

Fundamental clusters in spatial 2×2 games

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The notion of fundamental clusters is introduced, serving as a rule of thumb to characterize the statistical properties of the complex behaviour of cellular automata such as spatial 2×2 games. They represent the smallest cluster size determining the fate of the entire system. Checking simple growth criteria allows us to decide whether the cluster-individuals, e.g. some mutant family, are capable of surviving and invading a resident population. In biology, spatial 2×2 games have a broad spectrum of applications ranging from the evolution of cooperation and intraspecies competition to disease spread. This methodological study allows simple classifications and long-term predictions in various biological and social models to be made.

For minimal neighbourhood types, we show that the intuitive candidate, a 3×3 cluster, turns out to be fundamental with certain weak limitations for the Moore neighbourhood but not for the Von Neumann neighbourhood. However, in the latter case, 2×2 clusters generally serve as reliable indicators to whether a strategy survives.

Stochasticity is added to investigate the effects of varying fractions of one strategy present at initialization time and to discuss the rich dynamic properties in greater detail. Finally, we derive Liapunov exponents for the system and show that chaos reigns in a small region where the two strategies coexist in dynamical equilibrium.

Keywords: game theory; spatial 2×2 games; cellular automata; criteria for stability; persistence of strategies

1. INTRODUCTION

 2×2 games continue to receive ever increasing attention as simple models for biological, social and economic scenarios. Even though they are far too simple to capture every detail of such complex interactions, they represent a powerful tool for understanding the characteristics of such encounters. A well-known and well-studied member of these 2×2 games is the Prisoner's Dilemma, which explains the emergence of cooperative behaviour among selfish individuals (see, for example, Axelrod & Hamilton, 1981; Nowak & Sigmund, 1993; Milinski 1987; Wedekind & Milinski 1996; Fehr & Gächter 1999 and others). Perhaps even better known to behavioural ecologists is another 2×2 game called Chicken or the Hawk–Dove game, which describes intraspecies competition (Maynard Smith & Price, 1973).

Including spatial dimensions has proven to be a very fruitful extension to evolutionary game theory (see, for example, Nowak & May 1992; Lindgren & Nordahl 1994; Herz 1994; Killingback & Doebeli 1998; Eshel *et al.* 1999, 1998; Hartvigsen *et al.* 2000). Instead of considering a well mixed population where all individuals interact with each other, the individuals are bound to lattice sites and interact only with their neighbours. Each individual is engaged in a 2×2 game with each of its neighbours. In these games, the players have two options: they must choose between the strategies C and D. The pay-off matrix for the joint behaviour of the two players is then given by

$$\binom{RS}{TP},\tag{1}$$

where R denotes the pay-off for both players choosing C, P for mutual D, and for C against D the former gets S and the latter T. The rank ordering of the four pay-off values R, S, T and P define very different strategic

situations (Posch et al. 1999). For instance, T > R > P > S defines the Prisoner's Dilemma where C denotes cooperation and D defection. In this situation, rational players will opt for defection because it pays more, regardless of the opponent's decision. Consequentially, both players end up with P points only instead of the reward R for mutual cooperation; hence the dilemma.

Without loss of generality, we assume that R > P and normalize the pay-off values such that R = 1 and P = 0 holds. In case R > P does not hold, we simply interchange C and D. Using this convention, each game is represented by a point in the S, T-plane. The different rank ordering of R, S, T and P divides the plane into 12 regions as shown in figure 1; each region represents a certain type of game.

On our lattice, we consider only two kinds of players: those who always cooperate and those who always defect. An individual plays the game once with every nearest neighbour. Scenarios with repeated interactions have been studied by Nakamaru et al. (1997); Doebeli & Knowlton (1998) and Brauchli et al. (1999), for example. In each generation every individual plays with all its neighbours. At the end of a generation the score of each individual is determined by summing up its pay-offs against its neighbours. The scores in the neighbourhood, including the individual's own score, are ranked; in the following generation the individual adopts the strategy of the most successful player. In the case of a tie between the scores of C- and D-type players, the individual keeps its original strategy.

In biology, the score of an individual is interpreted in terms of reproductive success. For the above update rule, only the most successful strategy is able to reproduce by taking over neighbouring sites. An equally valid interpretation in social or economic contexts refers to individuals watching their neighbourhood and adapting the strategy of the most successful neighbour.

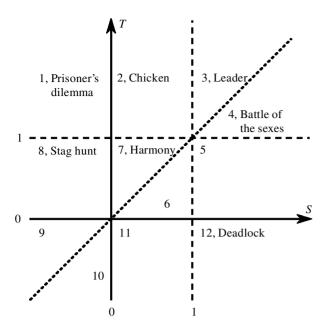


Figure 1. Partitioning of the S, T-plane according to the different rank ordering of R, S, T and P with R = 1, P = 0. Each of the 12 partitions refers to a specific type of 2×2 game. Those of particular interest are named as indicated in the diagram.

