Spatial evolutionary games with small selection coefficients I. General theory and two strategy examples

Rick Durrett

November 28, 2013

Abstract

Here we will use results of Cox, Durrett, and Perkins [42] for voter model perturbations to study spatial evolutionary games on $\mathbb{Z}^d$, $d \geq 3$ when the interaction kernel is finite range, symmetric, and has covariance matrix $\sigma^2 I$. The games we consider have matrices of the form $\mathbf{1} + wG$ where $\mathbf{1}$ is matrix of all 1's and w is small and positive. Since our population is infinite, we call our selection small rather than weak which usually means $w = O(1/N)$. We prove that the effect of space is equivalent to (i) changing the entries of the game matrix and (ii) replacing the replicator ODE by a related PDE. The first idea is due to Ohtsuki and Nowak [34] (for the pair approximation) while the second is well known in the theory of stochastic spatial processes [44, 16, 47, 48]. A remarkable aspect of our result is that the limiting PDE depends on the interaction kernel only through the values of two simple noncoalescence probabilities for an associated random walk. In this paper we develop theoretical results for n strategy games. However for applications, we restrict our attention here to two strategy games, because in that case existing PDE results allow us to analyze any example. Part II will deal with the more complicated case of three strategy games.

1 Introduction

Game theory was invented by John von Neumann and Oscar Morgenstern [1] to study strategic and economic decisions of humans. Maynard Smith and Price [2], see also [4], introduced the concept into ecology in order to explain why conflicts over territory between male animals of the same species are usually of the "limited war" type and do not cause serious damage. Axelrod and Hamilton [3] studied the evolution of cooperation by investigating the Prisoner's dilemma game. Since that time, evolutionary game theory has been used to study many biological problems. This is natural because evolutionary game theory provides a framework for the study of frequency dependent selection. For surveys see [7]–[10].

All of the references in the last paragraph study evolutionary games in homogeneously mixing populations, in which case the frequencies (in continuous time) follow the replicator equation. One can argue that long distance connections in human social network imply that spatial effects can be ignored, but this is not true for systems in ecology and cancer. Nowak and May [11, 13, 14] showed that having only local interactions in two dimensions enhanced the persistence of cooperators in Prisoner's dilemma. Their competition was deterministic and took place on the square lattice. In the references we list a representative sample of work of this type, [16]–[32]. There are literally hundreds of references, so we have restricted our attention to systems on the square lattice $\mathbb{Z}^d$, and chosen papers that are the most relevant to our investigations.

Twenty years ago, Durrett and Levin [16] studied evolutionary games and formulated rules for predicting the behavior of spatial models from the properties of the mean-field differential equations obtained by supposing that adjacent sites are independent, see [45] for an overview of this approach. Our main motivation for revisiting this question is that the recent work of Cox, Durrett, and Perkins [42] allows us to turn the heuristic principles of [16] into rigorous results for systems that are perturbations of the voter model. However, for the predictions of the heuristic to be accurate, one must take expected values with respect a voter model equilibrium rather than with respect to the product measure that gives rise to the mean-feild equation.

2 Voter Model Perturbations

Our goal here is to prove rigorous results for evolutionary games with matrices of the form $\bar{G} = \mathbf{1} + wG$, where $w > 0$ is small, and $\mathbf{1}$ is a matrix that consists of all 1's. We will study these games on $\mathbb{Z}^d$ where the interactions between an individual and its neighbors are given by an irreducible probability kernel $p(x)$ on $\mathbb{Z}^d$ that is finite range, symmetric $p(x) = p(-x)$, and has covariance matrix $\sigma^2 I$.

When $w = 0$ this reduces to the voter model, a system in which each site at rate 1 changes its state to that of a randomly chosen neighbor. When w is small, our spatial evolutionary game is a voter model perturbations in the sense of Cox, Durrett, and Perkins [42]. To formulate the class of models we consider, let $f_i(x,\xi) = \sum_y p(y-x) 1(\xi(y) = i)$ be the fraction of neighbors of x in state i. In the voter model, the rate at which the voter at x changes its opinion from i to j is

$$c^v_{i,j}(x,\xi) = 1_{(\xi(x)=i)} f_j(x,\xi)$$

The voter model perturbations that we consider have flip rates

$$c^v_{i,j}(x,\xi) + \varepsilon^2 h^\varepsilon_{i,j}(x,\xi)$$

The perturbation functions h^ε_{ij} may be negative (and will be for games with negative entries) but in order for the analysis in [42] to work, there must be a law q of $(Y^1, \dots Y^m) \in Z^m$ and functions $g^\varepsilon_{i,j} \geq 0$, which converge to limits $g_{i,j}$ as $\varepsilon \to 0$, so that for some $\gamma < \infty$, we have for $\varepsilon \leq \varepsilon_0$

$$h^\varepsilon_{i,j}(x,\xi) = -\gamma f_i(x,\xi) + E_Y[g^\varepsilon_{i,j}(\xi(x+Y^1), \dots \xi(x+Y^m))] \tag{1}$$

In words, we can make the perturbation positive by adding a positive multiple of the voter flip rates. This is needed so that [42] can use $g^\varepsilon_{i,j}$ to define jump rates of a Markov process. As we will see, the condition is harmless in our examples, and all our calculations can be done using the original perturbation

$$h_{i,j} = \lim_{\varepsilon \to 0} h^\varepsilon_{i,j}.$$

The next result is the key to the analysis of voter model perturbation. The result was proved in [42] for systems with two opinions but generalizes easily to more than two opinions.

Theorem 1. *If we rescale space to $\varepsilon\mathbb{Z}^d$ and speed up time by ε^{-2} then in $d \geq 3$*

$$u_i^\varepsilon(t,x) = P(\xi^\varepsilon_{t\varepsilon^{-2}}(x) = i)$$

converges to the solution of the system of partial differential equations:

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

where

$$\phi_i(u) = \sum_{j \neq i} \langle 1_{(\xi(0)=j)} h_{j,i}(0,\xi) - 1_{(\xi(0)=i)} h_{i,j}(0,\xi) \rangle_u$$

and the brackets are expected value with respect to the voter model stationary distribution ν_u in which the densities are given by the vector u.

Intuitively, since on the fast time scale the voter model runs at rate ε^{-2} versus the perturbation at rate 1, the process is always close to the voter equilibrium for the current density vector u. Thus, we can compute the rate of change of u_i by assuming the nearby sites are in that voter model equilibrium. The restriction to dimensions $d \geq 3$ is due to the fact that the voter model does not have nontrivial stationary distributions in $d \leq 2$. For readers not familiar with the voter model, we recall the relevant facts in Section 6

We will consider two versions of spatial evolutionary game dynamics.

