Spatial evolutionary games with weak selection

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Recently a rigorous mathematical theory has been developed for spatial games with weak selection, i.e., when the payoff differences between strategies are small. The key to the analysis is that when space and time are suitably rescaled the spatial model converges to the solution of a partial differential equation (PDE). This approach can be used to analyze all 2×2 games, but there are a number of 3×3 games for which the behavior of the limiting PDE is not known. In this paper we give rules for determining the behavior of a large class of 3×3 games and check their validity using simulation. In words, the effect of space is equivalent to making changes in the payoff matrix, and once this is done, the behavior of the spatial game can be predicted from the behavior the replicator equation for the modified game. We say predicted here because in some cases the behavior of the spatial game is different from that of the replicator equation for transformed game. For example, if a rock-paper-scissors game has a replicator equation that spirals out to the boundary, space stabilizes the system and produces an equilibrium.

voter model perturbation | reaction-diffusion equation | rock-paper-scissors

Evolutionary games are often studied assuming that the population is homogeneously mixing, i.e., each individual interacts equally with all the others. In this case, the frequencies of strategies evolve according to the replicator equation. See e.g., Hofbauer and Sigmund's book [1]. If u_i is the frequency of players using strategy i then

$$\frac{du_i}{dt} = u_i(F_i - \bar{F}) \qquad [1]$$

where $F_i = \sum_j G_{i,j}u_j$ is the fitness of strategy i, $G_{i,j}$ is the payoff for playing strategy i against an opponent who plays strategy j, and $\bar{F} = \sum_i u_iF_i$ is the average fitness. The homogeneous mixing assumption is not satisfied for the evolutionary games that arise in ecology or modeling solid cancer tumors, so it is important to understand how spatial structure changes the outcome of games. The goal of this paper is to facilitate applications of spatial evolutionary games by giving rules to determine the limiting behavior of a large class of 3×3 games.

Our spatial games will take place on the three-dimensional integer lattice $\mathbb{Z}^3$. The theory, see [2, 3] has been developed under the assumption that the interactions between an individual and its neighbors are given by an irreducible probability kernel $p(x)$ on $\mathbb{Z}^3$ with $p(0) = 0$, that is finite range, symmetric $p(x) = p(-x)$, and has covariance matrix $\sigma^2 I$. Here we will restrict our attention to the nearest neighbor case in which $p(x) = 1/6$ for $x = (1,0,0), (-1,0,0), \dots (0,0,-1)$.

To describe the dynamics we let $\xi_t(x)$ be the strategy used by the individual at x at time t and let

$$\psi_t(x) = \sum_y G(\xi_t(x), \xi_t(y))p(y-x)$$

be the fitness of x at time t. In Birth-Death dynamics, site x gives birth at rate $\psi_t(x)$ and sends its offspring to replace the individual at y with probability $p(y-x)$. In Death-Birth dynamics, the individual at x dies at rate 1, and is replaced by a copy of the one at y with probability proportional to $p(y-x)\psi_t(y)$. The theory developed in [3] can be applied to both cases. However, to save space we will only consider the birth-death case.

To motivate our study of evolutionary games we introduce two examples that will be used to illustrate the theory that has been developed.

A public goods game in pancreatic cancer. In this system, see [4], some cells (type 2's) produce insulin-like growth factor-II, while other cells (type 1's) free-ride on the growth factors produced by other cells. Since the 1's do not have to spend metabolic energy producing the growth factor they have a higher growth rate. This leads to the following very simple 2×2 game.

	1	**2**
1	0	λ
2	1	1

[2]

In words, 2's give birth at rate 1, independent of what is around them, while 1's give birth at rate equal to λ times the fraction of neighbors that are of type 1. If $\lambda > 1$ there is a mixed strategy equilibrium for the game $\rho_2 = 1/\lambda$, $\rho_1 = 1 - 1/\lambda$, which is the limit of the solution to the replicator equation when $0 < u_1 < 1$.

Multiple Myeloma. Normal bone remodeling is a consequence of a dynamic balance between osteoclast (OC) mediated bone resorption and bone formation due to osteoblast (OB) activity. Multiple myeloma (MM) cells disrupt this balance in two ways.

(i) MM cells produce a variety of cytokines that stimulate the growth of the OC population.

Significance Statement

Game theory, which was invented to study strategic and economic decisions of humans has for many years been used in ecology and more recently in cancer modeling. In the applications to ecology and cancer, the system is not homogeneously mixing so it is important to understand how space changes the outcome of evolutionary games. Here we present rules that can be used to determine the behavior of a wide class of three strategy games. In short, the behavior can be predicted form the behavior of the replicator equation for a modified equation. This theory will be useful for a number of applications.

M.N. and R.D. designed research. M.N. performed simulations and produced the graphics. R.D. wrote the paper with help from M.N.

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(ii) Secretion of $DKK1$ by MM cells inhibits OB activity.

OC cells produce osteoblast activating factors that stimulate the growth of MM cells where as MM cells are not effected by the presence of OB cells. These considerations led Dingli et al. [5] to the following game matrix. Here, $a, b, c, d, e > 0$.

$$\begin{array}{cccc} & OC & OB & MM \\ OC & 0 & a & b \\ OB & e & 0 & -d \\ MM & c & 0 & 0 \end{array} \qquad [3]$$

There are many other systems to which our methods can be applied. See e.g., [6] – [10].

1. Review of existing theory

We will study the dynamics of spatial games under the assumption of weak selection, i.e., when the game matrix

$$\bar{G}(i,j) = \mathbf{1} + wG_{i,j},$$

where $\mathbf{1}$ is a matrix of all 1's and w is small. Since multiplying a game matrix by a constant or adding a constant to all the entries in a column does not change the behavior of the replicator equation, $\bar{G}$ and G are equivalent from that point of view. Mathematical results for spatial games require that we take a limit in which $w \to 0$. However, simulations will show that the predictions are accurate in some cases when $w = 1/2$.

