EFFECTS OF SPACE IN 2 × 2 GAMES

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A systematic analysis of the effects of spatial extension on the equilibrium frequency of cooperators and defectors in 2 × 2 games is presented and compared to well mixed populations where spatial extension can be neglected. We demonstrate that often spatial extension is indeed capable of promoting cooperative behavior. This holds in particular for the prisoner's dilemma for a small but important parameter range. For the hawk–dove game, spatial extension may lead to both, increases of the hawk- as well as the dove-strategy. The outcome subtly depends on the parameters as well as on the degree of stochasticity in the different update rules. For rectangular lattices, the general conclusions are rather robust and hold for different neighborhood types i.e. for the von Neumann as well as the Moore neighborhood and, in addition, they appear to be almost independent of the update rule of the lattice. However, increasing stochasticity for the update rules of the players results in equilibrium frequencies more closely related to the mean field description.

Keywords: Cooperation; prisoner's dilemma; lattice games.

1. Introduction

The essence of various ecological interactions among animals can be modeled by so-called 2 × 2 games describing pairwise interactions between individuals with two behavioral strategies to choose from. Depending on their joint behavior, each individual obtains a certain payoff. In biology, this payoff is usually related to the fitness of an individual, i.e. to its reproductive success. Consequentially, in a population of interacting individuals, successful strategies achieving high payoffs will be prevalent.

The most prominent representative of such 2 × 2 games is certainly the prisoner's dilemma (PD) [Axelrod, 1984]. The PD has received widespread attention for explaining the emergence of cooperative and altruistic behavior among unrelated selfish individuals. In the PD, two players have to decide whether to cooperate (C) or defect (D). Mutual cooperation pays a reward R while mutual defection results in a punishment P. If one player opts for D and the other for C, then the former obtains the temptation to defect T and the latter is left with the sucker's payoff S. From the rank ordering of the four payoff values $T > R > P > S$ follows that a player is always better off defecting, regardless of the opponents decision. Consequentially, rational players will always end up with the punishment P instead of the higher reward for cooperation R. Nevertheless, cooperative behavior can establish through basic discrimination mechanisms that enable individuals to target their altruistic acts towards certain other individuals only. Since Axelrod's seminal work, numerous articles have been published on the subject suggesting different mechanisms to promote cooperative behavior. These mechanisms can be roughly divided into three

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categories: (a) repeated interactions of the same individuals, (b) identification through secondary traits such as reputation or (c) spatial extension. The latter will be the main topic of this article. In (a), individuals trigger their actions on the outcome of previous encounters (see e.g. [Nowak & Sigmund, 1993; Binmore & Samuelson, 1992; Lindgren, 1991; Milinski, 1987]). Memorizing the past, enables individuals to cooperate with cooperative opponents only. In (b), individuals interact only once but carry an image score summarizing their past actions (see e.g. [Nowak & Sigmund, 1998; Wedekind & Milinski, 2000]). The opponents reputation, i.e. its image score, again allows to discriminate between cooperators with high and defectors with low scores. In spatially extended systems (c), individuals interact only with their local neighborhood (see e.g. [Nowak & May, 1992; Doebeli & Knowlton, 1998; Killingback & Doebeli, 1998; Hauert, 2001a; Herz, 1994; Szabó *et al.*, 2000]). Cooperators may survive by forming clusters, thereby minimizing contacts with defecting players.

Closely related to the PD is another 2×2 game called chicken or hawk–dove game [Maynard Smith & Price, 1973] describing intra-species competition or, in the form of the snow-drift game [Sugden, 1986], explaining biproduct mutualism. Actually, it differs only in the payoff ranking with $T > R > S > P$ i.e. with the sucker's payoff S being more favorable than the punishment P.

In the general formulation, a 2×2 game is determined by the payoff matrix

$$\begin{pmatrix} R & S \\ T & P \end{pmatrix}, \qquad (1)$$

where the rank ordering of the four payoff values R, S, T, P determines the characteristics of the game. Without loss of generality we may assume $R > P$ (if this does not hold, we simply interchange C and D) and normalize the payoff values such that $R = 1$, $P = 0$ holds. This leads to 12 different rank orderings corresponding to very different strategic situations (see e.g. [Rapoport *et al.*, 1976; Binmore, 1992; Colman, 1995]). Each game corresponds to a region in the S, T-plane as shown in Fig. 1.

If we now consider large populations of interacting individuals, further assumptions concerning the structure of the population are required. In the simplest case, each individual interacts with every other one with equal probability i.e. the population is well mixed and has no structure at all. For populations consisting of only two types of players —
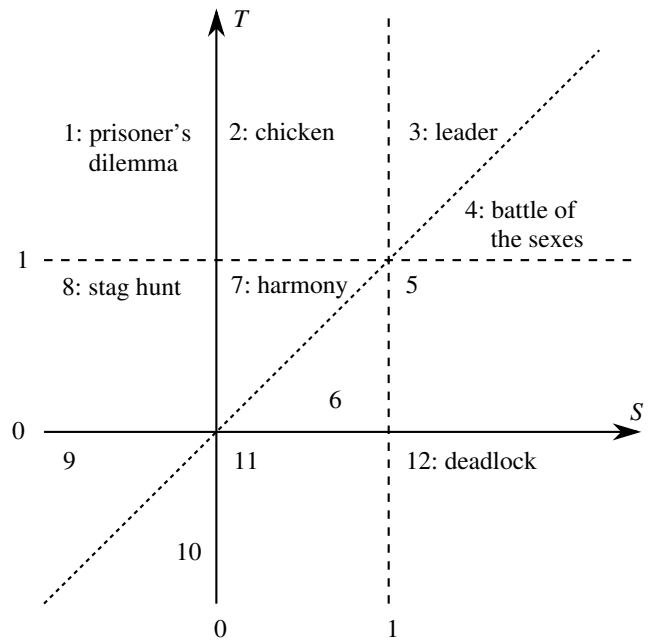

Fig. 1. The rank orderings of the parameters R, S, T and P with $R = 1$, $P = 0$ divide the S, T-plane into 12 different regions. Each region determines the parameter range for a particular 2×2 game.

those who always cooperate and those who always defect — the equilibrium distribution of the two strategies can be calculated analytically in the so-called mean field approximation [Posch *et al.*, 1999]. In the following section we briefly review this case and for the remaining sections, it provides a valuable basis for comparisons and discussions of our results for spatially structured populations.

The other extreme is represented by populations with rigid spatial structures such as regular lattices where each individual is bound to a single lattice site and interacts pairwise with its local neighbors only. Even though this provides only a crude approximation to ecological scenarios in nature, it turned out to be a fruitful extension providing substantial and interesting new insights. Spatial extension is not only capable of promoting cooperative behavior but also produces very complex dynamics [Nowak & May, 1993; Killingback & Doebeli, 1998]. In this article, however, we concentrate on the equilibrium frequencies of the strategies for different neighborhood types and different update rules on the player's as well as the lattice level. For the lattice, we consider random or asynchronous and synchronized updates that model populations with overlapping and nonoverlapping generations, respectively. For the players, we consider several update rules with different degrees of stochasticity.