Birth-Death dynamics. In this version of the model, a site x gives birth at a rate equal to its fitness

$$\sum_y p(y-x)\bar{G}(\xi(x), \xi(y))$$

and the offspring replaces a "randomly chosen neighbor of x." Here and in what follows, the phrase in quotes means z is chosen with probability $p(z-x)$. If we let $r_{i,j}(0,\xi)$ be the rate at which the state of 0 flips from i to j, then setting $w = \varepsilon^2$ and using symmetry $p(x) = p(-x)$

$$\begin{aligned} r_{i,j}(0,\xi) &= \sum_x p(x) 1(\xi(x) = j) \sum_y p(y-x)\bar{G}(j, \xi(y)) \\ &= \sum_x p(x) 1(\xi(x) = j) \left(1 + \varepsilon^2 \sum_k f_k(x,\xi) G_{j,k}\right) \\ &= f_j(0,\xi) + \varepsilon^2 \sum_k f^{(2)}_{j,k}(0,\xi) G_{j,k} \end{aligned} \tag{2}$$

where $f^{(2)}_{j,k}(0,\xi) = \sum_x \sum_y p(x)p(y-x) 1(\xi(x) = j, \xi(y) = k)$, so the perturbation, which does not depend on ε is

$$h_{i,j}(0,\xi) = \sum_k f^{(2)}_{j,k}(0,\xi) G_{j,k} \tag{3}$$

To see that this satisfies the technical condition (1) note that if $\gamma = \max_{i,j} G^-_{i,j}$ where $x^- = \max\{-x, 0\}$, and we let $g_{i,j}(k,\ell) = \gamma + 1_{(k=j)} G_{k,\ell}$ when $\xi(0) = i$ and 0 otherwise then

$$h^{\varepsilon}_{i,j}(0,\xi) = -\gamma f_i(0,\xi) + E_Y[g_{i,j}(\xi(Y^1), \xi(Y^2))]$$

where Y^1 is a randomly chosen neighbor of 0 and Y^2 is a randomly chosen neighbor of Y^1.

Death-Birth Dynamics. In this case, each site dies at rate one and is replaced by a neighbor chosen with probability proportional to its fitness. Using the notation in (2) the rate at which $\xi(0) = i$ jumps to state j is

$$\begin{aligned} \bar{r}_{i,j}(0,\xi) &= \frac{r_{i,j}(0,\xi)}{\sum_k r_{i,k}(0,\xi)} = \frac{f_j(0,\xi) + \varepsilon^2 h_{i,j}(0,\xi)}{1 + \varepsilon^2 \sum_k h_{i,k}(0,\xi)} \\ &= f_j + \varepsilon^2 h_{i,j}(0,\xi) - \varepsilon^2 f_j \sum_k h_{i,k}(0,\xi) + O(\varepsilon^4) \end{aligned} \tag{4}$$

The new perturbation, which depends on ε, is

$$\bar{h}_{i,j}(0,\xi) = h_{i,j}(0,\xi) - f_j \sum_k h_{i,k}(0,\xi) + O(\varepsilon^2) \tag{5}$$

It is not hard to see that it also satisfies the technical condition (1).

There are a number of other updates rules. In **Fermi updating**, a site x and a neighbor y are chosen at random. Then x adopts y's strategy with probability

$$[1 + \exp(\beta(F_x - F_y))]^{-1}$$

where $F_z = \sum_{z \sim w} G(\xi(z), \xi(w))$. When $\beta \to 0$ this reduces to Birth-Death updating. However the main reason for interest in this rule is the phase transition that occurs, for example in Prisoner's Dilemma games as β is increased, see [19, 24, 25].

In **Imitate the best** one adopts the strategy of the neighbor with the largest fitness. Changing the game matrix to $\bar{G} = 1 + wG$ does not change the dynamics, so this is not a voter model perturbation. In discrete time (i.e., with synchronous updates) the process is deterministic.

3 Voter Model Duality

Let $\xi_t(x)$ be the state of the voter at x at time t. The key to the study of the voter model is that we can define for each x and t, random walks $\xi^{x,t}_s$, $0 \le s \le t$ that move independently until they hit and then coalesce to 1 so that

$$\xi_t(x) = \xi_{t-s}(\zeta^{x,t}_s) \tag{6}$$

Intuitively, the $\zeta^{x,t}_s$ are genealogies that trace the origin of the opinion at x at time t. See Section 6 for more details about this and other facts about the voter model we cite in this section.

Consider now the case of two opinions. A consequence of this duality relation is that if we let $p(0|x)$ be the probability that two continuous time random walks with jump distribution p, one starting at the origin 0, and one starting at x never hit then

$$\langle \xi(0) = 1, \xi(x) = 0 \rangle_u = p(0|x)u(1-u)$$

To prove this, we recall that the stationary distribution ν_u is the limit in distribution as $t \to \infty$ of ξ_t^u, the voter model starting with sites that are independent and $= 1$ with probability u, and then observe that (6) implies

$$P(\xi_t^u(0) = 1, \xi_t^u(x) = 0) = P(\xi_0^u(\zeta_t^{0,t}) = 1, \xi_0^u(\zeta_t^{x,t}) = 0) = u(1-u)P(\zeta_t^{0,t} \neq \zeta_t^{x,t})$$

Letting $t \to \infty$ gives the desired identity.

To extend this reasoning to three sites, let $p(0|x|y)$ be the probability that the three random walks never hit and let $p(0|x, y)$ be the probability that the walks starting from x and y coalesce but they do not hit the one starting at 0. Considering the possibilities that the walks starting from x and y may or may not coalesce:

$$\langle \xi(0) = 1, \xi(x) = 0, \xi(y) = 0 \rangle_u = p(0|x|y)u(1-u)^2 + p(0|x, y)u(1-u)$$

Let v_1, v_2, v_3 be independent and chosen according to the distribution p. The coalescence probabilities satisfy some remarkable identities that will be useful for simplifying formulas later on. Let $\kappa = 1/P(v_1 + v_2 = 0)$ be the "effective number of neighbors." To explain this definition, note that if $p(x)$ is uniform over a set S that is symmetric $S = -S$ and does not contain 0 then $\kappa = |S|$. Since the v_i have the same distribution as steps in the random walk, simple arguments given in Section 7 show that

$$p(0|v_1) = p(0|v_1 + v_2) = p(v_1|v_2) \tag{7}$$
$$p(v_1|v_2 + v_3) = (1 + 1/\kappa)p(0|v_1) \tag{8}$$

It is easy to see that for any x, y, z coalescence probabilities must satisfy

$$p(x|z) = p(x, y|z) + p(x|y, z) + p(x|y|z) \tag{9}$$

Combining this with the identities for two sites leads to

$$p(0, v_1|v_1 + v_2) = p(0, v_1 + v_2|v_1) = p(v_1, v_1 + v_2|0) \tag{10}$$
$$p(v_1, v_2|v_2 + v_3) = p(v_2, v_2 + v_3|v_1) = p(v_1, v_2 + v_3|v_2) + (1/\kappa)p(0|v_1) \tag{11}$$

