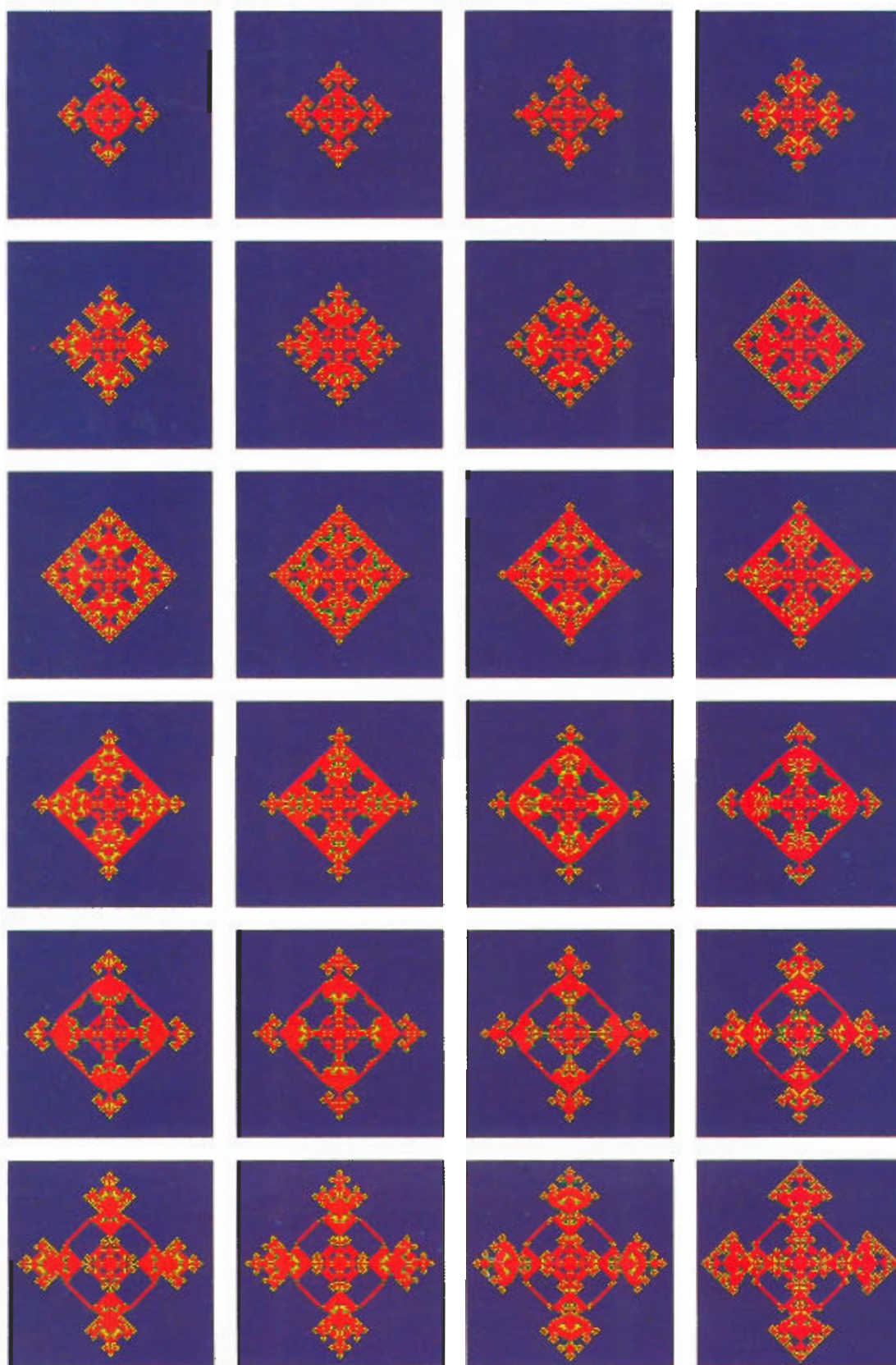
(d)

Fig. 10. (Continued)