2. Mean Field Games

In the mean field description all spatial correlations are neglected. This corresponds to well mixed populations where individuals are randomly matched. In order to determine the equilibrium frequencies of both, the always cooperate and the always defect strategies, we consider a homogeneous population of residents, and determine the fate of a mutant strategy with frequency x_m. In a well mixed population, the success of the mutant strategy depends only on x_m as well as on the parameters S, T. The frequency of the resident is simply given by $x_r = 1 - x_m$. For cooperative mutants attempting to invade a resident population of defectors we obtain the payoffs P_r and P_m for mutants and residents, respectively:

$$P_r = x_m T$$
$$P_m = x_r S + x_m .$$

In biological context, the payoff denotes the fitness and hence the reproductive success of mutants and residents. Similarly, in terms of cultural evolution, an individual imitates the strategy of a randomly chosen "model" member of the population with a probability proportional to the difference between the model's payoff and its own, provided the difference is positive and with probability 0 otherwise [Weibull, 1995; Schlag, 1998]. In the continuous time limit both approaches lead to the replicator equation [Hofbauer & Sigmund, 1998]:

$$\dot{x}_i = x_i(P_i - \overline{P}) \quad \text{with } i \in \{r, m\} . \tag{2}$$

The long term behavior of the population is determined by the three fixed points of Eq. (2): $\hat{f}_c^1 = 0$, $\hat{f}_c^2 = 1$ and $\hat{f}_c^3 = S/(S + T - 1)$, where $\hat{f}_c^i$ denotes the equilibrium fractions of cooperators in the population as a function of S, T (see Fig. 2). By inspection, four different dynamical domains are
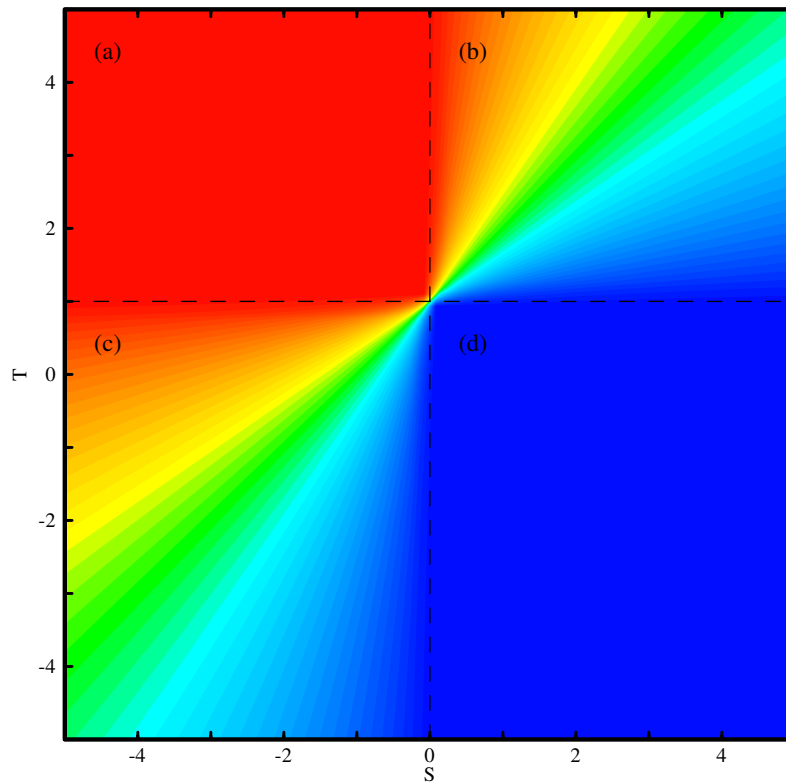

Fig. 2.   Fraction of cooperators $\hat{f}_c$ as a function of S, T in the mean field description. Regions with low $\hat{f}_c$ i.e. high fractions of defectors are colored red. Cooperative regions with $\hat{f}_c$ close to 1 are blue. Intermediate values of $\hat{f}_c$ are shown in yellow, green and light blue colors. The dashed lines divide the S, T-plane into four quadrants with different dynamical characteristics: (a) dominating defection, (b) coexistence, (c) bistability and (d) prevailing cooperation. In the case of bistability, the color codes indicate the size of the basin of attraction resulting in a cooperative state. In blue regions even a very small fraction of cooperators will spread and eventually dominate the population, while in reddish regions cooperators can spread only in populations that are already highly cooperative.

identified, each referring to one quadrant of the S, T-plane:

Defection: For $S < 0$, $T > 1$ the only stable fixed point is $\hat{f}_c = 0$. Therefore, the cooperative mutant gets eliminated regardless of its initial frequency. Note that the prisoner's dilemma falls into this category. As outlined in the beginning, without further assumptions, defection is the dominating strategy.

Cooperation: On the contrary, for $S > 0$, $T < 1$ the only stable fixed point is $\hat{f}_c = 1$. Thus, cooperative mutants eventually displace defective residents no matter how small its initial frequency.

Coexistence: For $S > 0$, $T > 1$, all configurations converge to the stable fixed point $\hat{f}_c^3 = S/(S+T-1)$ which now lies in the open interval $(0, 1)$. The other two fixed points, $\hat{f}_c^1 = 0$ and $\hat{f}_c^2 = 1$, are unstable. This means that after the occasional introduction of the missing strategy through random mutations, the mutant strategy will spread until the equilibrium frequency $\hat{f}_c^3$ is reached. Thus, such parameter values result in coexistence of cooperators and defectors. Note that the region with $0 < S < 1$ of this quadrant represents the chicken or hawk–dove game.

Bistability: For the remaining parameter range $S < 0$, $T < 1$ the fixed point $\hat{f}_c^3 = S/(S + T - 1)$ again lies in the open interval $(0, 1)$ but is now unstable. Any arbitrarily small deviation from $\hat{f}_c^3$ is amplified over time and eventually drives the system towards one of the stable fixed points $\hat{f}_c^1 = 0$ or $\hat{f}_c^2 = 1$. Therefore, the system is bistable and the initial frequencies of the two strategies determine which strategy invades and which one is driven to extinction. For initial frequencies of cooperators $f_c^0 > \hat{f}_c^3$, cooperators prosper but vanish otherwise.

In the remaining text, the mean field results provide a valuable basis for discussing differences in the equilibrium frequencies of cooperators and defectors due to spatial structuring of the population.

3. Spatial Games

We now turn to populations with rigid spatial structures as specified by regular lattices. Each individual is bound to a single lattice site and engages in pairwise interactions with its local neighbors. The total payoff accumulated in all interactions determines the score of an individual. Depending on its own score and the scores of its neighbors, each individual reconsiders its strategy and may adopt the strategy of one of its neighbors. The lattice is evolved in time by considering successive generations. In each generation, certain individuals are selected according to the update rule of the lattice, and interact with their neighbors. Each individual then gets the opportunity to update its strategy according to the respective update rule. For the lattice, we consider the following two update rules:

Synchronized updates: This corresponds to populations with nonoverlapping generations. All individuals interact pairwise with all their neighbors. Only then, all individuals update their strategy in a synchronized fashion. This implies that there exists a global pace maker that divides each generation into two stages, an interaction stage and a reproduction or imitation stage.

Asynchronous or random updates: Populations where reproduction or imitation is possible at all times are modeled by this update rule. Randomly selected individuals interact pairwise with all their neighbors and update their strategy according to their own score as well as the scores of their neighbors. Every generation is made up of N such updates, where N refers to the number of lattice sites, such that on average each player interacts once with all its neighbors. In the limit $N \to \infty$, this update rule results in a continuous time description of the lattice dynamics.

In all our simulations, we consider rectangular lattices with two different neighborhood types traditionally used in cellular automaton models:

von Neumann neighborhood: Each individual interacts with its four nearest neighbors to the north, east, south and west. This neighborhood puts a strong emphasis on the lattice structure. For a spreading strategy, it takes at least twice as long to cover the same distance in diagonal directions than in the orientations of the lattice.

Moore neighborhood: In the larger Moore-neighborhood each individual interacts with the eight neighbors reachable by a chess-king's move. This time, the maximum spreading speed is equal in all directions.

For the players, we consider three different update rules with varying degrees of stochasticity:

Best takes over: Each individual compares its score with the scores of all its neighbors and adopts the strategy of the most successful neighbor. In case of a tie the player sticks to its original strategy. In biological terms, this means that only the most successful neighbor has the opportunity to reproduce and the individual under consideration is replaced by a clonal offspring having the same strategy as its parent. Note that this is a fully deterministic update rule.

Imitate the better: In analogy to the imitation rule proposed by Weibull [1995] and Schlag [1998], the individual considers the difference between the scores of its neighbors and its own score. With a probability proportional to this difference it imitates the neighbors strategy, provided the difference is positive and with probability zero otherwise.

Proportional update: Individuals adopt the strategy of one of their neighbors with a probability proportional to their scores including their own score. Note that for this update rule, an individual occasionally switches to a strategy that returned a lower score to one of its neighbors than his own strategy has achieved.

The complexity of the emerging spatial patterns and their evolution in time is nicely illustrated in the picture of cellular automata (for a general introduction see e.g. [Wolfram, 1986] and with game theoretical background [Sigmund, 1995]). The state of one site in the next generation depends not only on the states of its immediate neighbors but also on their neighbors. For the von Neumann- and Moore-neighborhoods this adds up to 13 and 25 sites involved and hence to the huge number of $2^{13} \approx 10^4$ and $2^{25} \approx 10^7$ transitions rules, respectively. For an interactive introduction and a virtual lab on spatial 2×2 games, we refer to [Hauert, 2001b].