From (9) and (10) it follows that

$$p(0|v_1) = 2p(x, y|z) + p(0|v_1|v_1 + v_2) \tag{12}$$

where x, y, z is any ordering of $0, v_1, v_1+v_2$. Later, we will be interested in $p_1 = p(0|v_1|v_1+v_2)$ and $p_2 = p(0|v_1, v_1 + v_2)$. In this case, (12) implies

$$2p_1 + p_2 = p(0|v_1) \tag{13}$$

Similar reasoning to that used for (12) gives

$$p(v_1|v_2)(1+1/\kappa) = 2p(v_2, v_2+v_3|v_1) + p(v_1|v_2|v_2+v_3) \tag{14}$$
$$= 2p(v_1, v_2|v_2+v_3) + p(v_1|v_2|v_2+v_3) \tag{15}$$
$$p(v_1|v_2)(1-1/\kappa) = 2p(v_1, v_2+v_3|v_2) + p(v_1|v_2|v_2+v_3) \tag{16}$$

Later, we will be interested in $\bar{p}_1 = p(v_1|v_2|v_2+v_3)$ and $\bar{p}_2 = p(v_1|v_2, v_2+v_3)$. In this case, (14) implies that

$$2\bar{p}_1 + \bar{p}_1 = p(v_1|v_2)(1+1/\kappa) \tag{17}$$

We will also need the following consequence of (14) and (9)

$$\bar{p}_2 - p(v_1|v_2)/\kappa = p(v_1|v_2) - \bar{p}_1 - \bar{p}_2 = p(v_1, v_2+v_3|v_2) > 0 \tag{18}$$

Work of Tarnita et al. [30, 31] has shown that when selection is weak (i.e., $w \ll 1/N$ where N is the population size) one can determine whether a strategy in an n-strategy game is favored by selection (i.e., has frequency $> 1/n$) by using an inequality that is linear in the entries of the game matrix that involves one ($n=2$) or two ($n \geq 3$) constants that depend on the spatial structure. Our analysis will show that on $\mathbb{Z}^d$, $d \geq 3$, the only aspects of the spatial structure relevant for a complete analysis of the game with small selection are $p(0|v_1)$ and $p(0|v_1|v_1+v_2)$ for Birth-Death updating and $p(v_1|v_2)$ and $p(v_1|v_2|v_2+v_3)$ for Death-Birth updating.

The coalescence probabilities $p(0|v_1) = p(v_1|v_2)$ are easily calculated since the difference between the positions of the two walkers is a random walk. Let S_n be the discrete time random walk that has jumps according to p and let

$$\phi(t) = \sum_x e^{itx} p(x)$$

be its characteristic function (a.k.a Fourier transform). The inversion formula implies

$$P(S_n = 0) = (2\pi)^{-d} \int_{(-\pi,\pi)^d} \phi^n(t)\, dt$$

so summing we have

$$\chi \equiv \sum_{n=0}^{\infty} P(S_n = 0) = (2\pi)^{-d} \int_{(-\pi,\pi)^d} \frac{1}{1-\phi(t)}\, dt$$

For more details see pages 200–201 in [46]. Since the number of visits to 0 has a geometric distribution with success probability $p(0|v_1)$ it follows that

$$p(0|v_1) = \frac{1}{\chi}$$

In the three dimensional nearest neighbor case it is know that $\chi = 1.561386\ldots$ so we have

$$p(0|v_1) = p(v_1|v_2) = 0.6404566$$

To evaluate $p(0|v_1|v_1+v_2)$ and $p(v_1|v_2|v_2+v_3)$ we have to turn to simulation. Simulations of Yuan Zhang suggest that $p(0|v_1|v_1+v_2) \in [0.32, 0.33]$ and $p(v_1|v_2|v_2+v_3) \in [0.34, 0.35]$.

4 PDE limit

In a homogeneously mixing population the frequencies of the strategies in an evolutionary game follow the replicator equation, see e.g., Hofbauer and Sigmund's book [7]:

$$\frac{du_i}{dt} = \phi^i_R(u) \equiv u_i \left(\sum_k G_{i,k} u_k - \sum_{j,k} u_j G_{j,k} u_k \right). \tag{19}$$

Birth-Death dynamics. Let

$$p_1 = p(0|v_1|v_1 + v_2) \quad \text{and} \quad p_2 = p(0|v_1, v_1 + v_2)$$

In this case the limiting PDE in Theorem 1 is $\partial u_i / \partial_t = (1/2d)\Delta u + \phi^i_B(u)$ where

$$\phi^i_B(u) = p_1 \phi^i_R(u) + p_2 \sum_{j \neq i} u_i u_j (G_{i,i} - G_{j,i} + G_{i,j} - G_{j,j}) \tag{20}$$

Formula (12) implies that

$$2p(0|v_1, v_1 + v_2) = p(0|v_1) - p(0|v_1|v_1 + v_2)$$

so it is enough to know the two probabilities on the right-hand side.

If coalescence is impossible then $p_1 = 1$ and $p_2 = 0$ and the new equation reduces to the old one. There is a second more useful connection to the replicator equation. Let

$$A_{i,j} = \frac{p_2}{p_1}(G_{i,i} + G_{i,j} - G_{j,i} - G_{j,j})$$

This matrix is skew symmetric $A_{i,j} = -A_{j,i}$ so $\sum_{i,j} u_i A_{i,j} u_j = 0$ and it follows that $\phi^i_B(u)$ is p_1 times the RHS of the replicator equation for the game matrix $A+G$. This observation is due to Ohtsuki and Nowak [34] who studied the limiting ODE that arises from the nonrigorous pair approximation. In their case, the perturbing matrix, see their (14), is

$$\frac{1}{\kappa - 2}(G_{i,i} + G_{i,j} - G_{j,i} - G_{j,j})$$

To connect the two formulas note if space is a tree in which each site has κ neighbors then $p(0, v_1) = 1/(\kappa - 1)$. Under the pair approximation, the coalescence of 0 and v_1 is assumed independent of the coalescence of v_1 and $v_1 + v_2$, so

$$\frac{p_2}{p_1} = \frac{p(0|v_1, v_1 + v_2)}{p(0|v_1|v_1 + v - 2)} = \frac{p(v_1, v_1 + v_2)}{p(v_1|v_1 + v - 2)} = \frac{1}{\kappa - 2}.$$

Death-Birth Dynamics. Let

$$\bar{p}_1 = p(v_1|v_2|v_2 + v_3) \quad \text{and} \quad \bar{p}_2 = p(v_1|v_2, v_2 + v_3)$$

Note that in comparison with p_1 and p_2, 0 has been replaced by v_1 and then the other two v_i have been renumbered. In this case the limiting PDE is $\partial u_i/\partial t = (1/2d)\Delta u + \phi_D^i(u)$ where

$$\begin{aligned}\phi_D^i(u) &= \bar{p}_1 \phi_R^i(u) + \bar{p}_2 \sum_{j\neq i} u_i u_j (G_{i,i} - G_{j,i} + G_{i,j} - G_{j,j}) \\ &\quad - (1/\kappa) p(v_1|v_2) \sum_{j\neq i} u_i u_j (G_{i,j} - G_{j,i}) \end{aligned} \tag{21}$$

The first two terms are the ones in (20). The similarity is not surprising since the numerators of the flip rates in (4) are the flip rates in (2). The third term comes from the denominator in (4). Formula (12) implies that

$$2p(v_1|v_2, v_2 + v_3) = (1 + 1/\kappa)p(v_1|v_2) - p(v_1|v_2|v_2 + v_3)$$

so it is enough to know the two probabilities on the right-hand side.