When $w = 0$ either version of the dynamics reduces to the voter model, a system in which each site at rate 1 changes its state to that of a randomly chosen neighbor. The key to our analysis is that our spatial evolutionary game is a voter model perturbation in the sense of Cox, Durrett, and Perkins [2]. To make it easier to compare with [2] and the follow-up paper [3] that applied the theory to evolutionary games we will let $w = \varepsilon^2$. Here, we will simply state the facts that we will use. The reader can find the details in [3].

The key to the study of voter model perturbations is a result that says when we scale space by ε and run time at rate ε^{-2} then the spatial model converges to the solution of a PDE. In order to state the result we need to define the mode of convergence. Pick a small $r > 0$ and divide space $\varepsilon\mathbb{Z}^d$ into boxes with side ε^r. Given an $x \in \mathbb{R}^d$ let $B^\varepsilon(x)$ be the box that contains x and let $\bar{u}_i^\varepsilon(t,x)$ be the fraction of sites in state i in $B^\varepsilon(x)$ at time $t\varepsilon^{-2}$. We say that the spatial model converges to $u(t,x)$, if for any L

$$\sup_{x\in[-L,L]^d} |\bar{u}_i^\varepsilon(t,x) - u_i(t,x)| \to 0 \quad \text{as } \varepsilon \to 0.$$

Theorem 1 *Suppose $d \geq 3$. Let $v_i : \mathbb{R}^d \to [0,1]$ be continuous with $\sum_{i\in S} v_i = 1$. If the initial conditions $\xi_0^\varepsilon \to v_i$ in the sense described above then $\xi^\varepsilon_{\varepsilon^{-2}t}$ converges to the solution of the system of partial differential equations:*

$$\frac{\partial}{\partial t}u_i(t,x) = \frac{\sigma^2}{2}\Delta u_i(t,x) + \phi_i(u(t,x))$$

with initial conditions $u_i(0,x) = v_i(x)$.

The reaction term $\phi_i(u)$ in Theorem 1 is a constant times the replicator equation for the modified game $H = G + A$ where

$$A_{i,j} = \theta(G_{i,i} + G_{i,j} - G_{j,i} - G_{j,j}).$$

Note that if we add c_k to column k the perturbation matrix A is not changed.

The idea that the reaction term is the replicator equation for a modified games is inspired by Ohtsuki and Nowak [11] who found a similar result for the ODE that arises from the pair approximation. See Section 5 of [3] for more on this connection. As in the work of Tarnita et al. [12, 13], θ depends only on the spatial structure and not on the entries in the game matrix. In the three-dimensional nearest neighbor case it is known that $\theta \approx 0.5$. See Section 4 of [3] for more details.

2. Public goods game

Since the behavior of the replicator equation and of the weak selection limit for Birth-Death updating are not changed if we subtract a constant from each column, so we can restrict our attention to 2×2 games of the form.

$$\begin{array}{ccc} & \mathbf{1} & \mathbf{2} \\ \mathbf{1} & 0 & b \\ \mathbf{2} & c & 0 \end{array} \qquad [4]$$

Let u denote the frequency of strategy 1. In a homogeneously mixing population, u evolves according to the replicator equation Eq. (1):

$$\begin{aligned} \frac{du}{dt} &= u\{b(1-u) - ub(1-u) - (1-u)cu\} \\ &= u(1-u)[b - (b+c)u] \equiv \phi_R(u) \end{aligned} \qquad [5]$$

Note that $\phi_R(u)$ is a cubic with roots at 0 and at 1. If there is a fixed point in $(0,1)$ it occurs at $\rho = b/(b+c)$

A method for analyzing all 2×2 games is described in Section 6 of [3], so we will only consider the public goods game and suppose that $\lambda > 1$. Subtracting 1 from the second column the game G becomes

$$\begin{array}{ccc} G_1 & \mathbf{1} & \mathbf{2} \\ \mathbf{1} & 0 & b = \lambda - 1 \\ \mathbf{2} & c = 1 & 0 \end{array}$$

In the three dimensional nearest neighbor case the transformed game is given by H:

$$\begin{array}{ccc} H_1 & \mathbf{1} & \mathbf{2} \\ \mathbf{1} & 0 & \bar{b} = (3/2)\lambda - 2 \\ \mathbf{2} & \bar{c} = 2 - \lambda/2 & 0 \end{array}$$

- If $\lambda < 4/3$ then $\bar{b} < 0$ so strategy 2 domiinates strategy 1, $2 \gg 1$, and 2's take over the system.
- If $\lambda > 4$ then $\bar{c} < 0$ so $1 \gg 2$ and 1's take over the system.
- If $4/3 < \lambda < 4$ then $\rho = \bar{c}/(\bar{b} + \bar{c}) \in (0,1)$ is an attracting fixed point and there is coexistence in the spatial model.

Note that in contrast to [4] one does not need the growth rate of 1's to be a nonlinear function of the fraction of 2's to maintain coexistence.

To check the theoretical prediction we turn to simulation. The table gives the equilibrium frequencies of strategy 1.