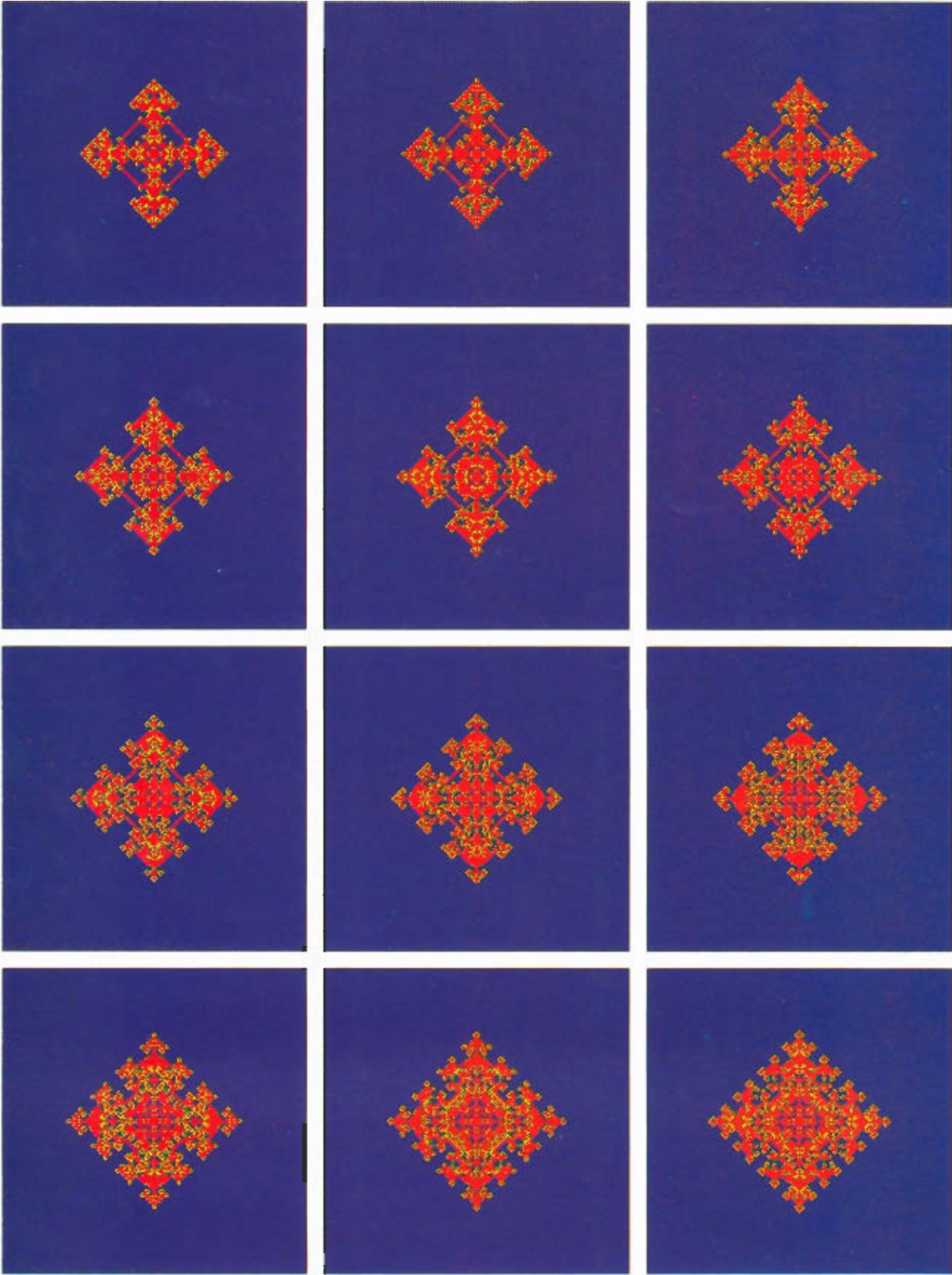
(a)

Fig. 11. Dynamic fractal for the 4 neighbour interaction. Generations  $t = 0 - 95$  are shown. Conditions: square lattice, no boundaries, 4 neighbours plus self-interaction, starting with a single defector, parameter region  $5/3 < b < 2$ .



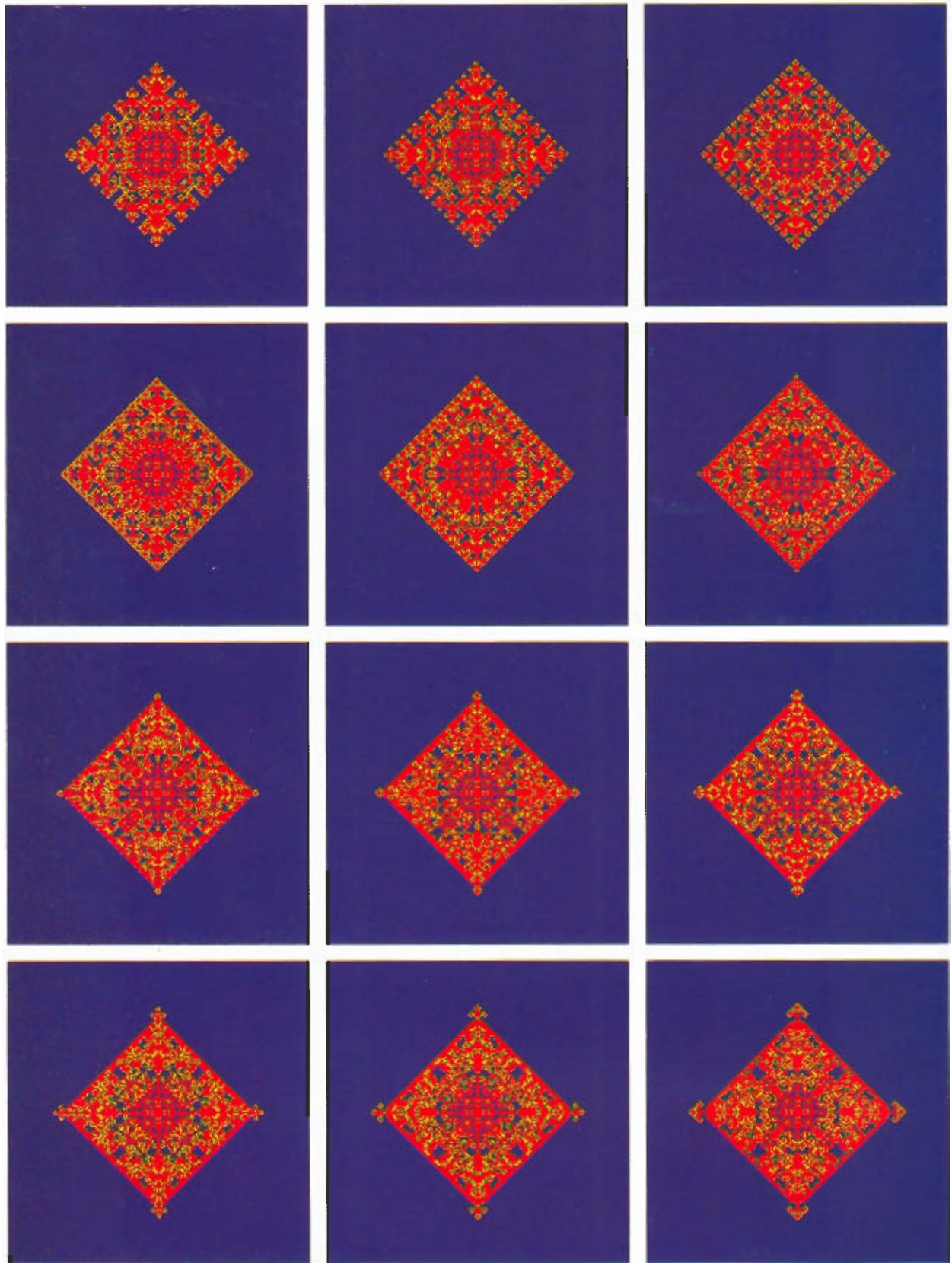
(b)