As in the Birth-Death case, if we let

$$\bar{A}_{i,j} = \frac{\bar{p}_2}{\bar{p}_1}(G_{i,i} + G_{i,j} - G_{j,i} - G_{j,j}) - \frac{p(v_1|v_2)}{\kappa \bar{p}_1}(G_{i,j} - G_{j,i})$$

then $\phi_i^D(u)$ is $\bar{p}_1$ times the RHS of the replicator equation for $\bar{A} + G$. Again, Ohtsuki and Nowak [34] have a similar result for the ODE resulting from the pair approximation. In their case the perturbing matrix, see their (23), is

$$\frac{1}{\kappa - 2}(G_{i,i} + G_{i,j} - G_{j,i} - G_{j,j}) - \frac{\kappa}{(\kappa+1)(\kappa-2)}(G_{i,j} - G_{j,i})$$

This time the connection is not exact since under the pair approximation

$$\frac{p(v_1|v_2)}{\kappa \bar{p}_1} = \frac{p(v_1|v_2)}{\kappa p(v_1|v_2|v_2 + v_3)} = \frac{1}{\kappa p(v_2|v_2 + v_3)} = \frac{\kappa - 1}{\kappa(\kappa - 2)}$$

5 Two strategy games

We now consider the special case of a 2×2 games.

$$\begin{array}{ccc} & 1 & 2 \\ 1 & \alpha & \beta \\ 2 & \gamma & \delta \end{array} \tag{22}$$

Let u denote the frequency of strategy 1. In a homogeneously mixing population, u evolves according to the replicator equation (19):

$$\begin{aligned}\frac{du}{dt} &= u\{\alpha u + \beta(1-u) + u[\alpha u + \beta(1-u)] + (1-u)[\gamma u + \delta(1-\delta)]\} \\ &= u(1-u)[\beta - \delta + \Gamma u] \equiv \phi_R(u) \end{aligned} \tag{23}$$

where we have introduced $\Gamma = \alpha - \beta - \gamma + \delta$. Note that if there is a fixed point in $(0,1)$ it occurs at

$$\bar{u} = \frac{\beta - \delta}{\beta - \delta + \alpha - \gamma} \tag{24}$$

Using results from the previous section gives the following.

Birth-Death dynamics. The limiting PDE is $\partial u/\partial t = (1/2d)\Delta u + \phi_B(u)$ where $\phi_B(u)$ is the RHS of the replicator equation for the game

$$\begin{pmatrix} \alpha & \beta + \Delta \\ \gamma - \Delta & \delta \end{pmatrix}$$

and $\Delta = (p_2/p_1)(\alpha + \beta - \gamma - \delta)$.

Death-Birth dynamics. The limiting PDE is $\partial u/\partial t = (1/2d)\Delta u + \phi_D(u)$ where $\phi_D(u)$ is the RHS of the replicator equation for the game

$$\begin{pmatrix} \alpha & \beta + \bar{\Delta} \\ \gamma - \bar{\Delta} & \delta \end{pmatrix}$$

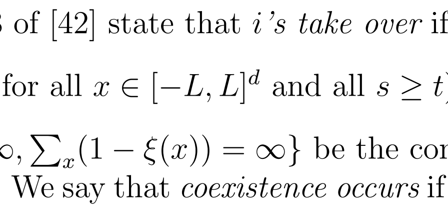
and $\bar{\Delta} = (\bar{p}_2/\bar{p}_1)(\alpha + \beta - \gamma - \delta) - (p(v_1|v_2)/\kappa\bar{p}_1)(\beta - \gamma)$.

5.1 Analysis of 2×2 games

Suppose that the limiting PDE is $\partial u/\partial t = (1/2d)\Delta u + \phi(u)$ where ϕ is a cubic with roots at 0 and 1. There are four possibilities

S_1	$\bar{u}$ attracting	$\phi'(0) > 0,\ \phi'(1) > 0$
S_2	$\bar{u}$ repelling	$\phi'(0) < 0,\ \phi'(1) < 0$
S_3	$\phi < 0$ on $(0,1)$	$\phi'(0) < 0,\ \phi'(1) > 0$
S_4	$\phi > 0$ on $(0,1)$	$\phi'(0) > 0,\ \phi'(1) < 0$

To see this, we draw a picture. For convenience, we have drawn the cubic as a piecewise linear function.



A definitions on page 8 of [42] state that *i's take over* if for all L

$$P(\xi_s(x) = i \text{ for all } x \in [-L, L]^d \text{ and all } s \geq t) \to 1 \quad \text{as } t \to \infty.$$

Let $\Omega_0 = \{\xi : \sum_x \xi(x) = \infty, \sum_x (1 - \xi(x)) = \infty\}$ be the configurations with infinitely many 1's and infinitely many 0's. We say that *coexistence occurs* if there is a stationary distribution ν for the spatial model with $\nu(\Omega_0) = 1$.

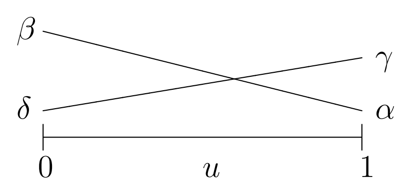
Theorem 2. *If $\varepsilon < \varepsilon_0(G)$, then:*
In case S_3, 2's take over. In case S_4, 1's take over.
In case S_2, 1's take over if $\bar{u} < 1/2$, and 2's take over if $\bar{u} > 1/2$.
In case S_1, coexistence occurs. Furthermore, if $\delta > 0$ and $\varepsilon < \varepsilon_0(G, \delta)$ then any stationary distribution with $\nu(\Omega_0) = 1$ has

$$\sup_x |\nu(\xi(x) = 1) - \bar{u}| < \delta.$$

To begin to apply this result we note that if ϕ is the RHS of the replicator equation for the game matrix in (2) then writing $i \gg j$ for strategy i dominates strategy j the cases are:

$$\begin{array}{ccc} & \beta > \delta & \beta < \delta \\ \alpha < \gamma & S_1.\ \text{Coexistence} & S_3.\ 2 \gg 1 \\ \alpha > \gamma & S_4.\ 1 \gg 2 & S_2.\ \text{Bistable} \end{array} \tag{25}$$

To check S_1 we draw a picture.



When the frequency of strategy 1 is $u \approx 0$ then strategy 1 has fitness $\approx \beta$ and strategy 2 has fitness $\approx \delta$, so u will increase. The condition $\alpha < \gamma$ implies that when $u \approx 1$ it will decrease and the fixed point is attracting. When both inequalities are reversed in S_2, the fixed point exists but is unstable. Finally the second strategy dominates the first in S_3, and the first strategy dominates the second in S_4.