4. Spatial Results

Due to the complexity of the spatial system, all the following results are obtained from extensive numerical simulations. All combinations of neighborhood types and update rules for the lattice as well as for the individuals are considered having the following common settings.

Similarly to the results of the mean field description, the equilibrium frequency of cooperators f_c is shown as a function of the parameters S, T in the interval $[-5, 5]$ sampled in steps of 0.2. For each pair of S, T-values a grid with 51×51 individuals and periodic boundary conditions was initialized with an average initial fraction of cooperators $f_c^0 = 0.2$ and $f_c^0 = 0.8$, respectively. After initialization, the system is relaxed over 24 generations and then the average fraction of cooperators $\bar{f}_c$ is determined over another 24 generations. This process is repeated 10 times in order to minimize effects of a particular realization of the initial state. Note that for a square lattice with $N \times N$ sites it takes at least $N/2$ generations to spread information i.e. a strategy across the entire lattice. It follows that after 24 generations, the system has not yet become aware of its finite dimensions. Therefore, in general, this should be sufficient time for a system to relax to its equilibrium state and return equilibrium frequencies that basically hold for arbitrary lattice sizes. However, also note that certain parameter values in the transition region between dominating defection and prevailing cooperation and in particular for update rules of the lattice and/or individuals involving stochastic elements, extremely long transient periods may be observed before the system relaxes into its equilibrium state [Killingback & Doebeli, 1998]. To make things worse, this behavior sensitively depends on the chosen grid size [Nowak & May, 1993]. Therefore, our approach minimizes finite size effects but at the same time tends to overestimate equilibrium frequencies of the less frequent strategy.

To simplify comparisons to the mean field description, some additional lines are shown in each graph. The dashed lines divide the S, T-plane into the four quadrants of qualitatively different mean field equilibrium outcomes. The dash-dotted line indicates the mean field solution for the respective initial fraction of cooperators f_c^0 (see also Fig. 2). For $S < 0$, $T < 1$ i.e. in the bistability quadrant, all combinations of S, T-values below this line lead to homogeneous states of cooperation $\hat{f}_c = 1$, whereas above this line defection dominates $\hat{f}_c = 0$.

Each of the following figures is made up of 2×3 graphs. The three rows refer to the three different update rules for the players with increasing stochasticity: the deterministic *best takes over* rule in the top row, *imitate the better* in the middle and finally to the *proportional* update rule in the bottom row. In the left column, the average fractions of

cooperators $\overline{f}_c$ are shown as a function of S, T. As in Fig. 2, regions with low $\overline{f}_c$ (dominating defection) are colored red while blue regions refer to high $\overline{f}_c$ (prevailing cooperation). Intermediate values of $\overline{f}_c$ are colored in ascending order yellow, green and light blue with green corresponding to $\overline{f}_c = 0.5$. In the right column differences to the mean field scenario are shown. These pictures highlight the effects of spatial structures on the equilibrium frequencies of cooperators and defectors. In white areas, space has virtually no effect i.e. for such parameter values spatial extension does not change the equilibrium frequencies. Generally this holds in the cooperation quadrant ($S > 0$, $T < 1$) and to a large extent for $S < 0$, $T > 1$ (defection quadrant). In the latter quadrant, however, important deviations are observed for small T and large S. They are addressed in detail together with the different simulation settings. Parameter regions where the spatial structures lead to higher $\overline{f}_c$ than in the mean field are colored blue while in red regions the spatial extension decreases the fraction of cooperators $\overline{f}_c$ compared to mean field. The intensity of the two colors indicates the strength of the spatial effects on the equilibrium frequencies.

4.1. *von Neumann-neighborhood*

For the von Neumann-neighborhood, Figs. 3 and 4 show $\overline{f}_c$ as a function of S, T with synchronized lattice updates and for initial fractions of cooperators $f_c^0 = 0.2$ and $f_c^0 = 0.8$, respectively. Similarly, results for asynchronous or random lattice updates are given in Figs. 5 and 6. In the two figures with $f_c^0 = 0.2$ (Figs. 3 and 5) significant changes in $\overline{f}_c$ appear for $S < 0$ roughly along the boundary indicated by a solid line. Above this boundary defection reigns (reddish colors) while below cooperators dominate (blue colors). This line refers to growth conditions of a particular spatial configuration: with the deterministic *best takes over*-update rule, corners of an isolated 2×2- or larger cluster of cooperators are able to grow if the following holds:

$$T < 2 + 2S \tag{3a}$$

$$S > -1\,. \tag{3b}$$

In the top row of the two figures we see that in this area spatial effects are particularly pronounced. Results for increased stochasticity for the player's update rule (middle and bottom rows) show that in the vicinity of the inequalities given by Eq. (3a)

changes in $\overline{f}_c$ are still observed but are less distinct. For parameter ranges $S < -1$, Eq. (3a) continues to have significant effects on f_c. This results from less homogeneous spatial configurations than outlined above. Higher initial fractions of cooperators $f_c^0 = 0.8$ as in Figs. 4 and 6 mostly hide effects of the above mentioned growth conditions. Only in a small area of the defection quadrant ($S < 0$, $T > 1$) its importance is preserved. Despite its small size, this area is of particular importance since it refers to the prisoner's dilemma, PD. The above conditions roughly delimit the range where spatial extension is capable of promoting cooperative behavior among selfish individuals. Stochastic elements in the update rules tend to further reduce this area such that for the *proportional* update rule (bottom row) cooperators can hardly persist in the PD.

Note that for the deterministic *best takes over* update rule and $1 < T < 2$, but outside the range delimited by Eq. (3a), isolated clusters of cooperators confined solely by diagonal boundaries are stable. For high initial f_c^0 such clusters are likely to be formed during the first few generations and will then persist for ever, regardless of the update rule of the lattice. This leads to the increased $\overline{f}_c$ in the top row of Figs. 4 and 6.

In the quadrant of coexistence ($S > 0$, $T > 1$) spatial extension generally reduces the equilibrium frequency of cooperators $\overline{f}_c$ compared to mean field calculations. This is of particular interest for the hawk–dove game ($0 < S < 1$) where spatial extension apparently tends to favor the hawk strategy. Another interesting effect concerns the formation of discrete levels of $\overline{f}_c$ for the *best takes over*- and *imitate the better*- update rules (top and middle rows). Proportional updates (bottom row) again lead to an almost continuous range of $\overline{f}_c$ as in the mean field approach.

In the quadrant of bistability ($S < 0$, $T < 1$), spatial extension tends to level out initial differences in f_c^0 for stochastic update rules (middle and bottom rows). In that case, space reduces the parameter range with dominating cooperation for high f_c^0 while increasing it for low f_c^0 with respect to mean field calculations. Recall that the dash-dotted line indicates the basin of attraction for the initial frequency of cooperators f_c^0. In mean field calculations, parameter values below this line lead to states of homogenous cooperation while above defectors reign.