Fig. 11. (Continued)



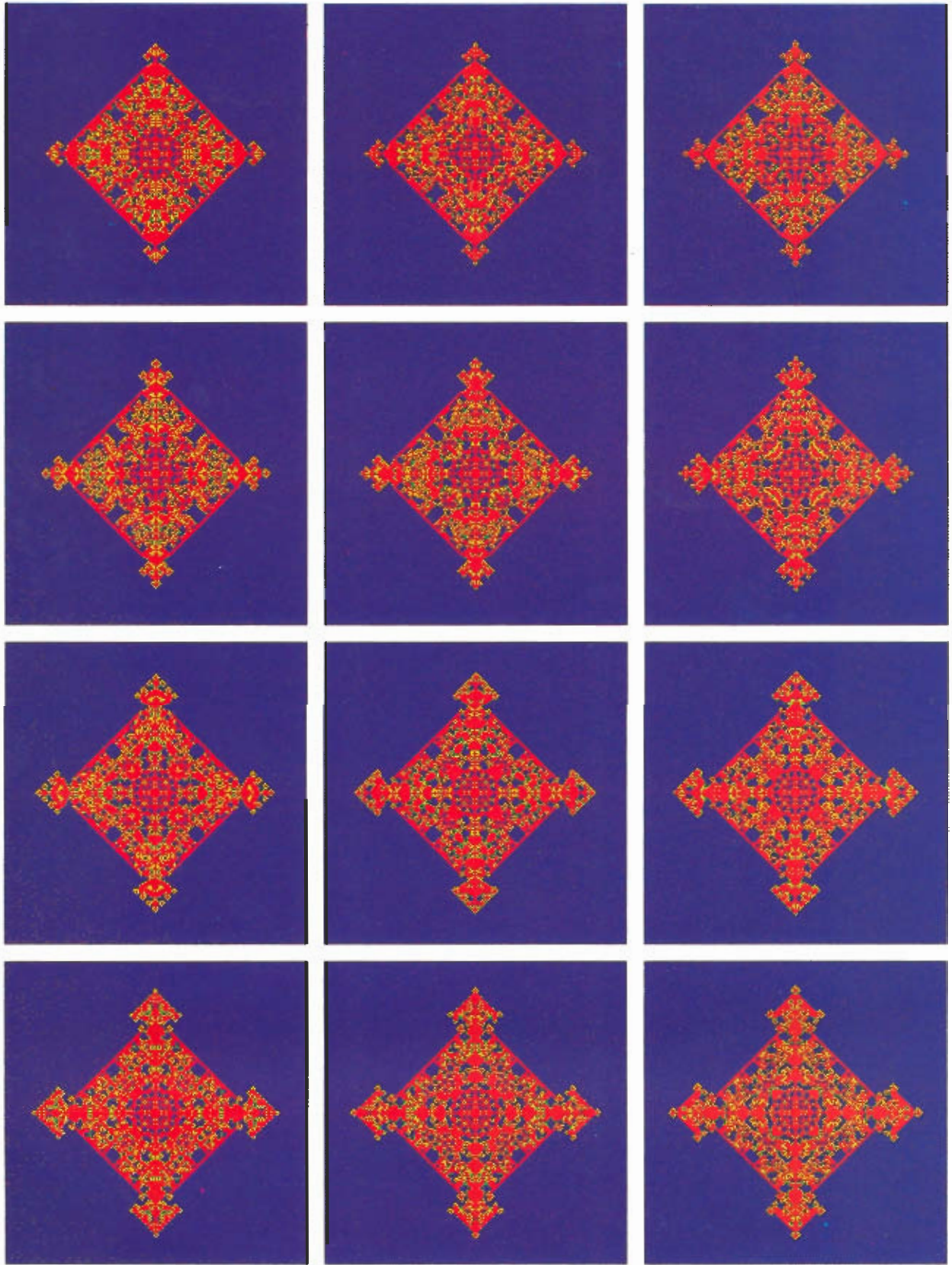
(c)