5.2 Phase Diagram

At this point, we can analyze the spatial version of any two strategy game. In the literature on 2×2 games it is common to use the following notation for payoffs, which was introduced in the classic paper by Axelrod and Hamilton [3].

$$\begin{array}{ccc} & \text{C} & \text{D} \\ \text{C} & R & S \\ \text{D} & T & P \end{array}$$

Here T = temptation, S = sucker payoff, R = reward for cooperation, P = punishment for defection. If we assume, without loss of generality, that $R > P$ then there are 12 possible orderings for the payoffs. However, from the viewpoint of Theorem 2, there are only four cases.

Hauert simulates spatial games with $R = 1$ and $P = 0$ for a large number of values of S and T. He considers three update rules: (a) switch to the strategy of the best neighbor,

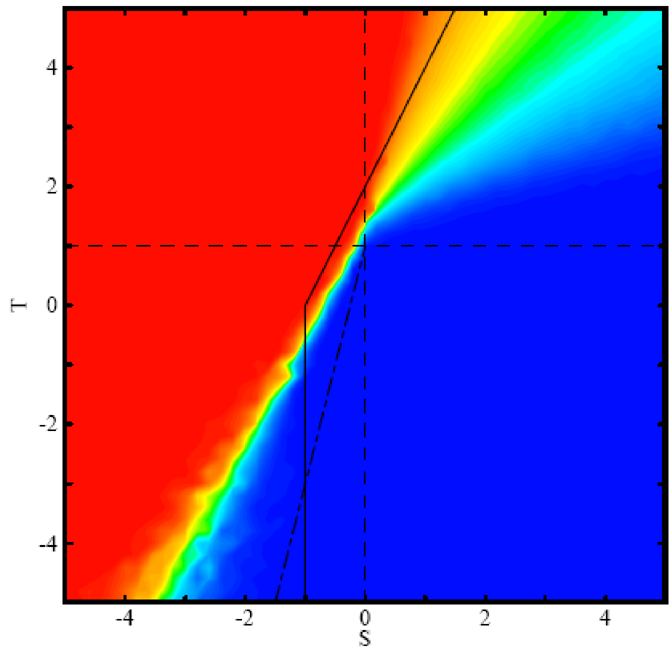


Figure 1: Phase diagram from Hauert's simulations

(b) pick a neighbor's strategy with probability proportional to the difference in scores, and (c) pick a neighbor's strategy with probability proportional to its fitness, or in our terms Death-Birth updating. He considers discrete and continuous time updates using the von Neumann neighborhood (four nearest neighbors) and the Moore neighborhood (which also includes the diagonally adjacent neighbors). The picture most relevant our investigation here is the graph in the lower left corner of his Figure 5, reproduced here as Figure 1, which shows equilibrium frequencies of the two strategies in continuous time for update rule (c) on the von Neumann neighborhood. Similar pictures can be found in the work of Roca, Cuesta, and Sanchez [28, 29].

Our situation is different from his, since the games we consider are small perturbations of the voter model game **1**, bu,t as we will see, the qualitative features of the phase diagrams are the same. Under either update the game matrix changes to

$$\begin{array}{lll} & \text{C} & \text{D} \\ \text{C} & \alpha = R & \beta = S + \theta \\ \text{D} & \gamma = T - \theta & \delta = P \end{array}$$

Birth-Death updating. In this case

$$\theta = \Delta = \frac{p_2}{p_1}(R + S - T - P) \tag{26}$$

We will now find the boundaries between the four cases using (25). Letting $\lambda = p_2/p_1 \in (0, 1)$, we have $\alpha = \gamma$ when

$$R - T = -\theta = -\lambda(R + S - T - P)$$

Rearranging gives $\lambda(S-T) = (1+\lambda)(T-R)$, and we have

$$T - R = \frac{\lambda}{\lambda+1}(S-P) \tag{27}$$

Repeating this calculation shows that $\beta = \delta$ when

$$T - R = \frac{\lambda+1}{\lambda}(S-P) \tag{28}$$

This leads to the four regions drawn in Figure 2. Note that the coexistence region is smaller than in the homogenenously mixing case.

In the coexistence region, the equilibrium is

$$\bar{u} = \frac{S-P+\theta}{S-P+T-R} \tag{29}$$

Plugging in the value of θ from (26) this becomes

$$\bar{u} = \frac{(1+\lambda)(S-P)+\lambda(R-T)}{S-P+T-R} \tag{30}$$

Note that in the coexistence region, $\bar{u}$ is constant on lines through $(S,T) = (P,R)$.

In the lower left region where there is bistability, 1's win if $\bar{u} < 1/2$ or what is the same if strategy 1 is better than strategy 2 when $u = 1/2$, that is,

$$R + S + \theta > T - \theta + P$$

Plugging in the value of θ this becomes $(1+2\lambda)(R+S-T-P) > 0$ or

$$R - T > P - S. \tag{31}$$

Writing this as $R + S > T + P$, we see that the population converges to when it is "risk dominant", a term introduced by Harsanyi and Selten [6]. Note that bistablity in the replicator equation disappears in the spatial model, an observation that goes back to Durrett and Levin [16]. If you rotate Figure 1 by 180 degrees it is very similar to the phase diagram for the Lotka-Volterra model given in Figure 1.1 of [42].

Death-Birth updating. The phase diagram is similar to that for Birth-Death updating but the regions are shifted over in space. Since the algebra in the derivation is messier, we state the result here and hide the details away in Section 9. If we let $\mu = \bar{p}_2/\bar{p}_1$, $\nu = p(v_1|v_2)/\kappa\bar{p}_1)$,

$$P^* = P - \frac{\nu(R-P)}{1+2(\mu-\nu)}, \qquad R^* = R + \frac{\nu(R-P)}{1+2(\mu-\nu)},$$

and let $\lambda = \mu - \nu$, then the two lines $\alpha = \gamma$ and $\beta = \delta$ can be written as

$$T - R^* = \frac{\lambda}{1+\lambda}(S - P^*) \quad \text{and} \quad T - R^* = \frac{1+\lambda}{\lambda}(S-P^*).$$

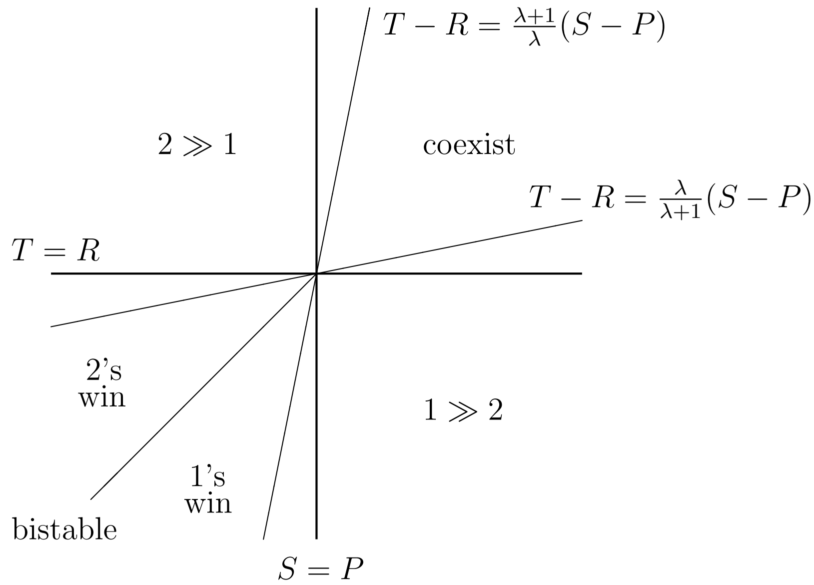


Figure 2: Phase diagram for Birth-Death Updating.