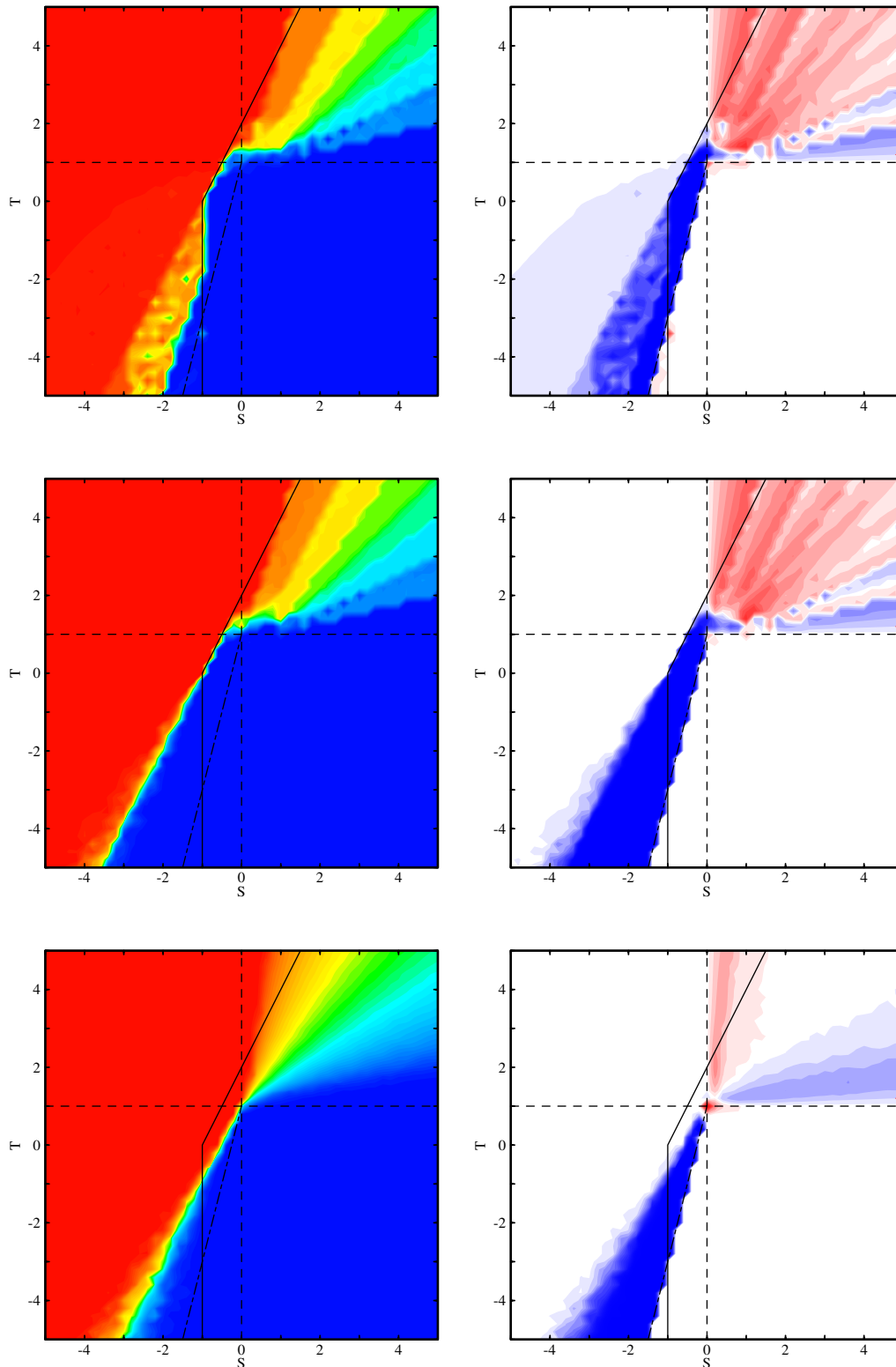Generally, surprisingly little differences were observed for the synchronized and the asynchronous