λ	4/3	3/2	3	3.5	4
Original game	0.11	0.25	0.75	0.83	0.89
w **= 1/2**	0.01	0.19	0.79	0.88	0.96
w **= 1/10**	0.00	0.16	0.82	0.92	0.98
$w \to 0$ **limit**	0	0.17	0.83	0.93	1

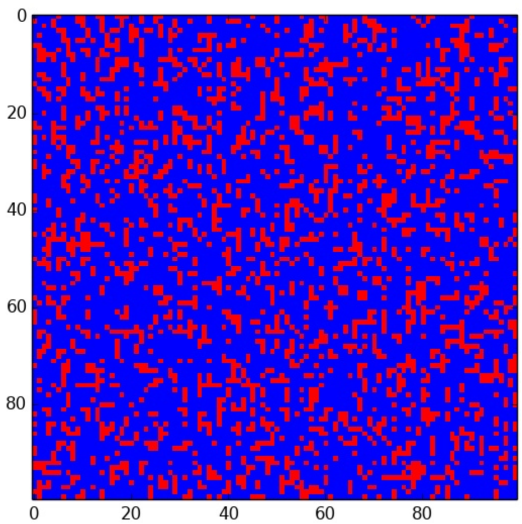

Fig. 1. Simulation of public goods game G_1 with $\lambda = 3$. There is very little spatial structure in equilibrium. Here and in Figures 4, 5, and 7, the picture gives the state of slice through a $100 \times 100 \times 100$ grid.

Note that the agreement with the limiting result is very good when $w = 1/10$ and good when $w = 1/2$.

Simulations were done using a standard algorithm for simulating continuous time Markov chains. Details can be found in a 1994 survey paper by Durrett and Levin [15]. The method is described in Section S1 of the supporting information.

3. Three strategy games

We will suppose that the game is written in the form.

$$G = \begin{array}{c|ccc} & \mathbf{1} & \mathbf{2} & \mathbf{3} \\ \mathbf{1} & 0 & \alpha_3 & \beta_2 \\ \mathbf{2} & \beta_3 & 0 & \alpha_1 \\ \mathbf{3} & \alpha_2 & \beta_1 & 0 \end{array} \qquad [6]$$

The subscripts indicate the strategy that has been left out in the various 2×2 subgames.

In the 2×2 case there are only four possibilities 1 dominates 2, 2 dominates 1, stable mixed strategy fixed point, and unstable mixed strategy fixed point. Bomze [14, 16] lists more than 40 possibilities for the 3×3 case. Here, we do not consider games with unstable edge fixed points and only. consider generic examples in which the six off-diagonal entries are non-zero and distinct, so we end up with 11 cases described in Section S2 of the supporting information. In the next three sections we consider games with "rock-paper scissors' relationships between the strategies and two examples in which the replicator equation has two locally attracting fixed points (bistability).

4. Rock-paper-scissors

Suppose that the $\beta_i > 0$ and the $\alpha_i < 0$ in Eq. (6). In this situation there is an interior fixed point with all coordinates positive. Theorem 7.7.2 in Hofbauer and Sigmund [1] describes the asymptotic behavior of the replicator equations for these games.

Theorem 2 *Let $\Delta = \beta_1\beta_2\beta_3 + \alpha_1\alpha_2\alpha_3$. If $\Delta > 0$ solutions converge to the fixed point (stable spiral). If $\Delta < 0$ their distance from the boundary tends to 0 (unstable spiral). If $\Delta = 0$ there is a one-parameter family of periodic orbits.*

In [3] the following result is proved which covers some situations with stable spirals.

Theorem 3 *Suppose that the modified three strategy game H has (i) zeros on the diagonal, (ii) an interior equilibrium ρ, and that H is almost constant sum: $H_{ij} + H_{ji} = \gamma + \eta_{ij}$ with $\gamma > 0$ and $\max_{i,j} |\eta_{i,j}| < \gamma/2$. Then there is coexistence and furthermore for any $\delta > 0$ if $\varepsilon < \varepsilon_0(\delta)$ and μ is any stationary distribution concentrating on configurations with infinitely many 1's, 2's and 3's we have*

$$\sup_x |\mu(\xi(x) = i) - \rho_i| < \delta$$

In words, the equilibrium frequencies are close to those of the replicator equation for the modified game.

Turning to simulation we first consider the constant sum game (which is covered by Theorem 3).

G_2	**1**	**2**	**3**
1	0	4	−3
2	−1	0	5
3	6	−2	0

H_2	**1**	**2**	**3**
1	0	6.5	−7.5
2	−3.5	0	8.5
3	10.5	−5.5	0

Note that H_2 is again constant sum. It has $\Delta > 0$ so the replicator equation spirals in to the fixed point and Theorem 3 implies there is coexistence in the spatial game with weak selection.

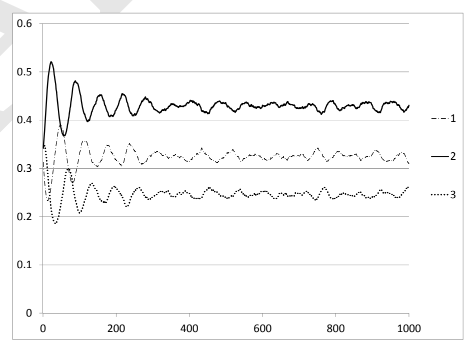

Fig. 2. Simulation confirms that in the spatial game $1 + 0.2G_2$ there is coexistence.

For our second example we consider a game G_3 for which the modified game H_3 has $\Delta < 0$, and hence the solution to the replicator equation spirals out to the boundary.

G_3	**1**	**2**	**3**
1	0	1	−2
2	−3	0	2
3	3	−2	0

H_3	**1**	**2**	**3**
1	0	3	−4.5
2	−5	0	4
3	5.5	−4	0

Figure 3 shows that spatial structure stabilizes the system. The apparent periodic behavior will disappear when a large enough system is simulated. For a discussion of this see Section 5 of a 1998 paper by Durrett and Levin [17]. As explained in Section S3 of the supporting information sufficiently large means that the side of the cube is much larger than the correlation length.