This leads to the four regions drawn in Figure 3. In the coexistence region, the equilibrium $\bar{u}$ is constant on lines through $(S,T) = (R^*, P^*)$. In the lower left region where there is bistability, 1's win if

$$R^* - T > P^* - S.$$

Even though Hauert's games do not have weak selection, there are many similarities with Figure 1. The equilibrium frequencies are linear in the coexistence region, and in the lower left, the equilibrium state goes from all 1's to all 2's over a very small distance.

Tarnita's formula. Tarnita et al. [30] say that strategy C is favored over D in a structured population, and write $C > D$, if the frequency of C in equilibrium is $> 1/2$ in the game $\bar{G} = \mathbf{1} + wG$ when w is small. Assuming that

(i) the transition probabilities are differentiable at $w = 0$,

(ii) the update rule is symmetric for the two strategies, and

(iii) in the game given by the matrix with $\beta = 1$, $\alpha = \gamma = \delta = 0$, strategy A is not disfavored,

they argued that

I. *$C > D$ is equivalent to $\sigma R + S > T + \sigma P$ where σ is a constant that only depends on the spatial structure and update rule.*

By using results for the phase diagram given above, we can show that

Theorem 3. *I holds for the Birth-Death updating with $\sigma = 1$ and for the Death-Birth updating with $\sigma = (\kappa + 1)/(\kappa - 1)$.*

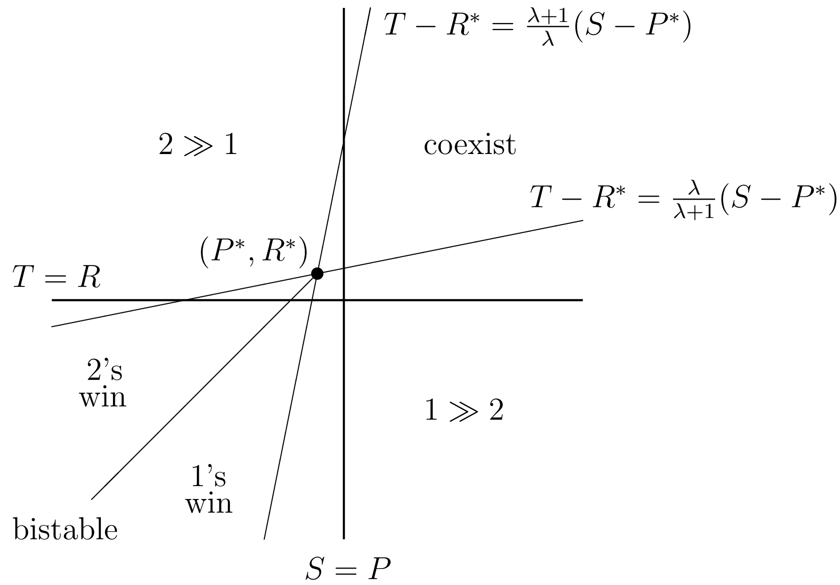


Figure 3: Phase diagram for Death-Birth Updating.

Proof. For Birth-Death updating it follows from (31) that this is the correct condition in the bistable quadrant. By (30), in the coexistence quadrant,

$$\bar{u} = \frac{(1+\lambda)(S-P) + \lambda(R-T)}{S-P+T-R}$$

Cross-multiplying we see that $\bar{u} > 1/2$ when we have

$$0 < (1/2+\lambda)(S-P) + (\lambda+1/2)(R-T) = (1/2+\lambda)(R+S-T-P)$$

Thus in both quadrants the condition is $R + S > T + P$. The proof of the formula for Death-Birth updating is similar but requires more algebra, so again we hide the details away in Section 9. Since the derivation of the formula from the phase diagram in the Death-Birth case is messy, we also give a simple self-contained proof of Theorem 3 in this case. □

5.3 Concrete Examples

In this, we present calculations for concrete examples to complement the general conclusions from the phase diagram. Before we begin, recall that the original and modified games are

$$\begin{array}{ccc} & C & D \\ C & R & S \\ D & T & P \end{array} \qquad \begin{array}{ccc} & C & D \\ C & \alpha = R & \beta = S + \theta \\ D & \gamma = T - \theta & \delta = P \end{array}$$

where $\theta = (p_2/p_1)(R + S - T - P)$ for Birth-Death updating and

$$\theta = \frac{\bar{p}_2}{\bar{p}_1}(R+S-T-P) - \frac{p(v_1|v_2)}{\kappa \bar{p}_1}(S-P)$$

for Death-Birth updating.

Example 1. Prisoner's Dilemma. Consider the following game between cooperators and defectors. Here c is the cost that cooperators pay to provide a benefit b to the other player.

$$\begin{array}{ccc} & \text{C} & \text{D} \\ \text{C} & R = b - c & S = -c \\ \text{D} & T = b & P = 0 \end{array}$$

In this formulation there are no prisoner's deciding whether to confess (D) or not (C), but if $b > c$ there is still the dilemma that strategy D dominates C but the (D, D) payoff is worse than the one for (C, C).

Under either updating the matrix changes to

$$\begin{array}{ccc} & \text{C} & \text{D} \\ \text{C} & \alpha = b - c & \beta = -c + \theta \\ \text{D} & \gamma = b - \theta & \delta = 0 \end{array}$$

In the Birth-death case, $\theta = (p_2/p_1)(b - c - c - b) = -2cp_2/p_1$. In this modified game $\Gamma = \alpha - \beta - \gamma + \delta = 0$ and $\beta - \delta < 0$ so recalling $\phi_R(u) = u(1-u)[\beta - \delta + \Gamma u$, the cooperators always die out. Under Death-Birth updating

$$\theta = -2c\frac{\bar{p}_2}{\bar{p}_1} - (-c - b)\frac{p(v_1|v_2)}{\kappa \bar{p}_1}.$$

Again $\Gamma = 0$ so the victor is determined by the sign of

$$\bar{p}_1(\beta - \delta) = -c\bar{p}_1 - 2c\bar{p}_2 + (c + b)\frac{p(v_1|v_2)}{\kappa}$$

Identity (14) implies that $2\bar{p}_2 + \bar{p}_1 = p(v_1|v_2)(1 + 1/\kappa)$ so cooperators will persist if

$$(-c + b/\kappa)p(v_1|v_2) > 0.$$

Since $p(v_1|v_2) > 0$ the condition is just $b/c > \kappa$ giving a proof of the result of Ohtsuki et al. [35], which has already appeared in Cox, Durrett, and Perkins [42].