Fig. 3. von Neumann-neighborhood with synchronized lattice update. The stochasticity of the individual update rules increases from top to bottom: (a) *best takes over*, (b) *imitate the better* and (c) *proportional*. The left column shows the equilibrium frequencies of cooperators $\overline{f}_c$ as a function of S, T. The right column shows differences to the mean field results $(\overline{f}_c - \hat{f}_c)$ i.e. highlights the effects of spatial extension. Blue and red colors refer to cooperators and defectors, respectively. On the left, blue color denotes high $\overline{f}_c$ and on the right it indicates that space favors cooperators i.e. increases $\overline{f}_c$. In analogy, on the left, reddish color refers to parameter values leading to low $\overline{f}_c$ and on the right it indicates that space favors defectors i.e. lowers $\overline{f}_c$. Details on the simulations, the additional lines and more information on the color code are given in the text.
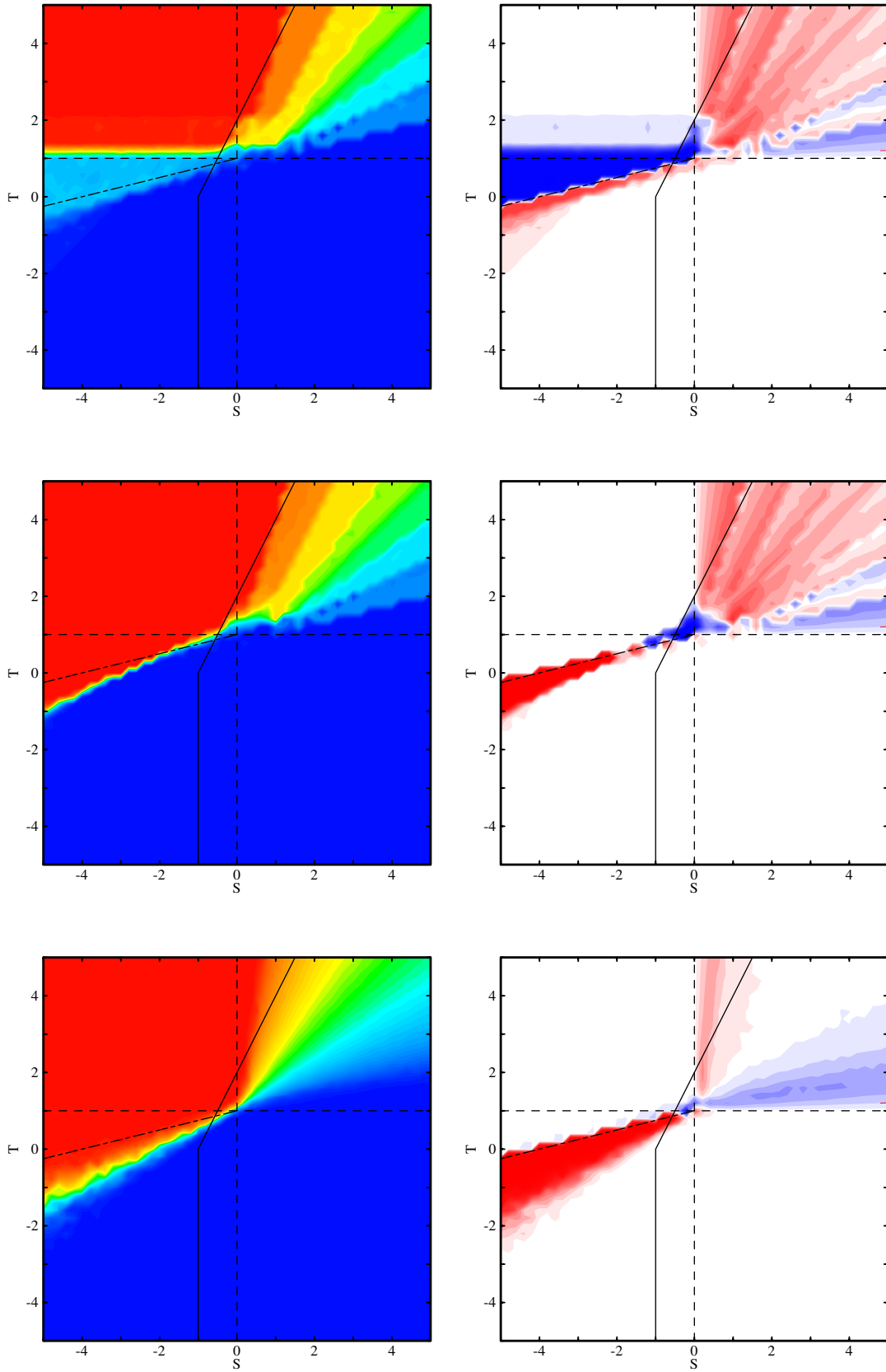