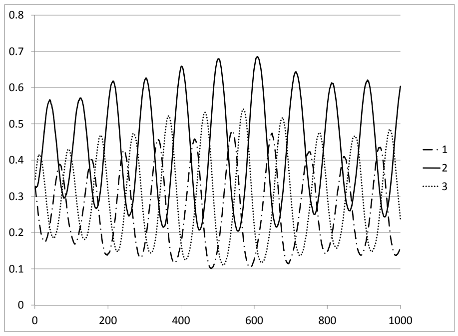

Fig. 3. Simulation of unstable rock-paper scissors game $1 + 0.2G_2$

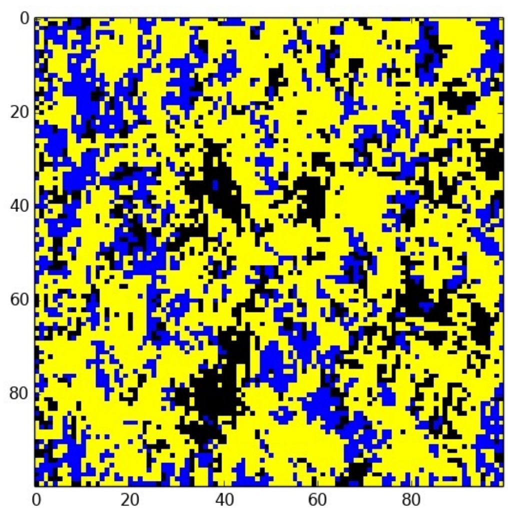

Fig. 4. Final state in the simulation in Figure 3. Note that there is significant correlation in contrast to the simulation of the public goods game in Figure 1.

5. Stag Hunt

To prepare for the discussion of bistable 3×3 games we begin with a 2×2 example.

	Stag	*Hare*
Stag	4	0
Hare	2	1

To explain the matrix: you can go hunt Stag (a large male deer) but if you go alone then you have no chance to get one. If you hunt Hare and the other player hunts Stag you get to keep all the rabbits. If you hunt Hare and the other player does also then you split the kill

If we transform so that there are 0's on the diagonal and replace the strategy names by numbers, the game becomes G. The modified game is H.

G	**1**	**2**
1	0	−1
2	−2	0

H	**1**	**2**
1	0	−0.5
2	−2.5	0

In H, $(\rho_1, \rho_2) = (1/6, 5/6)$ is an unstable equilibrium. If $u_1 > 1/6$, the first strategy becomes more attractive and increases further.

It was shown in Section 6 of [3] that if $\rho_1 < 1/2$ then the 1's take over the system. This is proved by considering the limiting PDE for the local density of strategy 1 which is

$$\frac{du}{dt} = \sigma^2 u''/2 + \phi(u) \quad \text{with} \quad \phi(u) = u(1-u)[b - (b+c)u]$$

where $b = -0.5$, $c = -2.5$. When $b, c < 0$ this equation has a traveling wave solution that moves with velocity v

$$u(t,x) = w(x - vt), \quad u(-\infty) = 1, \quad u(\infty) = 0.$$

1's take over if and only if $v > 0$ which is equivalent to $\int_0^1 \phi(x)\,dx > 0$. Since ϕ is a cubic with zeros at 0 and 1 this holds if and only if the interior equilibrium $\rho = b/(b+c) < 1/2$.

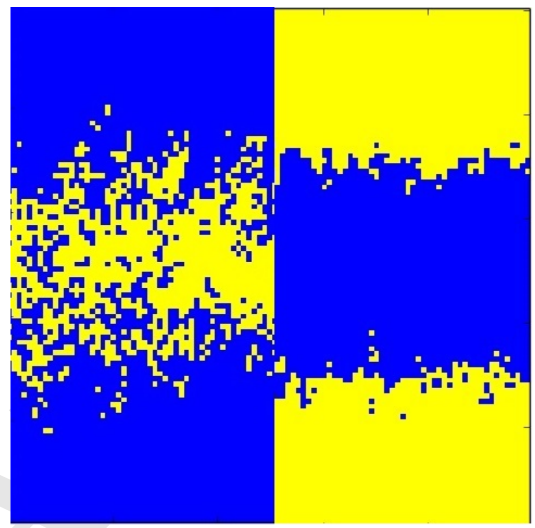

Fig. 5. The simulations were started with a strip of one strategy in between two strips of the opposite type. In the public goods game on the left the interface melts down and we have coexistence. In the Stag Hunt on the right the interface stays tight. For an explanation of the relevance of the behavior of interfaces to properties of stochastic spatial models see the 1999 paper by Molofsky et al [18]

6. Multiple myeloma

The original matrix, which we will call G_4 is given in Eq. (3). The modified game has entries

H_4	**1**	**2**	**3**
1	0	A	B
2	E	0	$-D$
3	C	F	0

where $A = (1+\theta)a - \theta e \ldots D = (1+\theta)d$, and $F = \theta d$. The modification of the game does not change the sign of D but it puts a positive entry F in $G_{3,2}$. It may also change the signs of one or two of the other four non-zero entries. Noting that $A < 0$ if $e > (1+\theta)a/\theta$ while $E < 0$ if $e < \theta a/(1+\theta)$ we see that if one of these two entries is negative the other one is positive. The same holds for B and C so there are nine possibilities for the signs of A, B, C, E and a wide variety of possible behaviors for the spatial game that are not found in the replicator equation. In particular it is possible for all three strategies to coexist in the spatial model but not in the replicator equation. These possibilities were systematically considered in Section 9.1 of [3]. Given the dramatic differences between the properties of the spatial game and the replicator equation, this casts doubt on the proposed insights into therapy that emerge from the analysis of Dingli et al [5]. See the discussion that begins on page 1134.