Example 2. Nowak and May [11] considered the "weak" Prisoner's Dilemma game with payoff matrix:

$$\begin{array}{ccc} & \text{C} & \text{D} \\ \text{C} & R = 1 & S = 0 \\ \text{D} & T = b & P = 0 \end{array}$$

As you can see from Figure 3, if Death-Birth updating is used, these games will show a dramatic departure from the homogeneously mixing case. Nowak and May used "imitate the best dynamics" so the process was deterministic and there are only finitely many different evolutions. See Section 2.1 of [13] for locations of the transitions and pictures of the various cases. When $1.8 < b < 2$, if the process starts with a single D in a sea of C's, and color the sites based on the values of $(\xi_{n-1}(x), \xi_n(x)$ a kaleidoscope of Persian carpet style patterns results. As Huberman and Glance [12] have pointed out, these patterns disappear if asynchronous updating is used. However, work of Nowak, Bonhoeffer and May [14, 15] showed that their conclusion that spatial structure enhanced cooperation remained true with stochastic updating or when games were played on random lattices.

Example 3. The Harmony game has $P < S$ and $T < R$. In this game strategy 1 dominates strategy 2, but in contrast to Prisoner's dilemma the payoff for the outcome (C, C) is the largest in the matrix. Licht [57] used this game to explain the proliferation of MOUs (memoranda of understanding) between securities agencies involved in international antifraud regulation. From Figures 2 and 3, we see that in the spatial model cooperators take over the system.

Example 4. Snowdrift game. In this game, two motorists are stuck in their cars on opposite sides of a snowdrift. They can get out of their car and start shoveling (C) or do nothing (D). The payoff matrix is

$$\begin{array}{ccc} & \text{C} & \text{D} \\ \text{C} & R = b - c/2 & S = b - c \\ \text{D} & T = b & P = 0 \end{array}$$

That is, if both players shovel then the work is cut in half, but if one player cooperates and the other defects then the C player gains the benefit of sleeping in his bed rather than in his car.

The story behind the game makes it sound frivolous, however, in a paper published in Nature [27], the snowdrift game has been used to study "facultative cheating in yeast." For yeast to grow on sucrose, a disaccharide, the sugar has to be hydrolyzed, but when a yeast cell does this, most of the resulting monosaccharide diffuses away. None the less, due to the fact that the hydrolyzing cell reaps some benefit, cooperators can invade a population of cheaters.

If $b > c$ then the game has a mixed strategy equilibrium, which by (24) is

$$\frac{S - P}{S - P + T - R} = \frac{b - c}{b - (c/2)}$$

Under either update rule the modified payoff becomes

$$\begin{array}{ccc} & \text{C} & \text{D} \\ \text{C} & b - c/2 & b - c + \theta \\ \text{D} & b - \theta & 0 \end{array}$$

and using (24) again the equilibrium changes to

$$\bar{u} = \frac{S - P + \theta}{S - P + T - R} = \frac{b - c + \theta}{b - (c/2)}$$

assuming that this stays in $(0, 1)$. If this $\bar{u} > 1$, then 1 becomes an attracting fixed point; if $\bar{u} < 0$, then 0 is attracting.

If $\theta > 0$ then spatial structure enhances cooperation. If we use Birth-Death updating:

$$\theta = \frac{p_2}{p_1}(R + S - T - P) = \frac{p_2}{p_1}(b - 3c/2)$$

If we use Death-Birth updating:

$$\theta = \frac{\bar{p}_2}{\bar{p}_1}(R+S-T-P) - \frac{p(v_1|v_2)}{\kappa \bar{p}_1}(S-P)$$
$$= \frac{\bar{p}_2}{\bar{p}_1}(b-3c/2) - \frac{p(v_1|v_2)}{\kappa \bar{p}_1}(b-c)$$

Hauert and Doebeli [23] have used simulation to show that spatial structure can inhibit the eovlution of cooperation in the snowdrfit game. One of their examples has $R=1$, $S=0.38$, $T=1.62$, and $P=0$ in which case $\theta<0$ for both update rules. At the end of their article they conclude that "space should benefit cooperation for low cost to benefit ratios," which is consistent with our calculation. For more discussion of the contrasting effects on cooperation in Prisoner's Dilemma and Snowdrift games, see the review by Doebeli and Hauert [26].

Example 5. Hawk-dove game. As formulated in Maynard-Smith's classic book [4], when a confrontation occurs, Hawks escalate and continue until injured or until an opponent retreats, while Doves make a display of force but retreat at once if the opponent escalates. The payoff matrix is

	Hawk	Dove
Hawk	$(V-C)/2$	V
Dove	0	$V/2$

Here V is the value of the resource, which two doves split, and C is the cost of competition. If we suppose that $C>V$ then again the replicator equation has an attracting fixed point. Killingback and Doebli [17] studied the spatial version of the game and set $V=2$, $\beta=C/2$ to arrive at the payoff matrix

	Hawk	Dove
Hawk	$1-\beta$	2
Dove	0	1

We will assume $\beta>1$. In this case, (24) implies that the equilibrium mixed strategy plays Hawk with probability $\bar{u}=1/\beta$. To put this game into our phase diagram we need to label the Dove strategy as Cooperate and the Hawk strategy as Defect:

	C	D
C	$R=1$	$S=0$
Dove	$T=2$	$P=1-\beta$

Under either of our update rules the payoff matrix changes to

	H	D
H	$1-\beta$	$2+\theta$
D	$-\theta$	1

where $\theta=(p_2/p_1)(2-\beta)$ in the Birth-Death case and

$$\theta = \frac{\bar{p}_2}{\bar{p}_1}(2-\beta) - \frac{p(v_1|v_2)}{\kappa \bar{p}_1}\cdot 1$$

for Death-Birth updating. In one of Killingback and Doebli's favorite cases, $\beta = 2.2$, both of these terms are negative, so by (47) the frequency of Hawks in equilibrium is reduced, in agreement with their simulations.

While the conclusions may be similar, the updates used in the models are very different. In [17], a discrete time dynamic ("synchornous updating") was used in which the state of a cell at time $t+1$ is that of the eight Moore neighbors with the best payoff. As in the pioneering work of Nowak and May [11] this makes the system deterministic and there are only finitely many different behaviors as β is varied with changes at β passes through 9/7, 5/3, 2, and 7/3. Figure 1 in [17] shows spatial chaos, i.e., the dynamics show a sensitive dependence on initial conditions. For more on this see [18]. In continuous time with small selection our results predict that as long as the mixed strategy equilibrium is preserved in the perturbed game we will get coexistence of Hawks and Doves in an equilibrium with density of Hawks and Doves close to that predicted by the perturbed game matrix.

Example 6. The Battle of the Sexes is another game that leads to an attracting fixed point in the replicator equation. The story is that the man wants to go to a sporting event while the woman wants to go to the opera. In an age before cell phones they make their choices without communicating with each other. If C is the choice to go to the other person's favorite and D is go to your own then the game matrix might be

$$\begin{array}{ccc} & \text{C} & \text{D} \\ \text{C} & R = 0 & S = 1 \\ \text{D} & T = 2 & P = -1 \end{array}$$

In Hauert's scheme this case is defined by $T > S > R > P$ in contrast to the inequalities $T > R > S > P$ for the snowdrift game, and Hawks-Doves.