Even in this simple and completely deterministic situation, where individuals have no means to develop complex strategies, lattice dynamics turns out to be complex (see, for example, Killingback & Doebeli 1998), leading to intriguing dynamic patterns. Recent developments and some extensions are given in Nowak & Sigmund (2000).

The following investigations are aimed at determining the minimal requirements for a strategy to survive and invade a world of opponents. These requirements are a combination of suitable pairs of S, T-values together with a minimal cluster size. The study of such minimal clusters in spatial games was initiated by Killingback et al. (1999). We continue this work and extend it to 2×2 games in general.

2. GROWING CLUSTERS

Before studying the dynamic properties of certain cluster types, we must define the neighbourhood of an individual, i.e. its competitors. Because such games on grids are actually cellular automata, we consider the two minimal and commonly used neighbourhood types for cellular automata: the Von Neumann and the Moore neighbourhoods. The former consists of the four nearest neighbours, while the latter includes interactions with the eight nearest neighbours. For a good introduction to the pioneering work of Von Neumann and games in general see Sigmund (1995).

The dynamic behaviour of the cellular automata under consideration is very complex, e.g. the subsequent state of one site depends not only on its neighbourhood but also on the neighbours of its neighbours. With the Moore neighbourhood, this adds up to 25 cells involved and thus to 225 transition rules. For this reason we are interested in simple rules of thumb to determine the long-term statistical behaviour of the system. We therefore introduce

the notion of fundamental clusters. They must satisfy the following conditions: first, if certain growth criteria are met (see §§ (a) and (b) below), expansion must continue indefinitely and guarantee the survival of the strategy. Second, no smaller cluster is able to fulfil the first condition. The role of such clusters, and 3×3 clusters in particular, in determining the long-term dynamic behaviour of spatial games was first pointed out by Killingback et al. (1999).

Note that the size and shape of fundamental clusters generally depends on the values of S and T. However, to obtain simple rules of thumb, we limit our investigations to clusters of cooperators of square shape. On rectangular lattices, they have the smallest perimeter-to-area ratio. This minimizes the line of interference with the surroundings, and therefore represents the most favourable situation for cluster individuals in a hostile environment, i.e. surrounded by defectors. Thus, if square clusters are unable to grow in this situation, then no other cluster shape will be formed.

In the following, we derive the conditions imposed on S and T such that 3×3 clusters grow along the edges and/or the corners while parrying attacks by opponents. Then we investigate for 2×2 games in general whether expansion and invasion continue indefinitely, given that the growth criteria are satisfied for 3×3 clusters, i.e. if 3 × 3 clusters are fundamental or at least a good approximation.

(a) The Von Neumann neighbourhood

The Von Neumann neighbourhood consists of the four nearest neighbours: on the left, right, above and below. In the following, we derive inequality relations for S and Tsuch that 1×1 , 2×2 and 3×3 clusters grow. For that purpose, we determine and compare the achieved scores of a player and its neighbours. We derive sufficient conditions that the player sticks to its strategy (persistence) and also neighbours switch to the player's strategy (expansion). The small figures to the right of the equations indicate the type of interaction considered.

(i) 1×1 clusters grow if

$$\begin{vmatrix} 4S > T \text{ (persistence)} \\ 4S > 0. \end{vmatrix}$$
 C D (2)

(ii) 2 × 2 clusters grow if

$$2 + 2S > T$$
 (persistence)
 $2 + 2S > 0$.

(iii) 3×3 clusters:

(a) Corners persist if

$$3 + S > T. \tag{4}$$

(b) Corners grow if

(c) Edges persist if either

$$2 + 2S > T,$$
or
$$4 > T.$$
(6)

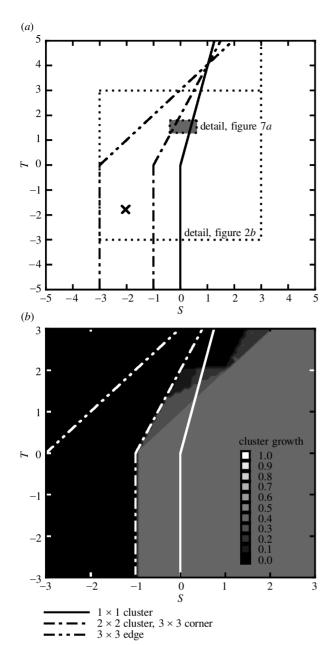


Figure 2. Von Neumann neighbourhood. (a) Boundaries in the S, T-plane indicating maximal T- and minimal S-values for different cluster sizes and cluster parts to grow. (b) Fraction of cooperators f_c^t originating from a single 3×3 cluster of cooperators in an infinite world of defectors. Black denotes low f_c^t while white indicates f_c^t close to 1. Intermediate values are displayed in different shades of grey. Technical details: f_c^t is calculated on a 49 × 49 grid after t = 22 generations as a function of S, T. For $t \le 22$ the system evolves as on an infinite grid.