Here, our interest in this model is as an example with bistability. Suppose that $A, B, C, E > 0$ and $DC/BE > F/A$, which holds for the original game entries. Results from [3], which are described in Section S4 of the supporting information shows that there are three cases:

Case 1. $C/E > 1 - F/A$. The replicator equation converges to the 1,3 equilibrium.

Case 2. $1 - F/A > C/E > 1 - DC/BE$. There is an interior fixed point that is a saddle point, and the replicator equation exhibits bistability.

Case 3. $1 - DC/BE > C/E$. The replicator equation converges to the 1,2 equilibrium.

Simulation of Case 2. We take $a = e = 2$, $d = 1$, and vary $b = c$. The perturbed game is very simple in this case: $A = E = a = e$, $B = C = b = c$, $D = 1.5$, $F = 0.5$. Since $B = C = c$ the condition for case 2 is

$$1 - \frac{0.5}{2} > \frac{c}{2} > 1 - \frac{1.5}{2}$$

or $1.5 > c > 0.5$. When $c = 1.5$ the 1,3 equilibrium wins. When $c = 1$ the 1,2 equilibrium wins. When $c = 1.25$ the 1,2 equilibrium wins, see Figure 6 but takes a long time to do so, suggesting that this value is near the point where the winner changes. In principle we could find this tipping point by showing that the limiting system of PDE has traveling wave solutions and finding the, parameter value where the velocity changes sign but this seems to be difficult mathematical problem.

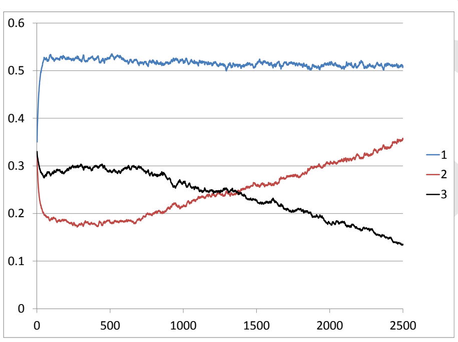

Fig. 6. Frequencies versus time in a $100 \times 100 \times 100$ simulation of the weak selection multiple myeloma game $1 + (1/3)G_4$, with $a = e = 2$, $d = 1$, and $b = c = 1.25$. Note that the frequencies first get close to the unstable fixed point at $(0.531, 0.306, 0.1633)$ and then start heading toward the boundary equilibrium.

7. Summary

In this paper we have used simulation and heuristic arguments to make predictions about the behavior of games that cannot be analyzed rigorously using the methods of [3]. The main contribution is to describe a procedure for determining the behavior of spatial three strategy games with weak selection,

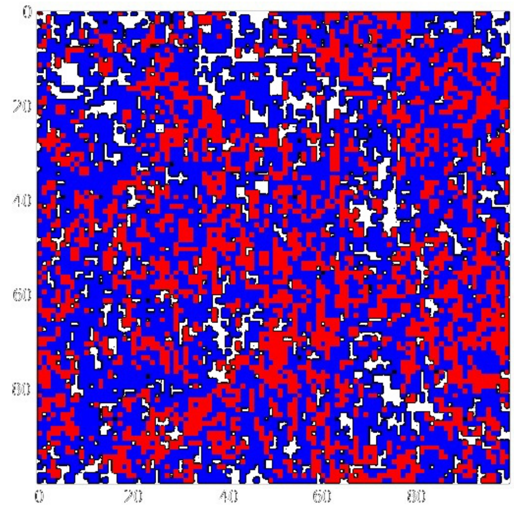

Fig. 7. Picture of final configuration for the simulation in Figure 6. Note that the blues (1s) are spread throughout the space while the reds (2s) and whites (3s) are segregated.

when the game matrix G has no unstable edge fixed points. One first forms the modified game $H_{ij} = (1 + \theta)G_{ij} - \theta G_{j,i}$, where θ is a constant that depends on the spatial structure but not on the entries in the game matrix. $\theta \approx 1/2$ in the three dimensional nearest neighbor case. The behavior of the spatial game with matrix G can then be predicted from that of the replicator equation for H. We say predicted because in some cases the behavior is not the same.

For three strategy games without unstable edge fixed points there are there are four major types:

1. When there are 1,2, or 3 stable edge fixed points and they can all be invaded there is coexistence in the spatial evolutionary game when selection is small. This was proved in [3]

2. As first observed by Durrett and Levin [19], when the replicator equation is bistable, i.e., the limit depends on the starting point, the spatial game has a stronger equilibrium that is the limit for generic initial conditions. In two strategy games, the victorious strategy is determined by the direction of movement of the traveling wave solution of the PDE. For three strategy games we do not know how to prove the existence of such traveling waves or compute their speeds, but simulations show that the same result holds.

3. In the case of rock-paper-scissors games, there is coexistence when the replicator equation converges to the interior fixed. This was proved in [3] when the game is “almost constant sum.” It is somewhat surprising that when the replicator equation trajectories that spiral out to the boundary, space exerts a stabilizing effect and the three strategies coexist. This has also been found recently by Ryser and Murgas [10].

4. Last, and least interesting is the situation in which the replicator equation converges to a boundary fixed point. Simulations show (see Section S5 of the supporting information) that the same behavior occurs in the spatial evolutionary game.

Work remains to be done on three strategy games with unstable boundary fixed points, however the work presented here can be used to analyze all of the games in all the papers we have cited except for one example in [10]. In many cases the behavior of the spatial game differs from that of the replicator equation, so it is important to consider the impact of spatial structure in order to obtain correct conclusions. The results we have presented here are derived in the limit that the selection $w \to 0$, but simulations show that in many cases the conclusions are accurate when $w = 0.1$ or event 0.25.