Fig. 11. (Continued)



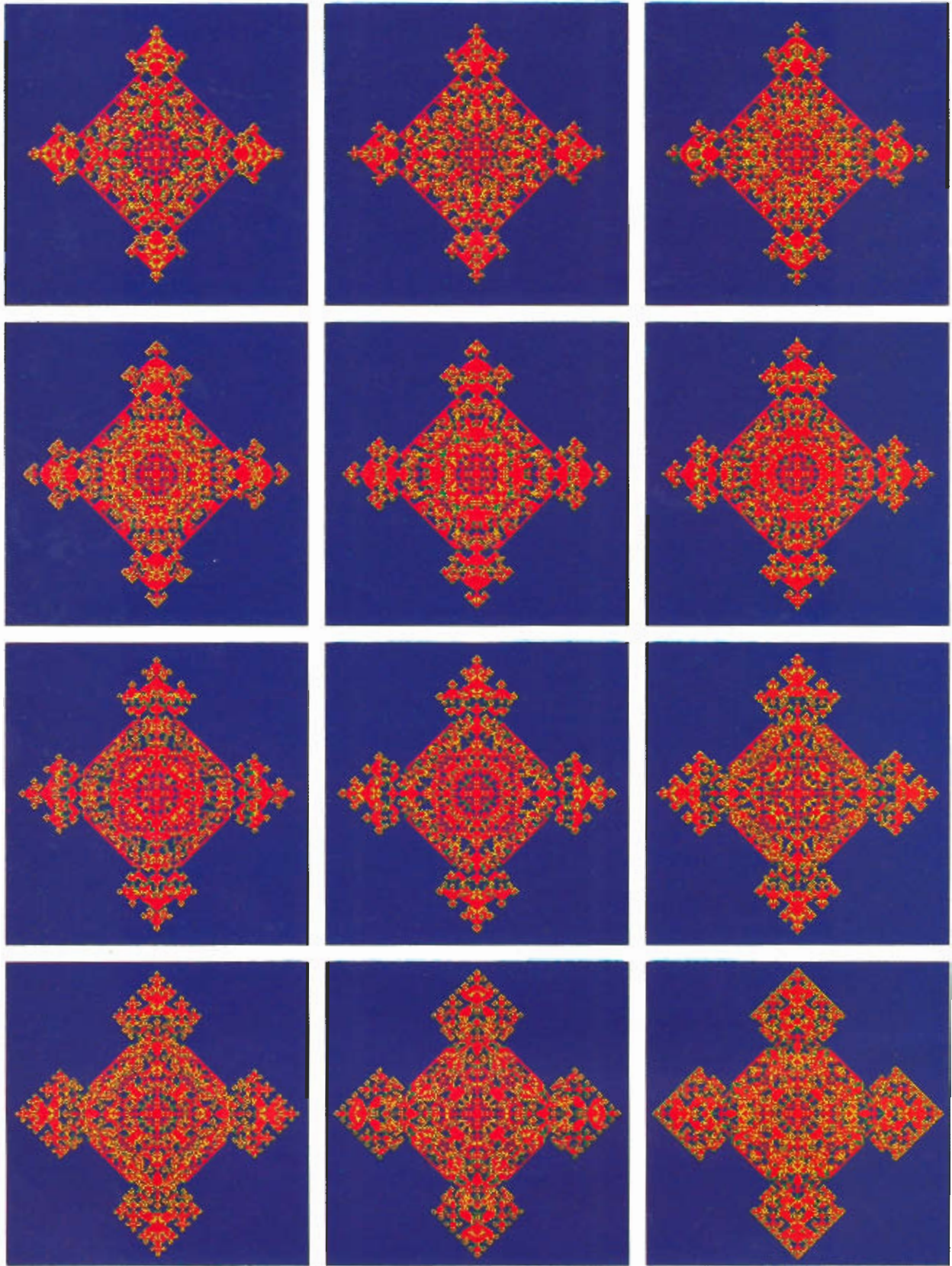
(d)

Fig. 11. (Continued)



(e)

Fig. 11. (Continued)



(f)

Fig. 11. (Continued)

is given by  $br^2\pi$ , and the payoff for a cooperator surrounded by cooperators is given by  $r^2\pi$ . Without loss of generality we can assume that the radius of interaction,  $r$ , is the unit of length, i.e.,  $r = 1$ .

Let us consider a circular cluster of cooperators of radius  $R$  which is entirely surrounded by defectors. The defectors just outside the boundary of the circle receive the payoff  $b\alpha(R)\pi$ . Here  $\alpha(R)$  is the area of the intersection between the circle of cooperators and the payoff circle of the defectors. For  $R > 1/2$ , this is

$$\alpha(R) = R^2\left(\theta - \frac{1}{2} \sin 2\theta\right) + \phi - \frac{1}{2} \sin 2\phi \quad (5)$$

with  $\phi = \arccos(1/2R)$  and  $\theta = \pi - 2\phi$ . This payoff has to be compared with the payoff given to cooperators, whose payoffs come from the circle lying entirely inside the cluster of cooperators. This payoff is  $\pi$ . Thus the cluster of cooperators will expand if

$$b < \frac{1}{\alpha(R)}. \quad (6)$$

For  $1/2 < R < 1$ ,  $C$ -clusters will grow if

$$b < \frac{R^2}{\alpha(R)}. \quad (7)$$

For  $R < 1/2$ ,  $C$ -clusters only grow if  $b < 1$ .