(d) Edges grow if

$$\begin{vmatrix} 3 + S > T \\ 3 + S > 0. \end{vmatrix}$$



The different regions in the S, T-plane resulting from the above equations are shown in figure 2a. Comparisons of the above equations yield the following results:

(i) Growth conditions for 2×2 clusters and corners of 3 × 3 clusters are identical (cf. equations (3) and (5)).

- (ii) If corners of 3×3 clusters grow, edges persist and vice versa (cf. equations (5), (6) and equations (4), (7), respectively).
- (iii) Inequalities involving the central site occur only in the second line of equation (6). Note that this condition can be dropped because the first part is always satisfied if corners can grow.
- (iv) In contrast to the Moore neighbourhood (see equations (16)–(18)), neither corners nor edges growing in one direction become defeated by defectors attacking from another side.

As a next step, we investigate the fate of a single 3×3 cluster evolved over several generations as a function of S and T. This is done by systematically sampling the S, Tplane and calculating the fraction of cooperators f_{c}^{t} after a specified number of generations t. The result is displayed in figure 2b.

Comparisons of the growth criteria and the expansion properties in figure 2a,b determine whether 3×3 clusters are fundamental. The short answer is 'no'. In a more detailed view, consider the following: for a considerable area in the S, T-plane, the growth criteria are met, i.e. edges grow and thus corners persist. Nevertheless, the cluster dies out after few generations. In figure 2a this area is marked with a cross.

According to the results derived above, it is straightforward to check whether 2×2 clusters could meet the criteria for fundamental clusters. This time the answer is 'almost'. With the exception of a small area with 2 < T < 4 and close to the boundary delimited by equation (3), we could not find any further areas where 2×2 clusters vanish. Near this boundary, a large number of dynamic domains can be identified. They range from isolated C patches and simple growing C clusters to connected C networks and dynamic fractals. Note that for T > 4, growth criteria for 1×1 clusters are weaker than for 2×2 clusters (see figure 2a). In conclusion, if the growth criteria for 2×2 clusters hold, the chances are good that the strategy is able to invade a world of opponents and will survive forever.

(b) The Moore neighbourhood

The Moore neighbourhood consists of the eight nearest neighbours including all neighbours reachable by a chess-kings move. In analogy to the Von Neumann neighbourhood we derive similar but (because of the larger neighbourhood) slightly more complicated inequality relationships. As before, the small figures to the right of the equations indicate the type of interaction considered.

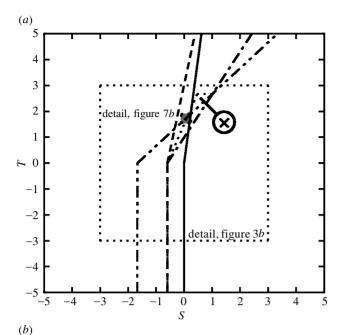
(i) 1×1 clusters grow if

(ii) 2×2 clusters persist if

$$3 + 5S > 2T
3 + 5S > T.$$
(9)

(iii) 2×2 clusters grow if

$$\begin{vmatrix} 3 + 5S > 2T \\ 3 + 5S > 0. \end{vmatrix}$$
 (10)



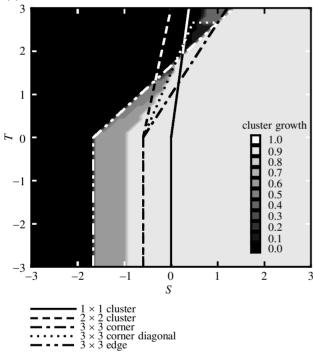
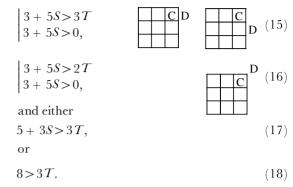


Figure 3. Moore neighbourhood. (a) Boundaries in the S, Tplane indicating the maximal *T*- and minimal *S*-values for different cluster sizes and cluster parts to grow. (b) Fraction of cooperators f_c^t originating from a single 3×3 cluster of cooperators in an infinite world of defectors. Note that the boundary S = -1, T < 0 is not explained by the growth conditions of the 3×3 cluster. It is the result of differing growth conditions of subsequent structures. Colour code for f_c^t and technical details are as in figure 2.

(iv)
$$3 \times 3$$
 clusters:
(a) Corners persist if
$$\begin{vmatrix}
5 + 3S > 3T \\
5 + 3S > T,
\end{aligned}$$
or
$$\begin{vmatrix}
8 > 3T \\
8 > T.
\end{vmatrix}$$
(12)



(c) Corners grow in the indicated directions if



(d) Edges grow in the indicated directions if

$$\begin{vmatrix}
5 + 3S > 3T \\
5 + 3S > 0.
\end{vmatrix}$$

$$\begin{vmatrix}
D \\
C
\end{vmatrix}$$

Equations (8)–(19) divide the S, T-plane into different regions as shown in figure 3a. Comparing the different inequality relationships, the following results obtained.