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Supporting Information

S1. Simulation algorithm

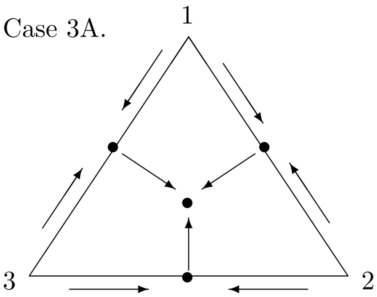
The algorithm is a variant of a technique called uniformization, which can reduce a continuous time Markov chain to discrete time. To expalin the Markov chain fact, let $q(i, j)$ is the rate for jumps from i to j, $\lambda_i = \sum_{j \neq i} q(i, j)$, and $\Lambda = \max_i \lambda_i$. If the chain is in state i at the nth step of the simulation, then $X_{n+1} = j$ with probability $q(i, j)/\Lambda$ if $j \neq i$ and $X_{n+1} = i$ with probability $1 - \lambda_i/\Lambda$. Since some transitions do not result in state changes this is inefficient, but this has the advantage that the times between jumps are exponential with rate Λ, so there is no need to create the exponential random variables. If n is large then the elapsed time after n simulation steps $T_n \sim n/\Lambda$, where $a_n \sim b_n$ means $a_n/b_n \to 1$.

The simulation method adapts easily to interacting particle systems and to evolutionary games in particular. Let $c_{ij}(x, \xi)$ be the rate at which site x changes from i to j when the configuration is ξ, let $\lambda_i(x, \xi) = \sum_{j \neq i} c_{ij}(x, \xi)$ and let $\Lambda = \max_{i,x} \lambda_i(x, \xi)$. On each simulation step we pick a site x at random. If it is in state i it changes to j with probability $c_{ij}(x, \xi)/\Lambda$ and does not change with probability $1 - \lambda_i(x, \xi)/\Lambda$. If there are N sites then the time until the next site tries to change is a minimum of N exponential(Λ) random variables, and hence exponential($N\Lambda$) Thus if n is large the elapsed time after n simulation steps $T_n \sim n/(N\Lambda)$.

S2. Classification of 3 by 3 games

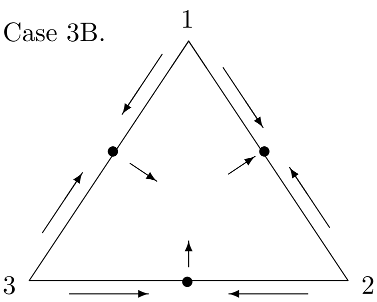
Here we describe the division of generic 3×3 games without unstable edge fixed points into 11 cases. The number in the name of each case gives the number of stable edge fixed points. Cases are further subdivided according to the number of edge fixed points that can be invaded, i.e., the freqeuncy of the third strategy will increase when rare. Whether a fixed point is invadable or not is indicated by the arrows next to the fixed points. On the other edges without fixed points, arrows give the direction of the dominance relations. Proofs of the statements we make about the behavior of the replicator equation can be found in Section 7 of [3].

Case 3A.



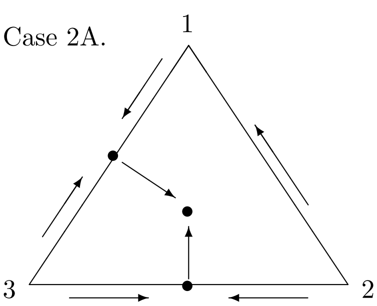
In Case 3A, all three edge equilibria can be invaded. The replicator equation converges to the interior fixed point and it was shown in [3] that there is coexistence in the spatial game when selection is weak.

Case 3B.



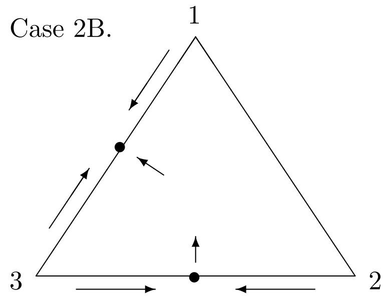
In case 3B, two of the three edge fixed points can be invaded. The replicator equation converges to the equilibrium on the 1, 2 edge, which we call $e_{1,2}$. It is impossible to have three stable edge fixed points and only 1 or 0 of them invadable.

Case 2A.



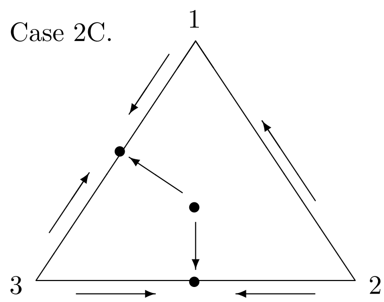
In case 2A, both edge equilibria can be invaded. The replicator equation converges to the interior fixed point and it was shown in [3] that there is coexistence in the spatial model.

Case 2B.



In case 2B, one edge fixed point can be invaded. The replicator equation converges to $e_{1,3}$. There is no arrow on the $1, 2$ edge because it is not important in which direction it points.

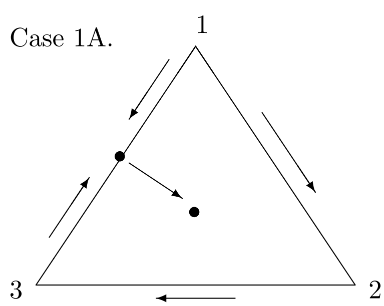
Case 2C.



In case 2C, neither edge fixed point can be invaded, so there is bistability, i.e., $e_{1,2}$ and $e_{1,3}$ are both locally stable.