Fig. 4. von Neumann-neighborhood with synchronized lattice update. All simulation settings are the same as in Fig. 3 but for an initial frequency of cooperators of $f_c^0 = 0.8$.
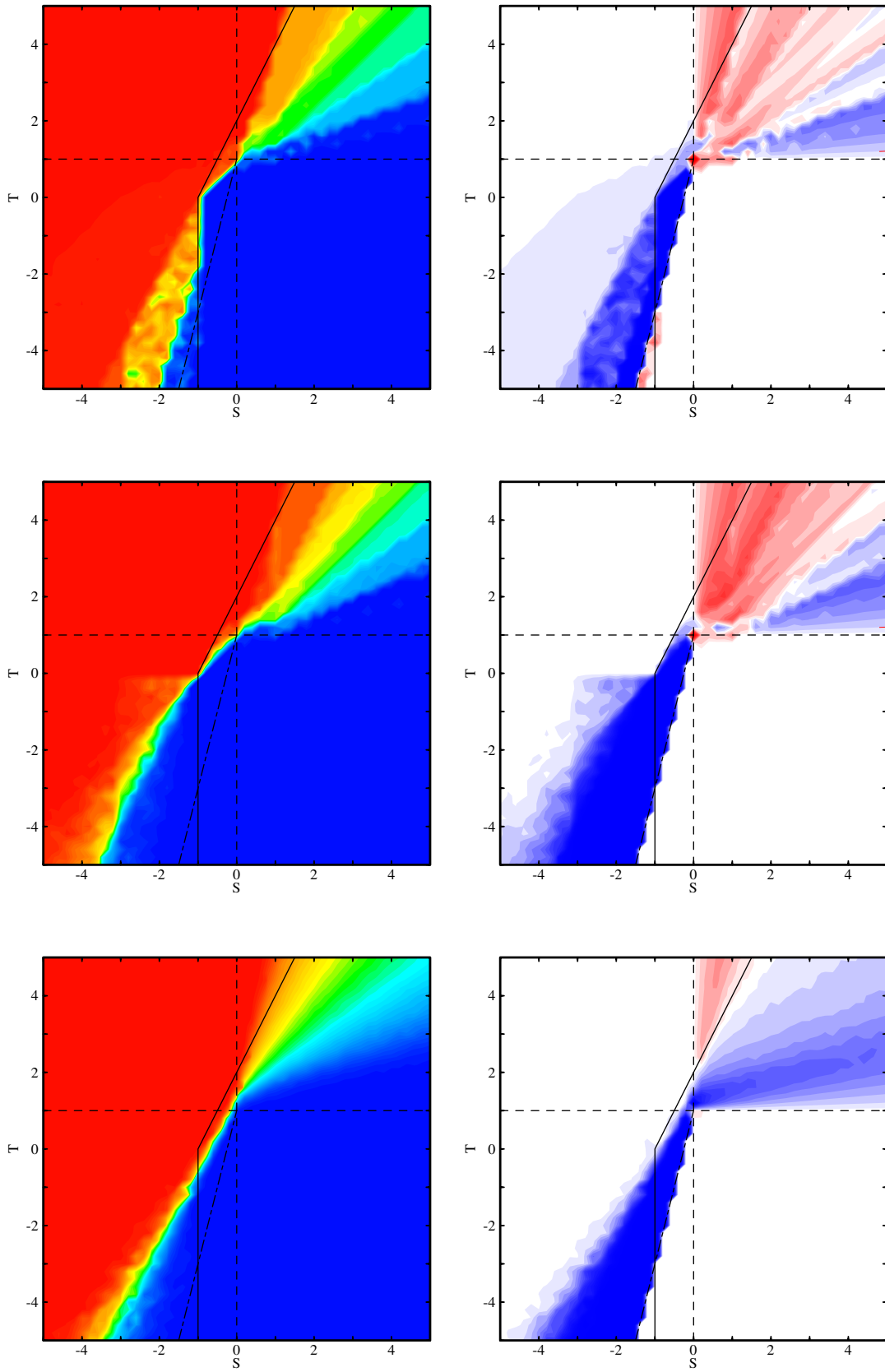
Fig. 5.   von Neumann-neighborhood with asynchronous or random lattice update. Simulation settings as in Fig. 3 ($f_c^0 = 0.2$).
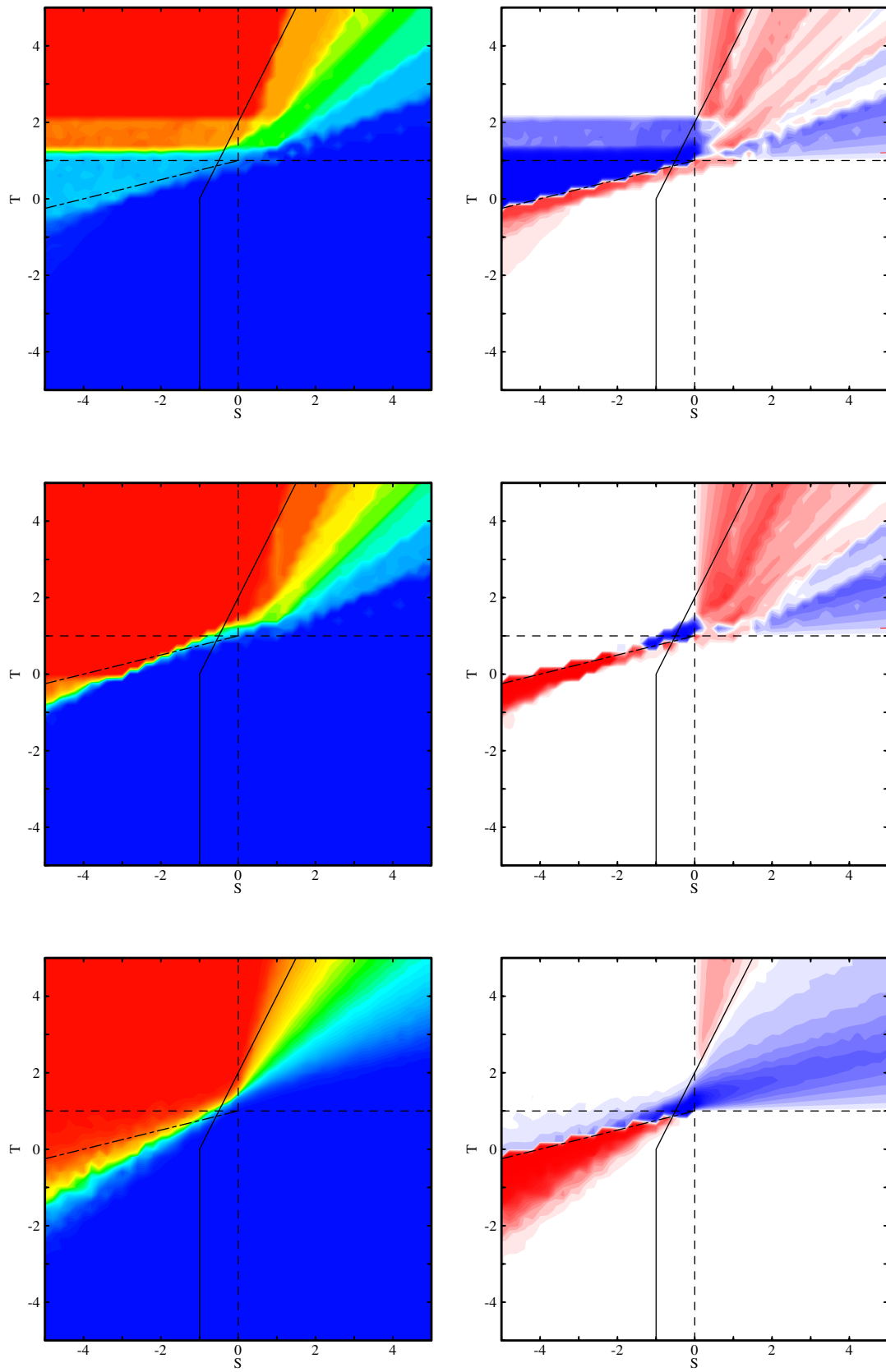
Fig. 6.   von Neumann-neighborhood with asynchronous or random lattice update. Simulation settings as in Fig. 4 ($f_c^0 = 0.8$).
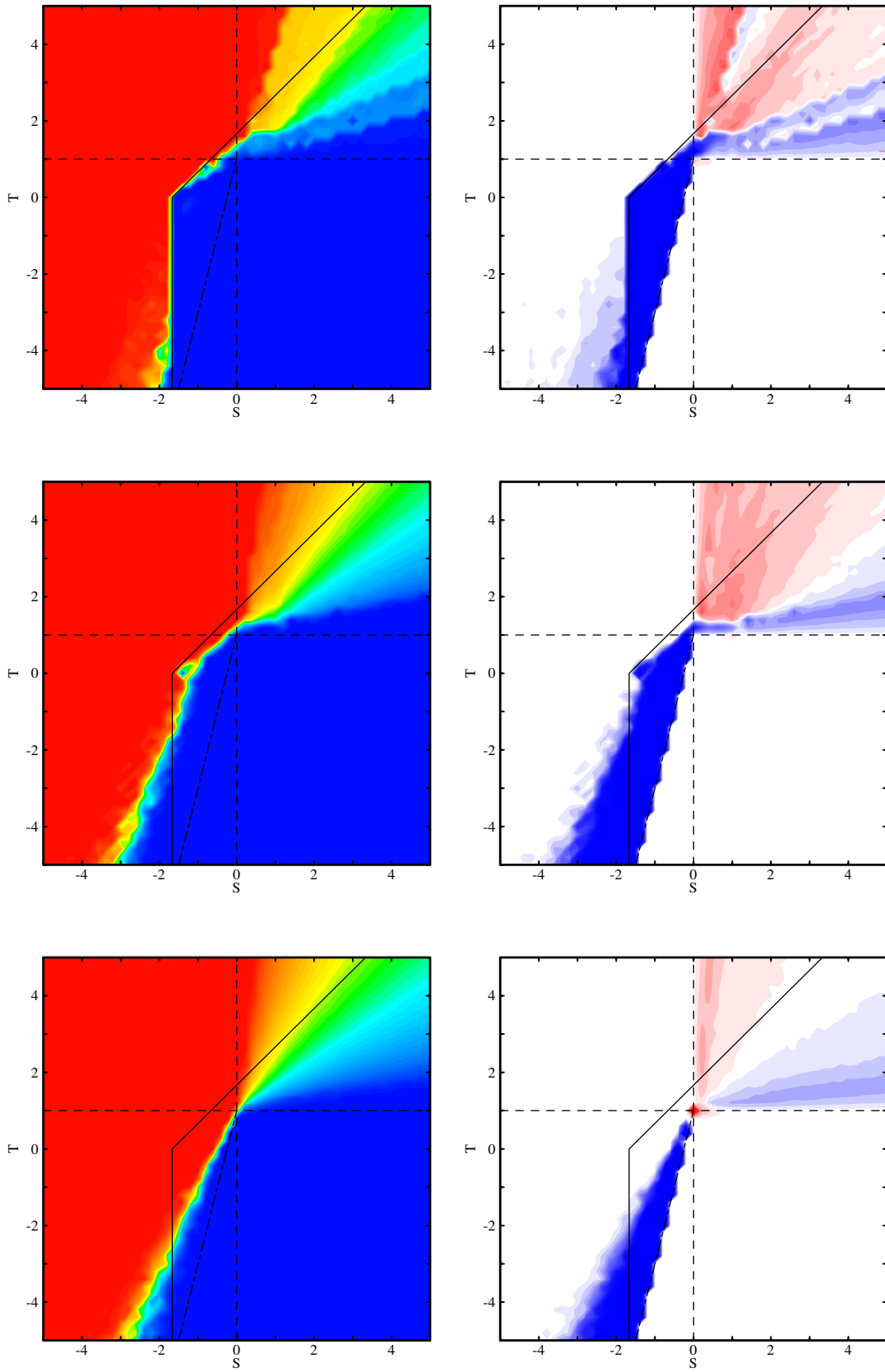
Fig. 7.   Moore-neighborhood with synchronized lattice update. Simulation settings as in Fig. 3 ($f_c^0 = 0.2$).
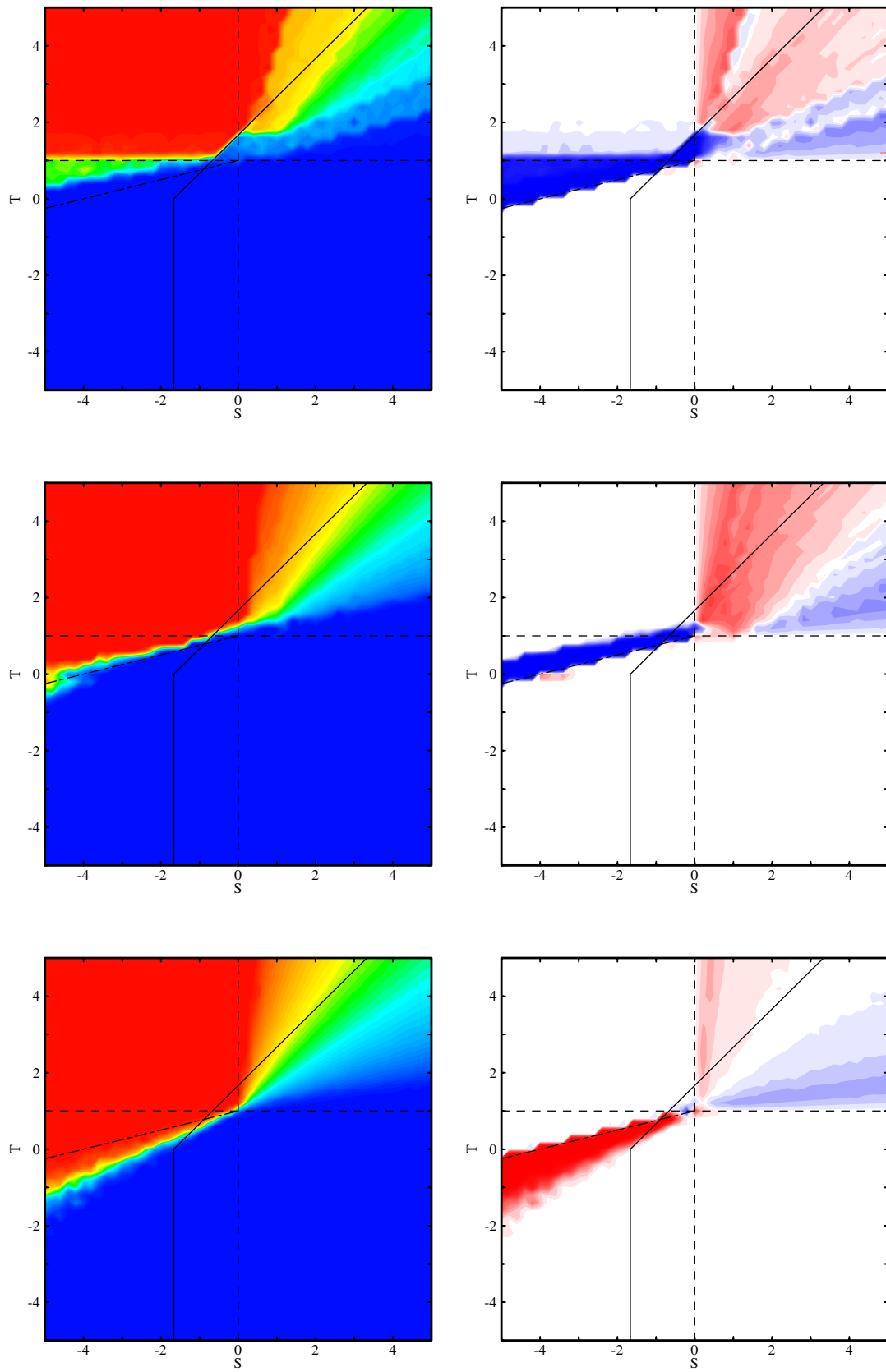
Fig. 8.   Moore-neighborhood with synchronized lattice update. Simulation settings as in Fig. 4 ($f_c^0 = 0.8$).
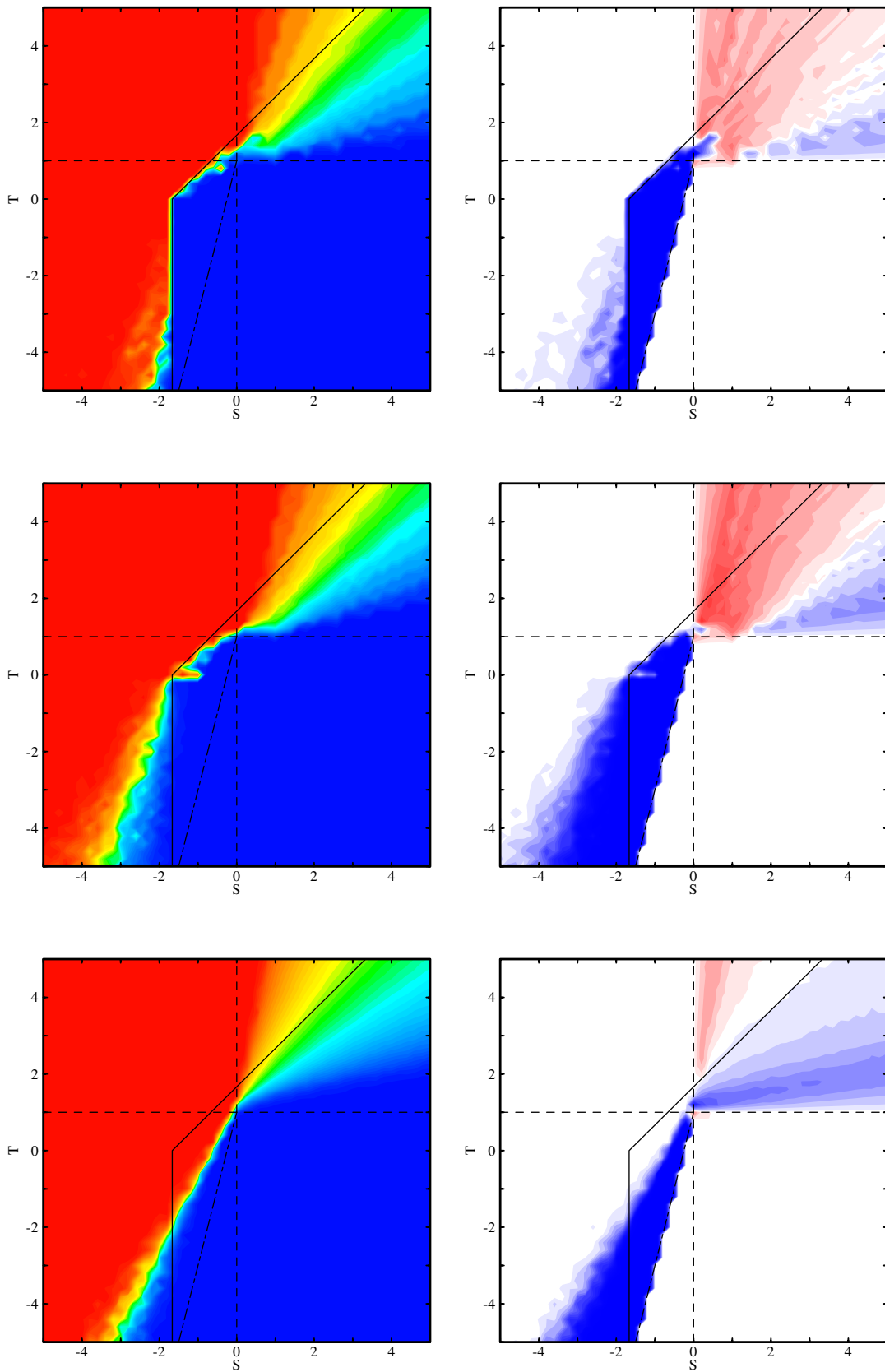
Fig. 9. Moore-neighborhood with asynchronous or random lattice updates. Simulation settings as in Fig. 5 ($f_c^0 = 0.2$).
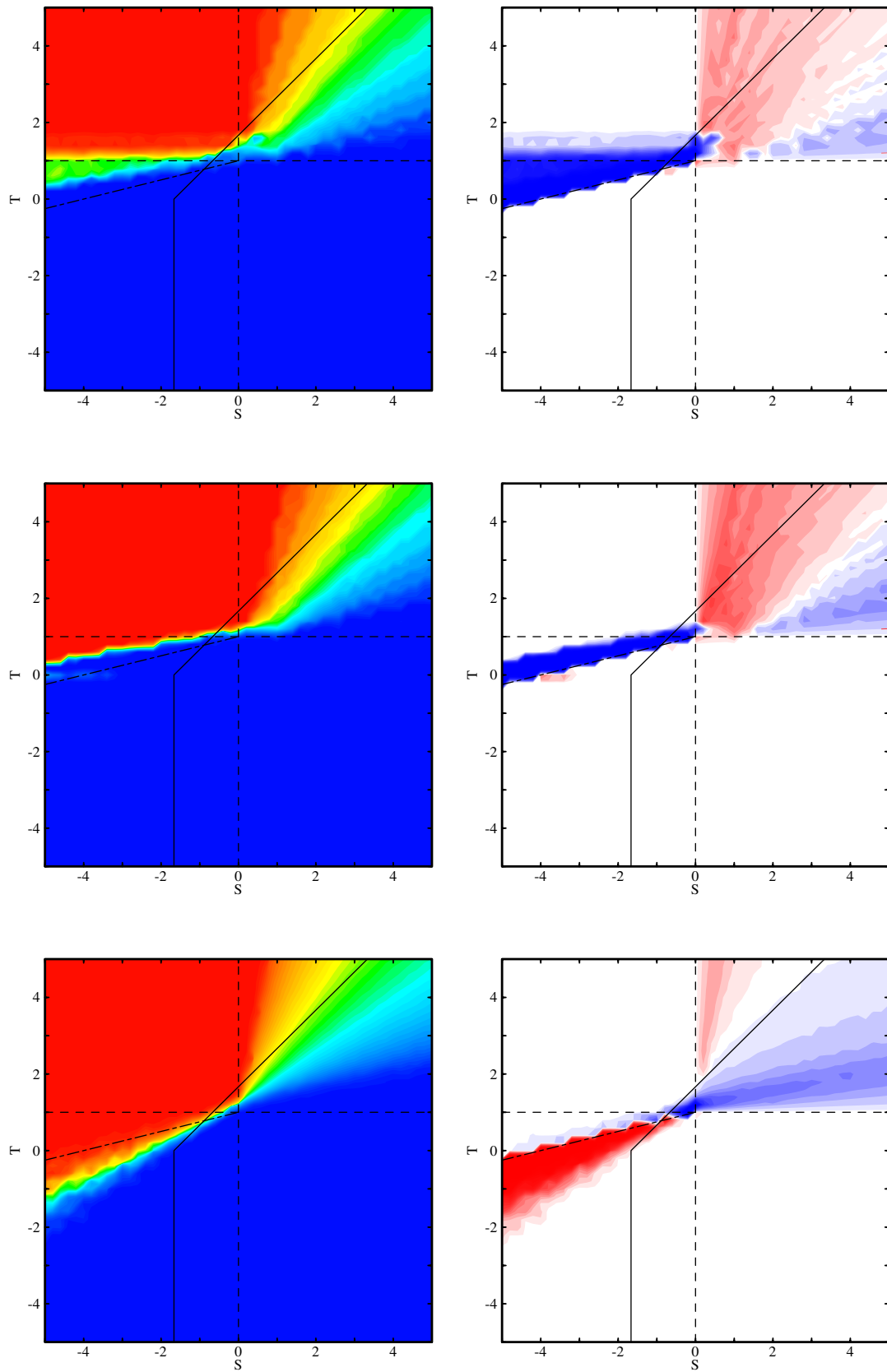
Fig. 10.   Moore-neighborhood with asynchronous or random lattice updates. Simulation settings as in Fig. 6 ($f_c^0 = 0.8$).