- (i) According to equation (19), an edge either invades all three or none of the accessible sites of opponents.
- (ii) If corners grow, they occupy either all five accessible sites or only the diagonal site (cf. equation (16) and minor restrictions according to the following two remarks).
- (iii) The diagonal growth of a corner (see equation (16)) requires special attention. Even though the corner may grow successfully, further conditions must hold to guarantee that the corner itself persists. For certain values of S and T, the corner can be successfully attacked by the defector in the middle of the edge. In that case, the persistence of the edge must be guaranteed by either the central site (equation (18)) or the cooperator on the edge (equation (17)).
- (iv) The role of the central site is of minor importance. Only in the tiny parameter region marked with a cross in figure 3a, where equation (16) holds but equation (17) does not, does the central site protect corners and edges against attacks.
- (v) Similar to the Von Neumann neighbourhood, corners of a 3 × 3 cluster persist if edges grow and vice versa (cf. equations (11)-(18)) with the aforementioned exception.

To complete the picture, we determine the fate of a single 3×3 cluster evolved over several generations. Figure 3b displays the fraction of cooperators f_c^t after t generations as a function of S and T. Comparisons of figure 3a and 3b show that 3×3 clusters expand where the growth criteria are met. Indeed, we did not find any S,Tvalues where cooperators vanished while satisfying the growth criteria. However, the following restrictions apply:

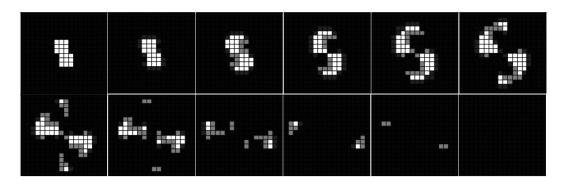


Figure 4. The Moore neighbourhood: two particularly arranged 3×3 clusters collide and annihilate producing a beautiful but fatal whirl-like pattern over ten generations (S=0.05, T=1.65). Black sites indicate defectors and white cooperators. Dark grey specifies cooperators that switched to defection in this generation and similarly, light grey denotes defectors that switched to cooperation. The two latter shades of grey are useful for estimating the activity in the system. Top row from left to right t=0-5; bottom row from left to right t=0-11.

- (i) For very small values of S in the region marked with a cross in figure 3a, 3×3 clusters are unable to grow. The corners expand diagonally but the initiated growth soon wears off, resulting in a periodic cycle.
- (ii) The growth capabilities of 1 × 1 clusters guarantee persistence and even growth of cooperators in some regions of the *S*, *T*-plane where 3 × 3 clusters cannot grow. Even though cooperation may spread, it remains impossible to form larger clusters. Usually isolated cooperators are surrounded by frustrated players constantly changing their strategy. Note that in this region equation (16) holds while violating equations (17) and (18).
- (iii) Even though we did not find regions where cooperators systematically vanished, we did find interesting configurations where cooperation dies out after several generations. Figure 4 shows an example of two colliding 3×3 clusters annihilating in a whirl-like pattern. On arbitrary but finite sized grids, cooperators may die out after some time. Interestingly, this was mainly observed for highly symmetrical configurations. For example, a single 3×3 cluster on a 49×49 grid dies out after 444 generations (e.g. S=0.05, T=1.65).

To conclude, the growth capability of 3×3 clusters generally guarantees infinite expansion and survival of a strategy on infinite grids. However, note that the reverse does not necessarily hold. As mentioned earlier, the diagonal growth of corners requires careful treatment. Although the above restrictions for 3×3 clusters are rather weak and rarely apply, they should be kept in mind, particularly when dealing with smaller grid sizes. Also note that the expansion criteria for 2×3 and 3×3 clusters are identical with the exception of the tiny region marked with a cross. Thus, it usually suffices to verify the growth conditions for 2×3 clusters. Therefore, both, 2×3 and 3×3 clusters serve as powerful approximations to fundamental clusters.

3. CLUSTER DYNAMICS

A closer look at the deterministic expansion of a single 3×3 cluster for Von Neumann and Moore neighbour-

hoods (figures 2a and 3a) reveals that growth is far less efficient for the former. The smaller Von Neumann neighbourhood reduces the speed of expansion and leads to intermediate values for f_c^t (indicated by the grey colouring) even for most favourable S, T-values (lower right corner). Many of the boundaries separating regions of different growth are readily identified as inequality relations introduced above. Each boundary specifies a particular type of encounter between cooperators and defectors. The side of higher S- and lower T-values favours cooperators, while on the other side defectors are better off. On the boundary itself, it is a draw and the players stick to their strategy. The most interesting parameter values are found along the transition region from dominating defection to prevailing cooperation. S, T-values from this region lead to fascinating dynamic patterns, often resembling an evolutionary kaleidoscope (Nowak & May, 1993).