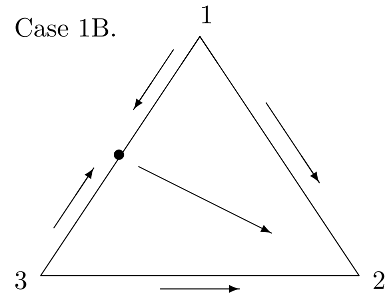
Next consider the situation in which there is one stable fixed point on the boundary. In first two cases it can be invaded.

Case 1A.



In case 1A, the pure strategy 2 can be invaded. The replicator equation converges to the interior fixed point. It was shown in [3] that there is coexistence in the spatial game when selection is weak.

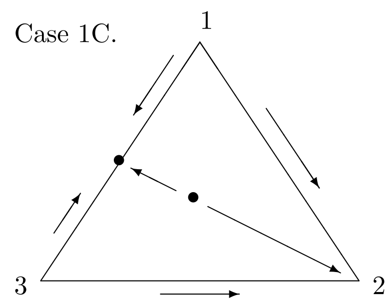
Case 1B.



In case 1B, the pure strategy 2 cannot be invaded. The replicator equation converges to the pure strategy 2.

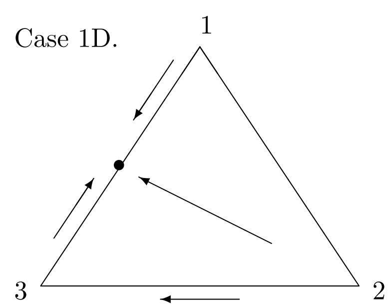
In the next two cases, there is one boundary fixed point and it cannot be invaded.

Case 1C.



In case 1C the interior equilibrium is bistable.

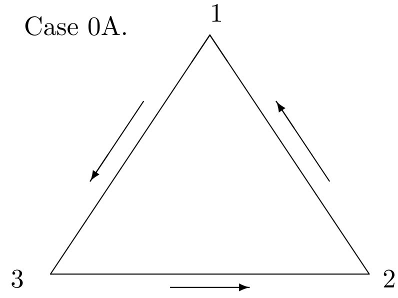
Case 1D.



In case 1D the replicator equation converges to $e_{1,3}$ There is no arrow on the $1, 2$ edge because the result does not depend on the direction it points.

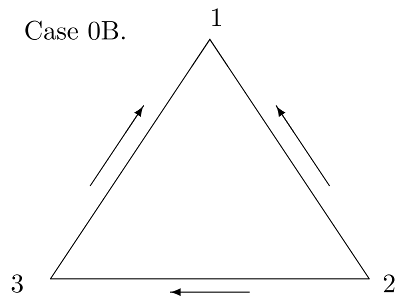
Finally we have the situation with no boundary fixed points. There are 8 possible orientations for the arrows on the edges. Two lead to rock-paper-scissor relationships between the strategies.

Case 0A.



In the other six combinations, two arrows point toward the same pure strategy equilibrium and that is the limit in the replicator equation.

Case 0B.



S3. Correlation length

For concreteness consider the Ising model. Let $\Lambda(L) = \{-L, -L+1, \ldots L\}^2$ and for each $\xi : \Lambda_L \to \{-1, -1\}$ define

$$\mu(\omega) = \frac{1}{Z(L)} \exp\left(\beta \sum_{x\sim y} \xi_x \xi_y\right)$$

where $x \sim y$ means x and y are nearest neighbors and $Z(L)$ is a normalizing constant to make p a probability measure on $\{-1, 1\}^{\Lambda(L)}$. It is a well known fact from statistical mechanics that one can let $L \to \infty$ to define probability measures on configurations $\omega : \mathbb{Z}^2 \to \{-1, 1\}$. When $\beta < \beta_c$ there is only one limit that has exponentially decaying correlations. That is if we let

$$\begin{aligned}\text{cov}\,(\xi(x), \xi(y)) &= P(\xi(x) = 1, \xi(y) = 1) \\ &\quad - P(\xi(x) = 1)P(\xi(y) = 1)\end{aligned}$$

which is ≥ 0 by the FKG inequality thenas $n \to \infty$

$$1/n \log \text{cov}\,(\xi(0,0), \xi(n,0)) = -\gamma(\beta).$$

The inverse of this exponential decay rate $\xi(\beta) = 1/\gamma(\beta)$ is the correlation length. Spins that are separated by one correlation length have covariance $\approx e^{-1}$ and hence have a tendency to be aligned. However, if we look at the fraction p_L of 1 spins in a box of side L which is much larger than the correlation length then the variance of p_L will be small and this will be close to its mean 1/2. In the stochastic Ising model, boxes that are the same size as the correlation length the feequency of 1's at time t, $p_L(t)$ will show fluctuations over time due to correlations, but when the length is much larger than the correlation length $p_L(t)$ wil stay approximately constant over time. This phenomenon is best understood in the well studied Ising but this is a general property of stochastic spatial models.

S4. Analysis of the Multiple myeloma game.

Boundary equilibria. To study the properties of the game we begin with the two strategy games it contains.

1 vs. 2. $(A/(A+E), E/(A+E))$ is a mixed strategy equilibrium. Since $A, E > 0$ it is attracting (on the 1,2 edge).

1 vs. 3. $(B/(B+C), C/(B+C))$ is a mixed strategy equilibrium. Since $B, C > 0$, it is attracting (on the 1,3 edge).

2 vs. 3. 3 dominates 2.

Invadability. The next step is to determine when the third strategy will increase when rare if the other two are equilibrium.

In the 1,2 equilibrium, fitnesses $F_1 = F_2 = AE/(A+E)$ while $F_3 = (CA + FE)/(A + E)$ so 3 can invade 1,2 (which we write as $3 \to 1,2$) if $CA + FE > AE$ or $C/E > 1 - F/A$.