or random lattice updates. The latter tends to level out abrupt changes in $\overline{f}_c$ and, additionally, tends to decrease $\overline{f}_c$. However, the qualitative results remain unaffected. This is of particular importance for the PD. For a detailed discussion on this topic we refer to Hubermann and Glance [1993] and Nowak *et al.* [1994].

4.2. *Moore-neighborhood*

For the larger Moore-neighborhood the analysis and discussion of the results are slightly more complex but can be performed along similar lines as for the von Neumann-neighborhood. In analogy, results for synchronized lattice updates with initial fractions of cooperators $f_c^0 = 0.2$ and $f_c^0 = 0.8$ are shown in Figs. 7 and 8 and for random or asynchronous lattice updates in Figs. 9 and 10, respectively. This time, for $S < 0$ significant changes of $\overline{f}_c$ appear along the boundary (solid line) resulting from growth conditions of an edge of a 3×3- or larger cluster of cooperators:

$$T < S + \frac{5}{3} \tag{4a}$$

$$S > -\frac{5}{3} \, . \tag{4b}$$

For the deterministic *best takes over* update rule (top row) effects of such spatial arrangements are clearly visible for low f_c^0 (Figs. 7 and 9) but are mostly hidden for high f_c^0 (Figs. 8 and 10). Equation (4a) is of particular importance for the PD (defection quadrant, $S < 0$, $T > 1$) where it roughly delimits the parameter range of persisting cooperative behavior. The significance of these boundaries decreases for stochastic update rules (middle and bottom rows).