To discuss the above results in a more general context and to test their relevance in more realistic scenarios, we consider randomly initialized grids with a certain fraction of cooperators $f_{\rm c}^{\,0}$. It turns out that for considerable regions of the S, T-plane, the average fraction of cooperators $\bar{f}_{\rm c}$ sensitively depends on $f_{\rm c}^{\,0}$. Figures 5 and 6 display \bar{f}_c as a function S, T for $f_c^0 = 0.8$ and $f_c^0 = 0.2$, respectively. As expected, the area where cooperation dominates is significantly larger for higher $f_{\rm c}^{\,0}$ (figure 5). In comparison to the clinical situation of a single cluster (figures 2 and 3), new boundaries appear, indicating that other inequality relations became relevant. The boundaries appearing for a single cluster are much more pronounced for small f_s^0 (figure 6). This follows from the rapidly decreasing probability of finding clusters of a certain size at initialization time for decreasing f_c^0 . Hence, it is very likely that only a few clusters of the fundamental size are formed.

Striking differences between high and low f_c^0 are observed in the region of low S- and T-values. Here, neither C nor D clusters of size 3×3 or smaller grow. The figures clearly show that the initially prevailing strategy outperforms and further diminishes the minority. Interestingly, in all other areas it takes only few generations for the dynamics to level out the initial differences, leading to very similar patterns.

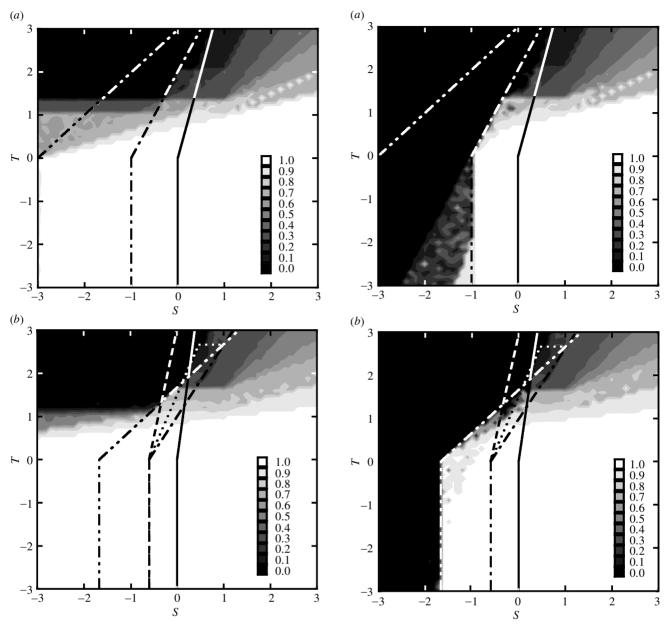


Figure 5. Cluster expansion in an inhomogenous environment. Average fraction of cooperators \bar{f}_c as a function of T, S for (a) Von Neumann and (b) Moore neighbourhood. At t = 0 the grid was initialized at random with a fraction of $f_c^0 = 80\%$ cooperators. To ease comparisons, the various dashed lines represent the boundaries introduced in figures 2a and 3a, respectively. Light areas again denote high fractions of cooperators and dark areas high fractions of defectors.

Technical details: \bar{f}_c was calculated on a 49 × 49 grid, averaged over 22 generations after a relaxation time of 24 generations and repeated for three realizations. Both, averaging and relaxation times were chosen to minimize effects of the finite size of the system.

For most S, T pairs the random initial configurations evolve towards static patterns with an overwhelming majority of one strategy together with patchy distributions of small clusters of the other strategy. In stark contrast to these rather uninteresting domains, fascinating dynamic patterns emerge for parameters within the transition region between cooperation and defection. The dynamic equilibrium between the two strategies

Figure 6. Cluster expansion in an inhomogenous environment. Same set-up as in figure 5, only for a lower initial fraction of cooperators $f_c^0 = 20\%$. Note that the boundary S = -1, T < 0 appearing in figure 3 has almost vanished for inhomogenous configurations. This stresses the importance of the growth conditions for the initial 3×3 cluster.

generates a variety of dynamic patterns, such as waves of cooperators travelling across the grid or small growing clusters of cooperators splitting periodically. In addition, similar to Conway's Game of Life (Berlekamp et al. 1982), special structures such as blinkers, gliders and rotators are observed. Generally, the dynamic coexistence of cooperators and defectors appears to be stable with the exception of smaller grid sizes (as noted above). Note that for S,T values within the transition region, no part of the grid ever becomes static and frozen. Every now and then the strategy of every player gets challenged and possibly changes. In agreement with our results, the different dynamic domains have already been discussed by Nowak & May (1992, 1993) for T > 1