Next we consider a circular  $D$ -cluster of radius  $R > 1/2$ . The defectors on the boundary of this cluster receive the payoff  $b(1 - \alpha(R))\pi$ . This must be compared with the payoff,  $\pi$ , which is given to cooperators, whose interaction area lies completely outside the  $D$ -cluster. Thus the  $D$ -cluster

can grow if

$$b > \frac{1}{1 - \alpha(R)}. \quad (8)$$

For  $R < 1/2$ , the circular  $D$ -cluster grows if

$$b > \frac{1}{1 - R^2}. \quad (9)$$

For large  $R$  we have

$$\alpha(R) \approx \frac{\phi}{\pi} = \frac{1}{\pi} \arccos \frac{1}{2R} \approx \frac{1}{2} - \frac{1}{2R\pi}. \quad (10)$$

For  $R \rightarrow \infty$  we have, of course,  $\alpha \rightarrow 1/2$ .

This means: For  $b < 1$ ,  $C$ -clusters grow to infinity and  $D$ -clusters disappear. For  $1 < b < 2$ ,  $C$ -clusters above a critical size grow to infinity;  $C$ -clusters which are too small, on the other hand, disappear.  $D$ -clusters grow or shrink to a certain stable size. For  $2 < b$ ,  $D$ -clusters grow to infinity. (For  $b = 2$ , both  $C$ - and  $D$ -clusters can grow to infinity.) For  $2 < b < 2.56$ ,  $C$ -clusters above a certain critical size grow or shrink to a given finite size. The threshold 2.56 is  $1/\alpha(1)$ . For  $2.56 < b$ , all  $C$ -clusters disappear.  $b = 2.56$  represents the highest advantage for the defectors which is compatible with cooperators still surviving in some clusters.

This represents some kind of continuous space approximation.

## 7. Other Games: On Hawks and Doves and ESS

Spatial games are not limited to the special payoff matrix given in Sec. 2. Any game can "become spatial" if played among neighbours in a spatial array.

Fig. 12. (following pages) Hawk-Dove games can also generate a large variety of different patterns. The figure shows the first 96 generations of two kaleidoscopes starting with a single dove ( $D$ ) invading a  $99 \times 99$  world of hawks ( $H$ ). The payoff matrices are

(a)

	$H$	$D$
$H$	31	20
$D$	50	10

(b)

	$H$	$D$
$H$	100	200
$D$	121	131

The colour code is as follows: blue: a  $H$  that was a  $H$  in the previous generation; green: a  $H$  that was a  $D$  in the previous generation; red: a  $D$  that was a  $D$  in the previous generation; yellow: a  $D$  that was a  $H$  in the previous generation.