In the 1,3 equilibrium, the fitnesses $F_1 = F_3 = BC/(B+C)$, while $F_2 = (EB-DC)/(B+C)$, so 2 can invade 1,3 if $EB - DC > BC$ or $1 - DC/BE > C/E$.

Case 1. $C/E > 1 - F/A$. $3 \to 1,2$ but $2 \not\to 1,3$ so the replicator converges to the 1,3 edge fixed point.

Case 2. $1 - F/A > C/E > 1 - DC/BE$ $3 \not\to 1,2$ but $2 \not\to 1,3$ so we have bistability.

Case 3. $1 - DC/BE > C/E$. $3 \not\to 1,2$ but $2 \to 1,3$ so the replicator converges to the 1,2 edge fixed point.

S5. Convergence to boundary fixed points

Coexistence has been proved in cases 3A, 2A, 1A. Rock-paper scissors and bistable cases were considered in the main paper. Here, will give simulations for the cases in which there is convergence to a boundary fixed point: 3B, 2B, 1B, 1D, 0B. In each case we give the original game matrix G and the transformed matrix H. The invadability conditions are as previously drawn for that case.

G_1	**1**	**2**	**3**
1	0	2.5	3.25
2	3.5	0	2.5
3	1.75	1.5	0

H_1	**1**	**2**	**3**
1	0	2	4
2	4	0	3
3	1	1	0

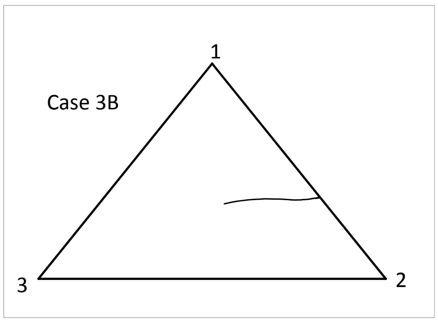


Figure 1: The replicator equation for $H_1 \to (1/3, 2/3, 0)$. In the spatial game G_1 frequencies $\to (0.378, 0.622, 0)$.

G_2	**1**	**2**	**3**
1	0	1.25	3.25
2	0.25	0	2.5
3	1.75	1.5	0

H_2	**1**	**2**	**3**
1	0	2	4
2	-1	0	3
3	1	1	0

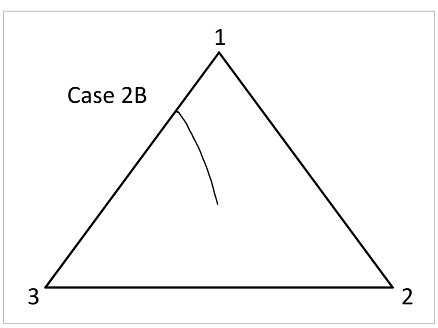


Figure 2: The replicator equation for $H_2 \to (3/4, 0, 1/4)$. In the spatial game $1 + (1/2.25)G_2$ frequencies $\to (0.7506, 0, 0.2494)$.

G_3	**1**	**2**	**3**
1	0	-1	3.25
2	1	0	0.5
3	1.75	-0.5	0

H_3	**1**	**2**	**3**
1	0	-2	4
2	2	0	1
3	1	-1	0

G_4	**1**	**2**	**3**
1	0	1.25	3.25
2	-0.25	0	0.125
3	2.5	-0.625	0

H_4	**1**	**2**	**3**
1	0	2	4
2	-1	0	-2
3	-2	1	0

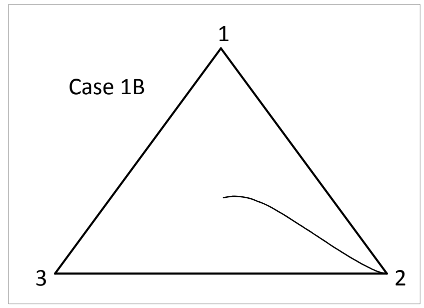


Figure 3: The replicator equation for H_3 and the frequencies in the spatial game $1 + (1/3)G_1 \to (0, 1, 0)$.

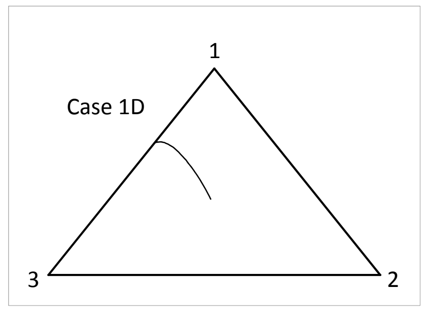


Figure 4: The replicator equation for $H_4 \to (2/3, 0, 1/3)$. In the spatial game $1 + (1/2.625)G_4$ frequencies $\to (0.636, 0, 0.364)$.

G_5	**1**	**2**	**3**
1	0	1.25	3.25
2	-0.25	0	-1.25
3	-0.5	0.25	0

H_5	**1**	**2**	**3**
1	0	2	4
2	-1	0	-2
3	2	1	0

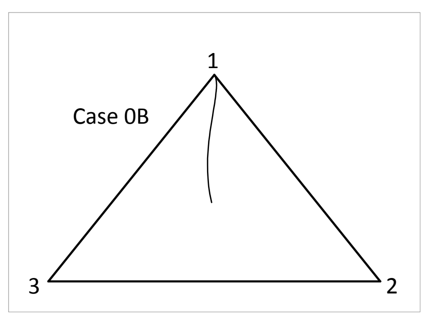


Figure 5: The replicator equation for H_5 and the frequencies in the spatial game $1 + (1/3.25)G_1 \to (1, 0, 0)$.