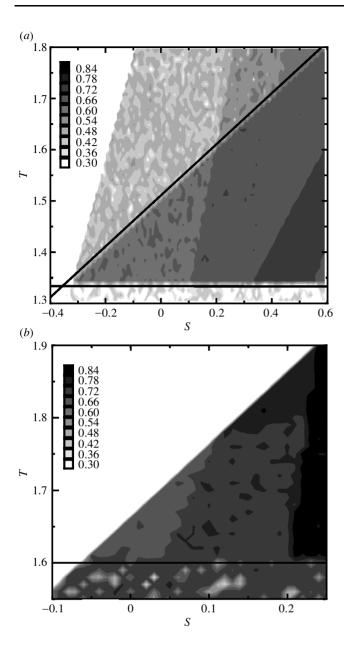


Figure 7. Liapunov exponent $\lambda_{\rm d}$ as a function of S, T in a small region of the S, T-plane, where C and D players coexist in dynamic equilibrium. $\lambda_{\rm d}$ for (a) the Von Neumann and (b) the Moore neighbourhoods. $\lambda_{\rm d} > 0$ indicates that the emerging rich dynamic patterns are produced by weakly chaotic dynamics. For constant T and increasing S, $\lambda_{\rm d}$ increases as the minimal cluster size capable of growing decreases. The peak (Von Neumann: $\lambda_{\rm d} \approx 0.75$; Moore: $\lambda_{\rm d} \approx 0.85$) lies shortly after the boundary where 1×1 clusters may additionally grow. For still larger S-values $\lambda_{\rm d}$ decreases again and soon returns to negative values.

in the limit $S \to 0$, focusing on the coexistence of C and D players. This limit separates the Prisoner's Dilemma and the Chicken Game. In the S,T-plane, different domains leading to specific dynamics can be identified. Interestingly, for both neighbourhood types, some small domains cross the boundary S = 0. Consequentially, within these parameter domains, the spatial dynamics of the two games are identical, even though they describe two rather different biological or social scenarios.

In the remaining text we derive quantitative measures for the dynamic properties of cluster expansion in a particularly interesting area where C and D players coexist in dynamic equilibrium. For the Von Neumann neighbourhood we focus on an area roughly delimited by the conditions that C corners (see equation (3)) and D peaks (D surrounded by three C) grow (3T > 3 + S, 3T > 4). Similarly, for the Moore neighbourhood the area under consideration is roughly bounded by the conditions that C edges (see equation (15)) and D corners grow (5T > 5 + 3S, 3T > 8). In the lower right part of both areas chaos reigns, indicated by Liapunov exponents $\lambda_d > 0$. Details on the definition and calculation of λ_d are relegated to Appendix A. Figures 7a and b display λ_d as a function of S, T for the appropriate area of the S, T-plane.

To draw a crude picture of the rich dynamics of these systems, we outline the characteristics for some constant T (Von Neumann: $T \approx 1.5$; Moore: $T \approx 1.7$) and increasing S: for small S, near the left boundary of the displayed areas, cooperators quickly vanish resulting in static configurations with an overwhelming majority of defectors. These rather uninteresting states are characterized by $\lambda_d < 0$. Increasing S eventually allows C clusters to grow and to build C networks for the Von Neumann neighbourhood with $\lambda_d \approx 0$. Once we cross a crucial boundary (Von Neumann: 2T < 3 + S; Moore: 3T < 5 + 3S) the dynamics change completely. Here we observe dynamic equilibrium producing intriguing patterns such as waves of cooperators travelling across the grid, but we also find structures such as growers, gliders, rotators and blinkers. In this area, the system displays chaotic dynamics with $\lambda_d > 0$. Further increases in S enable clusters of decreasing size to grow while increasing λ_d . The peak of λ_d (Von Neumann: $\lambda_d \approx 0.75$; Moore: $\lambda_d \approx 0.85$) lies shortly after the boundary where 1×1 clusters may additionally grow. For still larger S, the travelling waves eventually decay into many tiny static areas, mostly consisting of a single site, surrounded by players constantly changing their strategy. At this stage (not shown in the figures), the system has returned to a state with $\lambda_{\rm d} < 0$. Instead of taking the maximal Liapunov exponent, we could draw a very similar picture by considering other quantities such as the power spectrum and the autocorrelation. In accordance with chaotic dynamics, the former becomes continuous and the latter approximately constant with a δ peak around zero.

In spatially extended systems, the timing of the grid updates is usually of crucial importance. For a detailed discussion of synchronized versus sequential updating we refer to Hubermann & Glance (1993) and Nowak *et al* (1994a,b). In this paper we restrict our attention to synchronized grid updates. However, preliminary simulations have shown that the phase diagrams of the S,T-plane are hardly affected by the different update rules. Generally, the boundaries are slightly shifted in favour of defectors, and in some regions, where only small fractions of cooperators were able to survive, they vanish completely.