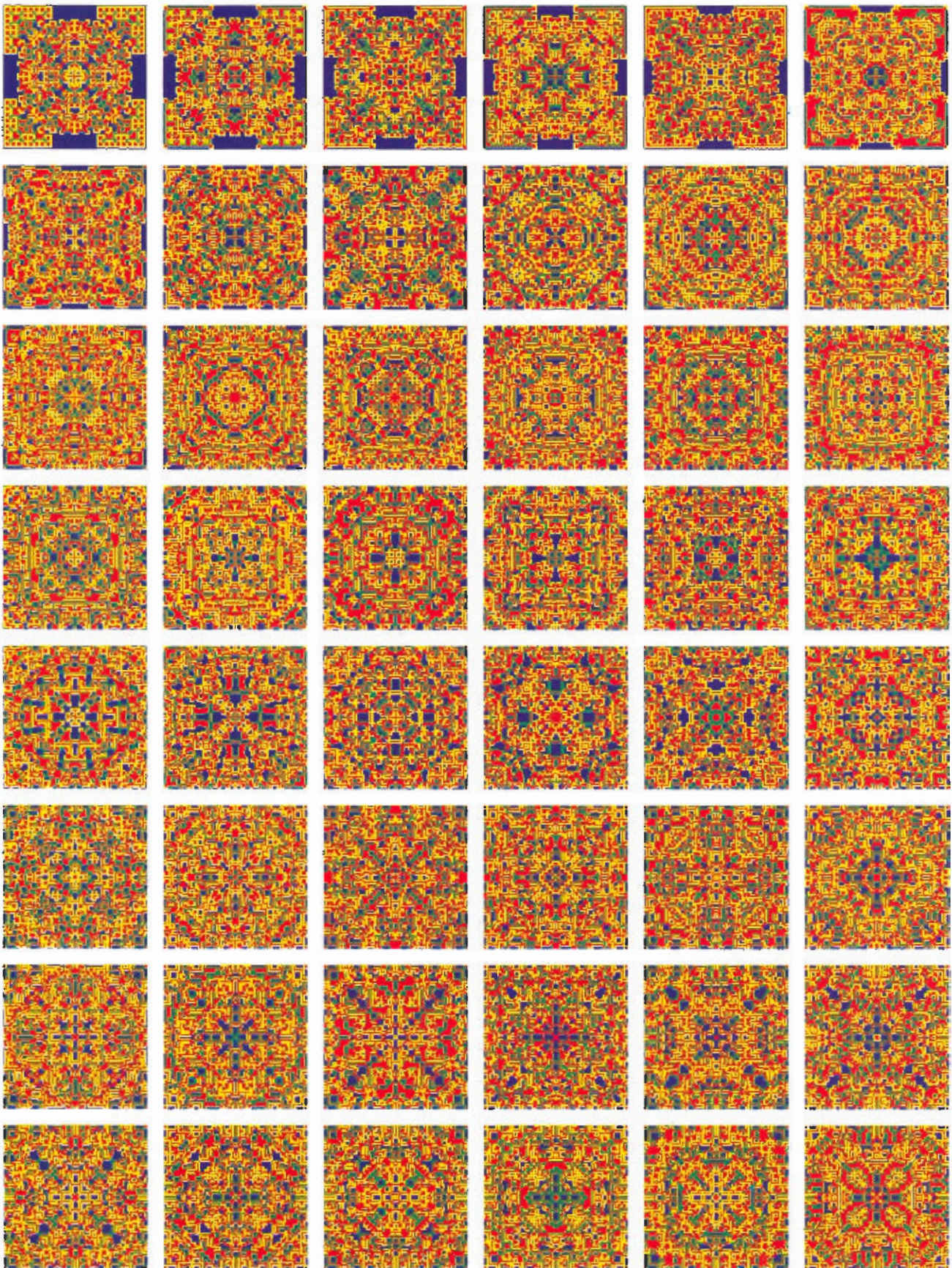


Fig. 12(a). (Continued)

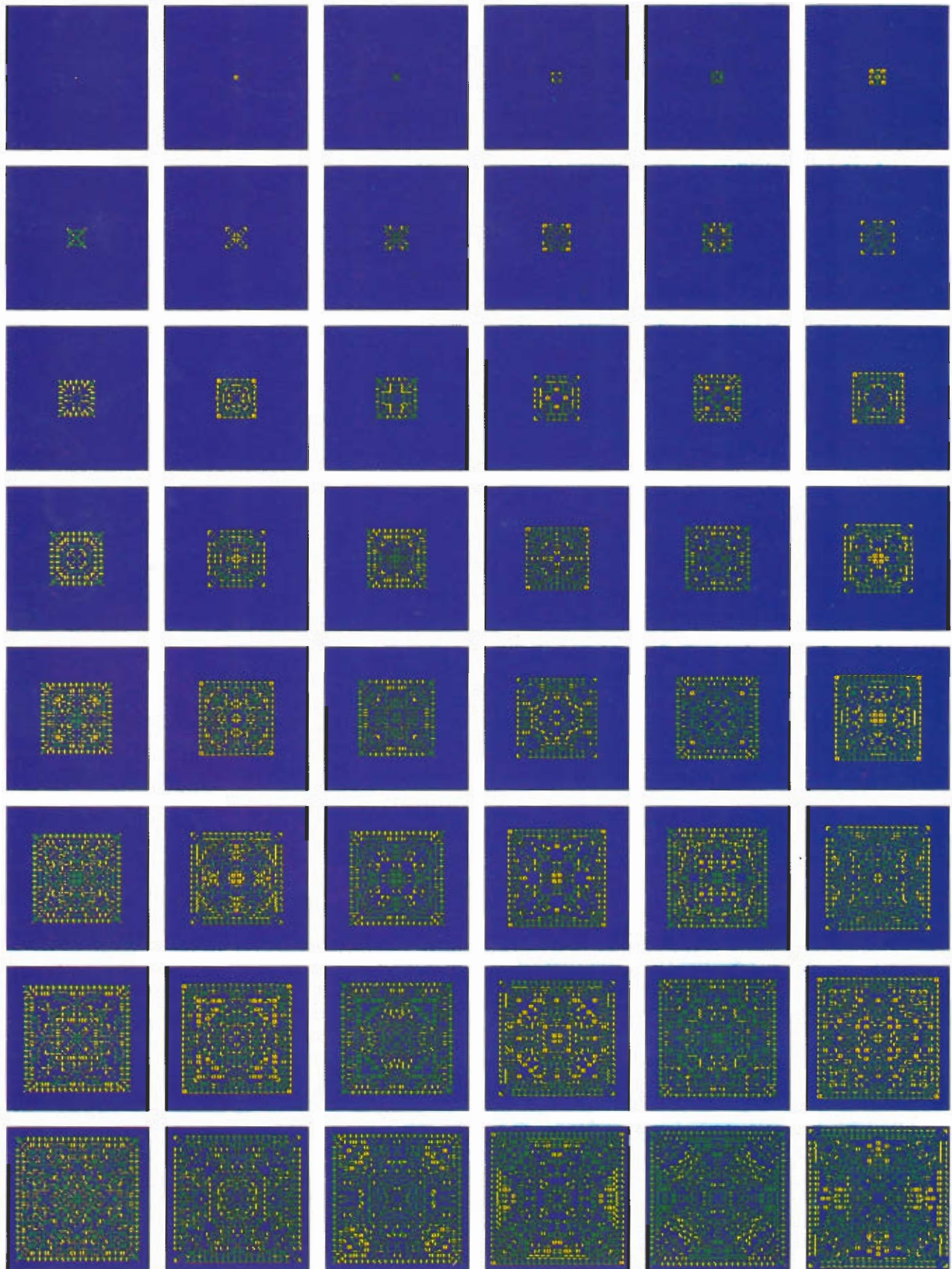


Fig. 12(b).