Note that in the defection quadrant for the *best takes over* update rule and $T < 2$, but outside the range delimited by Eq. (4a), isolated 3×3- or larger clusters of cooperators are stable. For higher f_c^0 the formation of such clusters during the first few generations is quite likely. This leads to the increased values of $\overline{f}_c$ in the top row of Figs. 8 and 10 and remains essentially unaffected by the update rule of the lattice. However, the stochastic component of the *imitate the better* update rule is enough to destroy these fragile structures and again defection reigns.

In the bistability quadrant ($S < 0$, $T < 1$), spatial extension again results in a tendency to level

out initial differences in the frequencies of cooperators f_c^0. As before, the dash-dotted line indicates the basin of attraction in mean field calculations for f_c^0 where parameter values below this line lead to homogenous cooperation while defection reigns above. Primarily for stochastic update rules (middle and bottom row), spatial extension increases the parameter range of prevailing cooperation for low f_c^0 while decreasing it for high f_c^0 with respect to mean field calculations.

Finally, in the quadrant of coexistence ($S > 0$, $T > 1$), spatial extension still tends to induce discrete levels of $\overline{f}_c$ but the effect is less pronounced than for the von Neumann-neighborhood. At the same time it again tends to decrease $\overline{f}_c$ compared to the mean field approach. Only for smaller T, cooperation may be favored. In particular, for the hawk–dove game ($0 < S < 1$) we obtain that roughly for $1 < T < 2$ the dove strategy is favored by spatial settings (see also [Killingback & Doebeli, 1996]) while for $T > 2$ the hawk strategy is far more frequent than expected from mean field calculations.

5. Discussion

The systematic analysis and comparison of the equilibrium frequencies of cooperators and defectors in populations without spatial structuring and others with rigid structures, as represented by rectangular lattices, yield several major conclusions: (a) including spatial extension in 2×2 games has indeed significant effects on the equilibrium frequencies of cooperators and defectors. In some parameter regions spatial extension promotes cooperative behavior while inhibiting it in others (see below); (b) differences in the initial frequencies of cooperators are readily leveled out and hardly affect the equilibrium frequencies except for $T < 1$, $S < 0$. In the mean field description, this quadrant refers to a bistable system where the initial frequencies determine the long term behavior, a feature that is generally preserved for the spatial setting (see below); (c) increasing stochasticity on the level of the lattice update, i.e. synchronized versus asynchronous or random updating, has surprisingly little effects on the long term dynamics of the system. Including stochastic elements in the individual's update rule has far more pronounced influences on the equilibrium frequencies. Generally speaking, introducing stochasticity tends to diminish effects of spatial

extension and results in equilibrium outcomes closer to the mean field description; (d) the size of the neighborhood obviously affects the spreading speed of successful strategies, but the equilibrium distribution is largely determined by (e) the fate of an isolated 3×3 cluster of cooperators or defectors in a sea of opponents. We have demonstrated that the parameter regions where spatial extension has the most pronounced effect on promoting cooperative behavior are roughly delimited by boundaries resulting from growth conditions of a single 3×3 cluster. Therefore, the fate of the cluster individuals provides a simple and useful rule of thumb to determine the long term behavior of the system [Killingback *et al.*, 1999; Hauert, 2001a]. However, also note that in the vicinity of abrupt changes in $\overline{f}_c$ and for stochastic update rules care must be taken since the system may have extremely long transient periods before it relaxes into its equilibrium state. In our simulations we attempted to minimize effects of the finite grid size and were thus unable to account for such situations.

In order to summarize the detailed effects of spatial extension, it is most convenient to address each of the four quadrants separately that lead to different equilibrium outcomes in the mean field description. For $S > 0$, $T < 1$ cooperation is the dominant strategy independent of the spatial structuring of the population. For $S < 0$ and $T < 1$ the mean field system is bistable and the initial frequencies of cooperators and defectors determine which strategy will win in the long run. In this quadrant, spatial extension has the most pronounced effect. For the deterministic *best takes over* update rule, cooperative behavior is promoted very efficiently and results in substantial increases of the basin of attraction of the cooperative state with respect to mean field calculations. Stochastic update rules, *imitate the better* and *proportional* update, however, have a very different effect. In fact, they tend to level out differences due to the initial f_c^0 i.e. the parameter range with dominating cooperation is increased for low f_c^0 and decreased for high f_c^0 with respect to mean field calculations.

The quadrant $S > 0$, $T > 1$ results in coexistence of cooperators and defectors with the mean field equilibrium frequencies $\hat{f}_c = S/(S + T - 1)$, $\hat{f}_d = 1 - \hat{f}_c = (T - 1)/(S + T - 1)$. Interestingly, spatial extension leads to discrete levels of f_c for the *best takes over*- and *imitate the better*-update rules

but remains continuous for the *proportional* update. At the same time, it turns out that spatial extension generally has a negative impact on the evolution of cooperative behavior. Only for small T, space is capable of promoting cooperation. In particular, this holds for the hawk–dove game ($0 < S < 1$), describing intra-species competitions. Compared to mean field calculations, spatial extension generally favors the hawk strategy. Consequentially, in spatially structured populations, we would expect to observe more frequent escalations of conflicts than predicted by mean field theory. However, also note that for $1 < T < 2$ and $0 < S < 1$, the outcome of the hawk–dove game sensitively depends on the initial conditions and update rules. For example, settings as shown in Fig. 8 favor the dove strategy. This particular situation has been discussed in detail by Killingback and Doebeli [1996].

Finally, for the remaining quadrant, $S < 0$, $T > 1$, defection is the dominant strategy according to mean field theory. Generally, this is equally true for populations with rigid spatial structures. However, for S and T close to 0 and 1, respectively, cooperators can survive and even dominate in a population. This area is roughly delimited by the conditions that an isolated 3×3 cluster of cooperators is able to grow in a sea of defectors along its corners (von Neumann-neighborhood: $T < 2 + 2S$) or edges (Moore-neighborhood: $T < S + 5/3$). Despite the small size of this region, it is of particular interest and importance since the prisoner's dilemma, modeling the emergence of cooperation among selfish individuals, falls into this category. It follows that for moderate temptations to defect T and small losses S for individuals played as a sucker, spatial extension provides powerful means to promote cooperative behavior without the need for sophisticated strategies. In addition, for the deterministic *best takes over* update rule and $1 < T < 2$ certain cluster arrangements of cooperators are stable. For high initial frequencies of cooperators f_c^0, the formation of such clusters is quite likely and leads to static islands of cooperators, irrespective of the lattice update. This results in a significant increase in $\overline{f}_c$. However, note that these states are very fragile — the least stochastic perturbation sweeps the cooperators away.

Mapping the traditional payoff values introduced by Axelrod and Hamilton [1981] and Nowak and Sigmund [1994] ($T = 5$ and 4, $R = 3$, $P = 1$, $S = 0$) onto the S, T-plane according to our

rescaling rules, we note that both lie outside the region where isolated 3×3 clusters are stable or even capable of growing and hence the spatial setting leads to states of homogeneous defection.

To conclude, we have demonstrated that for certain parameter ranges spatial extension is indeed capable of systematically promoting cooperative behavior whilst in others it leads to a systematic decrease. Growth conditions of an isolated 3×3 cluster turned out to serve as useful rules of thumb to estimate the long term fate of cooperators. Through comparisons with results from mean field systems we were able to pinpoint effects solely arising from the rigid spatial structure of the population. In particular, we have shown that for the prisoner's dilemma, space can outweigh the inherent advantage of defectors over cooperators — at least for a small parameter range. For the hawk–dove game, a counter-intuitive result was obtained that spatial structures tend to result in more frequent escalations in intra-species competitions.

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