4. CONCLUSIONS

Fundamental clusters play an important role in spatially extended systems. They allow us to predict certain features

of the long-term behaviour simply by checking the growth criteria of such clusters. If they are met, the clusterindividuals are able to survive and successfully invade a world of opponents. Usually such cluster-individuals are considered to be some sort of mutant family attempting to invade a resident population.

For instance, for the Prisoner's Dilemma we deduce from figures 5 and 6 that, regardless of the neighbourhood type, cooperative behaviour spreads only for large S and small T, i.e. $S \to 0$, $T \to 1$. For a small range of S, T-values cooperators and defectors coexist, but generally clusters of cooperators are without hope and vanish quickly.

For minimal neighbourhood types, such as the Von Neumann and Moore neighbourhoods, 3 × 3 clusters are intuitive candidates to serve as fundamental clusters. For the Von Neumann neighbourhood 3 × 3 clusters are not fundamental. For a considerable range of the parameter space S, T 3×3 clusters grow in the first generation, satisfying the growth criteria, but then they quickly vanish. However, the smaller 2×2 clusters turn out to be almost fundamental. With the exception of a tiny region in the S, T-plane we could not find further regions where 2×2 clusters vanish. Thus, the growth criteria for 2×2 clusters are reliable indicators regarding the long-term fate of the cluster individuals.

For the Moore neighbourhood, the growth of 3×3 clusters indeed guarantees infinite expansion with certain weak restrictions. We did not find areas in the S, T-plane where 3×3 clusters systematically vanished while satisfying the growth criteria. However, we found interesting configurations that did vanish. For example, two colliding 3 × 3 clusters may annihilate or, on smaller grids with periodic boundary conditions, highly symmetrical configurations suddenly disappear. Moreover, along one boundary of a tiny region (marked with a cross in figure 3a) growth is limited to a small area around 3×3 clusters and hence violates conditions for fundamental clusters. With the exception of this tiny region, 2×3 clusters satisfy identical growth criteria. Thus, for the Moore neighbourhood 2×3 and 3×3 clusters both serve as powerful approximations to fundamental clusters allowing for reliable predictions.

For stochastical initialization of the grid with a certain fraction of cooperators $f_{\,\mathrm{c}}^{\,\mathrm{0}},$ we show that for considerable regions of the S, T plane the average fraction of cooperators \bar{f}_c sensitively depends on f_c^0 . Mostly in areas where 3 × 3 or smaller clusters of neither C nor D players grow (low S and low T), the initial majority dominates and further diminishes the minority. In general, however, differences to results for a single cluster are surprisingly small. It appears that the growing clusters level out most of the initial differences.

Finally, we introduced a simple measure λ_d , by analogy to Liapunov exponents, to characterize dynamic properties of finite systems discrete in time and space. This indicates that chaotic dynamics $(\lambda_d > 0)$ are responsible for the fascinating patterns generated in the small region of the S,T-plane where C and D players coexist in dynamic equilibrium.

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APPENDIX A: METHODS

(a) Determining Liapunov exponents for systems discrete in time and space

The maximal Liapunov exponent λ_{max} is used to characterize dynamic properties of a system. For $\lambda_{max} > 0$ the system is chaotic, linear for $\lambda_{max} = 0$ and attractive for $\lambda_{max} < 0$, i.e. small disturbances undergo an exponential amplification, remain constant or vanish in short time. For a brief introduction we refer to Schuster (1995).

In this Appendix we derive an analogous quantity λ_d for systems discrete in time and space. Because λ_d allows for very similar classifications of the systems dynamics, we refer to it as a Liapunov exponent.

Consider an $n \times m$ grid, on which a specified fraction of cooperators f_c^0 is randomly distributed. Let the system relax by evolving it over at least $\max(n, m)/2$ generations. This corresponds to the minimal time it takes to spread information across the entire grid. In a next step, the relaxed state is duplicated and in one copy the strategy of $\varepsilon \ll n \cdot m$ randomly chosen players is changed from C to D and vice versa. The Hamming distance d_t is used to determine the difference of the two copies. It indicates the number of sites occupied by unequal strategies at time t. Thus, the initial distance of the two copies is $d_t \le \varepsilon$. λ_d is derived from the time evolution of d_t when evolving the two copies in

$$\lambda_{\rm d} = \frac{1}{\mathcal{N}} \sum_{l=0}^{\mathcal{N}} \ln \frac{d_{l+1}}{d_l}.\tag{20}$$

For the systems under consideration, two problems arise from equation (20): first, d_t cannot become arbitrarily large due to the finite size of the grid. This puts an upper limit to the meaningful number of updates N and consequentially the accuracy of $\lambda_{\rm d}$. Second, for $\varepsilon > 1$ disturbances initiated by the different seeds expand independently and interfere in an unpredictable manner. This puts further restrictions on \mathcal{N} . Also note that $\varepsilon > 1$ must hold to allow for negative values of λ_d .