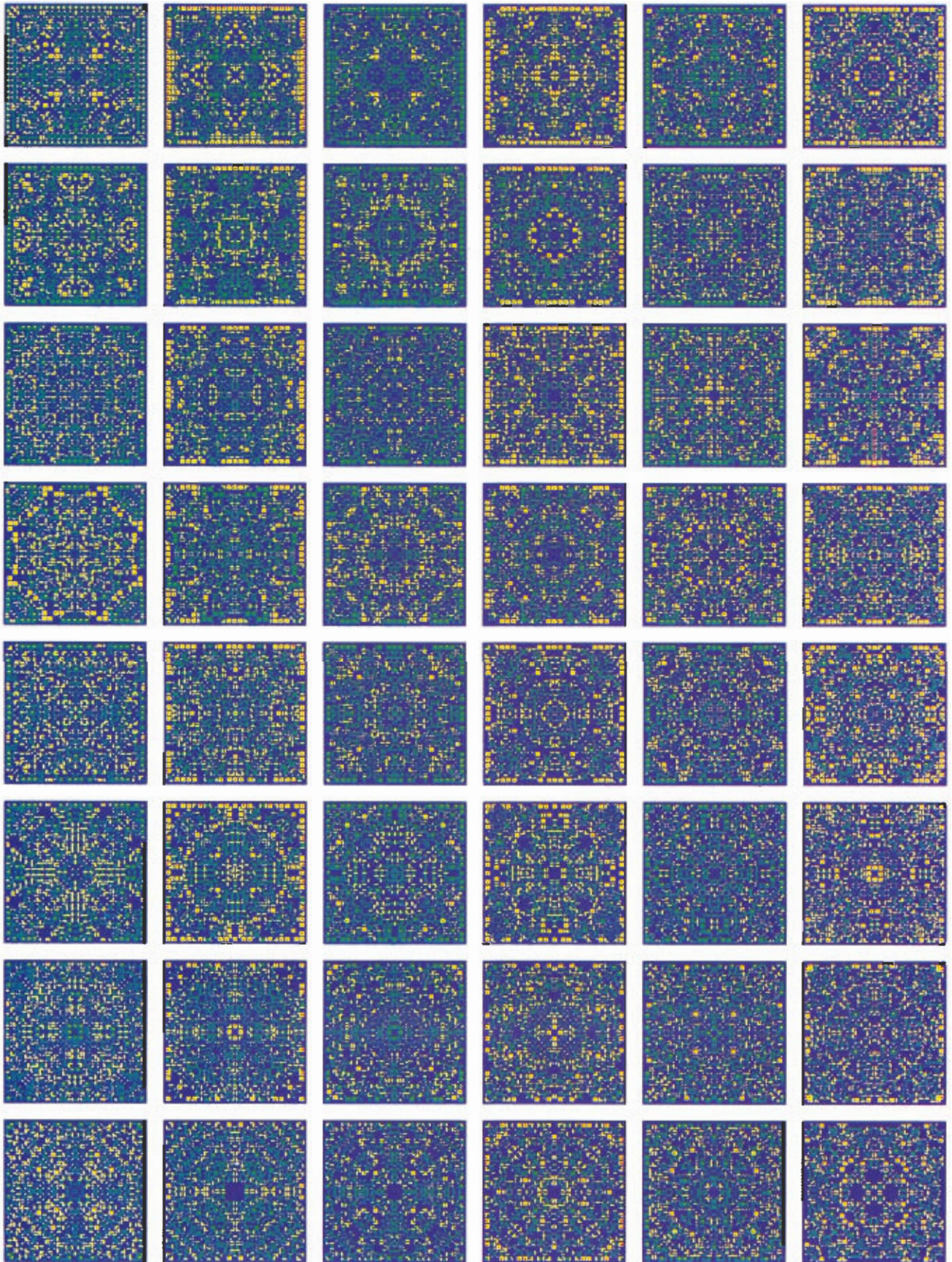


Fig. 12(b). (Continued)

Let us consider two strategies,  $A$  and  $B$ , and the payoff matrix

	$A$	$B$
$A$	$a$	$c$
$B$	$b$	$d$

In classical evolutionary game theory [Maynard Smith, 1982], a strategy,  $A$ , is said to be an evolutionarily stable strategy (ESS) if there is no mutant strategy,  $B$ , which can spread in a population that consists entirely of individuals adopting strategy  $A$ . For the above payoff matrix, this means that  $A$  is an ESS if

$$a > b$$

or

$$a = b \text{ and } c > d.$$

We can also define the ESS conditions for spatial games. There seem to be two different cases corresponding to a strong and a weak spatial ESS. We propose the following:

**Definition.** A strategy is a strong spatial ESS if any mutant strategy that is occupying a single cell is bound to disappear in the next generation. A strategy is a weak spatial ESS if any mutant strategy that is occupying a single cell is unable to spread.

For a geometry with  $N$  neighbours and self-interaction, we have:

$A$  is a strong ESS if  $Na + c > Nb + d$ .

$A$  is a weak ESS if  $(N + 1)a > Nb + d > Na + c$ .

$B$  can invade  $A$  if  $Nb + d > \max\{(N + 1)a, Na + c\}$ .