Problems arising from numerical overflow are usually solved by periodically rescaling d_t while preserving its direction in multidimensional systems. For cellular automata such rescaling is impossible because of the binary character of the system. For this reason, we repeat the above procedure and take the average to obtain λ_d . Averaging over different initial disturbances is important because often the time evolution of d_t sensitively depends on the immediate neighbourhood of the flipped sites.

An important restriction of the outlined procedure concerns parameter ranges with λ_d close to zero with static configurations of the grid. In those regions, small disturbances often lead to short bursts of activity with d_t quickly approaching a constant value. By inspection it is readily seen that $\lambda_d \to 0$, but the numerical procedure typically returns positive values. However, the unreliable results are revealed by a significantly higher standard deviation.

REFERENCES

Axelrod, R. & Hamilton, W. D. 1981 The evolution of cooperation. Science 211, 1390.

Berlekamp, E., Conway, J. & Guy, R. 1982 Winning ways for your mathematical plays. New York: Academic Press.

Brauchli, K., Killingback, T. & Doebeli, M. 1999 Evolution of cooperation in spatially structured populations. J. Theor. Biol. **200**, 405.

- Doebeli, M. & Knowlton, N. 1998 The evolution of interspecific mutualisms. Proc. Natl Acad. Sci. USA 95, 8676.
- Eshel, I., Samuelson, L. & Shaked, A. 1998 Altruists, egoists and hooligans in a local interaction model. Am. Econ. Rev. 88, 157.
- Eshel, I., Sansone, E. & Shaked, A. 1999 The emergence of kinship behaviour in structured populations of unrelated individuals. Int. 7. Game Theory 28, 447.
- Fehr, E. & Gächter, S. 2001 Cooperation and punishment in public goods experiments. Am. Econ. Rev. (In the press.)
- Hartvigsen, G., Worden, L. & Levin, S. A. 2000 Global cooperation achieved through small behavioural changes among strangers. Complexity 5, 14.
- Herz, A. V. M. 1994 Collective phenomena in spatially extended evolutionary games. J. Theor. Biol. 169, 65.
- Hubermann, B. A. & Glance, N. S. 1993 Evolutionary games and computer simulations. Proc. Natl Acad. Sci. USA 90, 7712.
- Killingback, T. & Doebeli, M. 1996 Spatial evolutionary game theory: Hawks and Doves revisited. Proc. R. Soc. Lond. B 263,
- Killingback, T. & Doebeli, M. 1998 Self-organized criticality in spatial evolutionary game theory. 7. Theor. Biol. 191, 335.
- Killingback, T., Doebeli, M. & Knowlton, N. 1999 Variable investment, the continuous Prisoner's Dilemma, and the origin of cooperation. Proc. R. Soc. Lond. B 266, 1723.
- Lindgren, K. & Nordahl, M. G. 1994 Evolutionary dynamics of spatial games. Physica D 75, 292.
- Maynard Smith, J. & Price, G. 1973 The logic of animal conflict. Nature 246, 15.

- Milinski, M. 1987 Tit for tat in sticklebacks and the evolution of cooperation. Nature 325, 433.
- Nakamaru, M., Matsuda, H. & Iwasa, Y. 1997 The evolution of cooperation in a lattice-structured population. J. Theor. Biol. **184** 65
- Nowak, M. A. & May, R. M. 1992 Evolutionary games and spatial chaos. Nature 359, 826.
- Nowak, M. A. & May, R. M. 1993 The spatial dilemmas of evolution. Int. J. Bifurcation Chaos 3, 35.
- Nowak, M. A. & Sigmund, K. 1993 A strategy of win-stay, lose-shift that outperforms tit-for-tat in the prisoner's dilemma game. Nature 364, 56.
- Nowak, M. A. & Sigmund, K. 2000 In The geometry of ecological interaction (ed. U. Dieckmann, R. Law & J. A. Metz), pp. 135-150. Cambridge University Press.
- Nowak, M. A., Bonhoeffer, S. & May, M. 1994a Spatial games and the maintenance of cooperation. Proc. Natl. Acad. Sci. USA
- Nowak, M. A., Bonhoeffer, S., & May, R. M. 1994b More spatial games. Int. J. Bifurcation Chaos 4, 33.
- Posch, M., Pichler, A. & Sigmund, K. 1999 The efficiency of adapting aspiration levels. Proc. R. Soc. Lond. B 266, 1427.
- Schuster, H. G. 1995 Deterministic chaos. Weinheim, Germany:
- Sigmund, K. 1995 Games of life. Harmondsworth, UK: Penguin. Wedekind, C. & Milinski, M. 1996 Human cooperation in the simultaneous and the alternating prisoner's dilemma: Pavlov versus generous tit-for-tat. Proc. Natl Acad. Sci. USA **93**, 2686.