For  $N$  neighbours without self-interaction, we have:

$A$  is a strong ESS if  $(N - 1)a + c > Nb$ .

$A$  is a weak ESS if  $Na > Nb > (N - 1)a + c$ .

$B$  can invade  $A$  if  $Nb > \max\{Na, (N - 1)a + c\}$ .

If we consider a square lattice with  $N = 8$  neighbours and self-interaction, the growth pattern of an individual  $B$  strategy will be fractal-like whenever the growing  $B$  cluster gains at the corners but loses along the lines. This happens if

$$5b + 4d > \max\{9a, 6a + 3c\} \quad (\text{Corner}),$$

$$6a + 3c > \max\{9a, 3b + 6d\} \quad (\text{Line}).$$

In the Hawk-Dove game [Maynard Smith, 1982] the payoff matrix is characterized by  $b > a$  and  $c > d$ . Figures 12 show the large variety of patterns that can be generated by Hawk-Dove games

on a square lattice (with 8 neighbours and self-interaction).

## 8. Conclusion: Spatial Cooperation, T-Shirts, and Carpets

For many kinds of "evolutionary games," we find that the outcome of frequency dependent selection can be changed (and reversed) if spatial effects are taken into account. Classical evolutionary game theory assumes randomly interacting populations. This is an abstraction. In real populations, individuals are more likely to interact with their neighbours.

The term "population viscosity" was coined by Hamilton [1964] in his fundamental paper on inclusive fitness. A population is viscous if individuals do not move far from their places of birth. This limited dispersal is thought to facilitate the evolution of cooperation (altruism) by increasing the *degree of relatedness* among interacting individuals (Hamilton, 1971, Wilson *et al.*, 1992). We show here, however, that local interactions within a spatial array can, by themselves, enable cooperative behaviour to persist indefinitely.

It is interesting to note that our spatial games can be thought of as showing elements of kin selection, group selection and reciprocal altruism (although it is, of course, not necessary to think of them in this way). Thus one may think of neighbouring individuals as being related by descent. Interactions occur among neighbours and hence among relatives. This suggests the interesting possibility of analysing the degree of kinship among neighbours and thence of using the concept of inclusive fitness [Hamilton, 1964] as a way of understanding some aspects of the dynamical properties of spatial games. It is also possible to evoke the formalism of reciprocal altruism: there are repeated encounters among neighbouring cells in successive rounds of the game. However, it is important to keep in mind that, in our models, individual cells do not have memory or elaborate strategies (although a spatial structure may be seen as a strategy with some kind of memory). One can also think of assigning fitness values to clusters of players of a certain strategy (cooperators). The success of such groups will depend on their detailed structure and their neighbourhood.

The need for cooperation is also a key feature of Eigen & Schuster's [1979] hypercycle theory. The early, prebiotic, self-replicating molecules are faced with an error threshold when they try to

accumulate more information in order to "encode" for more complex structures and more accurate replication devices. In the absence of an accurate, error-correcting machinery, the length of polymer molecules is quite limited and probably too small to encode for such machinery. This problem can be overcome if two, three or more different self-replicating molecules interact (cooperate) with each other in a cyclic way. Each member of such a "hypercycle" increases the replication rate (the fitness) of the subsequent member. This cyclic interaction seems to assure cooperation (and hence the accumulation of more information). Maynard Smith [1979] raised a devastating objection: hypercycles are vulnerable to defectors. Defectors are self-replicating molecules that use the catalytic support from their precursor molecule, but do *not* support any other molecule. Then the hypercycle obviously breaks down. In this sense a hypercycle is not an evolutionarily stable structure (see also Szathmary & Demeter [1987]).

Recently Boerlijst & Hogeweg [1991a, b] have performed computer simulations of hypercycles including spatial dimensions. They have found that larger hypercycles (with five or more members) form rotating spirals. These spirals have remarkable selection properties: they are able to eliminate defectors (parasites). Spirals can move and collide. Spirals can compete against each other. Selection favours faster rotating spirals. This can even lead to the selection of "altruistic" molecules with faster decay rates. There is still a problem. This selection based on spatial self-structuring favours shorter hypercycles over longer ones (because they rotate faster). This is exactly the opposite of what is required to accumulate information to overcome the error-threshold. Boerlijst & Hogeweg, however, have shown that selection can work in a counter-intuitive and surprising way if spatial structures are considered. This last point is very much in the spirit of our findings.

Hassel *et al.* [1991] have studied host-parasitoid interactions with limited, diffusive dispersal. They also find that local movement in a patchy environment can help otherwise-unstable host and parasitoid populations to persist together.

In short, we have shown that the simplest deterministic models of frequency dependent selection (or evolutionary games) can lead to a rich variety of spatial and temporal dynamics. Spatial chaos, dynamic fractals and kaleidoscopes are observed. The success of a given strategy depends on

the spatial structure of the population. Thus selection works on spatial structures.

Mathematics has had an inclination for nice structures since ancient times. The simplest mathematical models can generate very complicated dynamics whenever time (see May [1976]) or space is considered to be discrete. One of the appealing aesthetic elements in the present work is the combination between temporal chaos (the unpredictable oscillations of the frequencies of the individual strategies) and highly symmetric fractals. The kaleidoscopes of spatial evolutionary games have many applications in the "real world": there is a new industry for tiles, carpets, T-shirts, rose windows and lace doilies.

### Acknowledgments

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