Despite the difference in the inequalities the results are very similar. Again in either case the modified payoffs in this particular example are

$$\begin{array}{ccc} & \text{C} & \text{D} \\ \text{C} & \alpha = 0 & \beta = 1 + \theta \\ \text{D} & \gamma = 2 - \theta & \delta = -1 \end{array}$$

Under Birth-Death updating $\theta = 0$ since $R + S - T - P = 0$, while for Death-Birth updating

$$\theta = -\frac{2p(v_1|v_2)}{\kappa \bar{p}_1} < 0.$$

Since the equilibrium changes to

$$\bar{u} = \frac{S - P + \theta}{S - P + T - R}$$

spatial structure inhibits cooperation.

Example 7. Stag Hunt. The story of this game was briefly described by Rousseau in his 1755 book *A Discourse on Inequality.* If the two hunters cooperate to hunt stag (an adult male deer) then they will bring home a lot of food, but there is practically no chance of bagging a stag by oneself. If both hunters go after rabbit they split what they kill.

	Stag	Hare
Stag	$R = 3$	$S = 0$
Hare	$T = 2$	$P = 1$

In Hauert's scheme this case is defined by the inequalities $R > T > P > S$. Since $R > T$ and $P > S$, we are in the bistable situation. Returning to the general situation in either case the modified payoffs in this particular example are

	C	D
C	$\alpha = R$	$\beta = S + \theta$
D	$\gamma = T - \theta$	$\delta = P$

If $R + S > T + P$ then $\theta_{BD} > 0$ while for Death-Birth updating

$$\theta_{DB} = \theta_{BD} + (P - S)\frac{p(v_1|v_2)}{\kappa \bar{p}_1} > 0.$$

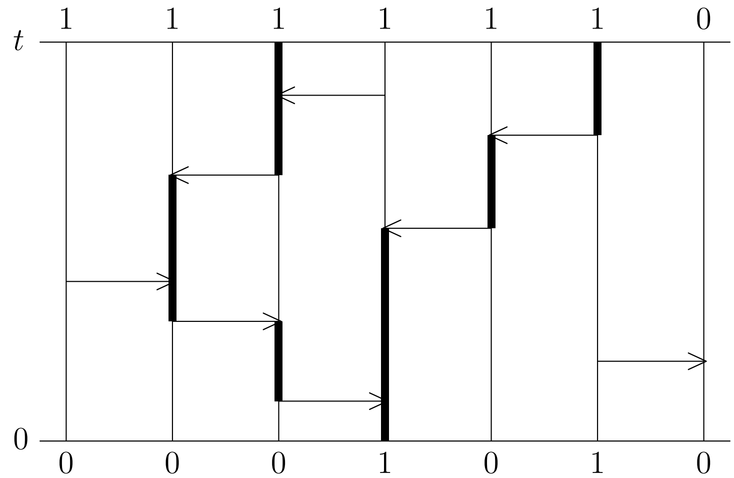
So the 1's win out. If $R + S < T + P$ then $\theta_{BD} < 0$ so the 2's win, but θ_{DB} may be positive or negative.

Under Birth-Death updating the winner is always the risk dominant strategy, and under Death-Birth updating it often is. This is consistent with results in the economics literature. See Kandori, Mailath, and Rob [56], Ellison [49] and Blume [40]. Blume uses a spatially explicit model with a log-linear strategy revision, which turns the system into an Ising model.

6 Voter model duality: details

In the degenerate case of an evolutionary game in which $G_{i,j} \equiv 1$, the system reduces to the voter model was introduced in the mid 1970s independently by Clifford and Sudbury [41] and Holley and Liggett [55] on the d-dimensional integer lattice. It is a very simple model for the spread of an opinion and has been investigated in great detail, see Liggett [58] for a survey. To define the model we let $p(y)$ be an irreducible probability kernel p on $\mathbb{Z}^d$ that is finite range, symmetric $p(y) = p(-y)$, and has covariance matrix $\sigma^2 I$.

In the voter model, each site x has an opinion $\xi_t(x)$ and at the times of a rate 1 Poisson process decides to change its opinion, imitating the voter at $x + y$ with probability $p(y)$. To study the voter model, it is useful to give an explicit construction called the graphical representation, see Harris [54] and Griffeath [53]. For each $x \in \mathbb{Z}^d$ and y with $p(y) > 0$ let $T_n^{x,y}$, $n \geq 1$ be the arrival times of a Poisson process with rate $p(y)$. At the times $T_n^{x,y}$, $n \geq 1$, x decides to change its opinion to match the one at $x + y$. To indicate this, we draw an arrow from $(x, T_n^{x,y})$ to $(x + y, T_n^{x,y})$.



To define the dual process $\zeta_s^{x,t}$, which we think of as the motion of a particle, we start with $\zeta_0^{x,t} = x$. To define the dynamics we start at x at time t and work down the graphical representation. The process stays at x until the first time $t-r$ that it encounters the tail of an arrow x. At this time, the particle jumps to the site $x+y$ at the head of the arrow, i.e., $\zeta_r^{x,t} = x+y$. The particle stays at $x+y$ until the next time the tail of an arrow is encountered and then jumps to the head of the arrow etc. The definition of the dual guarantees that if $\xi_t(x)$ is the opinion of x at time t in the voter model then we have the result called (6) in the introduction

$$\xi_t(x) = \xi_{t-s}(\zeta_s^{x,t})$$

For fixed x and t, $\zeta_s^{x,t}$ is a random walk that jumps at rate 1 and by an amount with distribution $p(y)$. It should be clear from the definition that if $\zeta_s^{x,t} = \zeta_s^{y,t}$ for some s then the two random walks will stay together at later times. For these reasons the $\zeta_s^{x,t}$ are called coalescing random walks.

Having a dual random walk starting from x for each t is useful for the derivation of (6). However for some computations it is more convenient to have a single set valued dual process ζ_t^B that starts with a particle at each point of B, particles move as independent random walks until they hit, at which time they coalesce to 1. Extending the reasoning that lead to (6)

$$P(\xi_t(x) = 1 \text{ for all } x \in B) = P(\xi_0(y) = 1 \text{ for all } y \in \xi_t^B) \tag{32}$$

Holley and Liggett (1975) have shown

Theorem 4. *In $d \leq 2$ the voter model approaches complete consensus, i.e., $P(\xi_t(x) = \xi_t(y)) \to 1$. In $d \geq 3$ if we start from product measure with density u (i.e., we assign opinions 1 and 0 independently to sites with probabilities u and $1-u$) then as $t \to \infty$, ξ_t^u converges in distribution to ξ_∞^u, a stationary distribution, ν_u, in which a fraction u of the sites have opinion 1.*

Proof. We will give the proof here since it is short and we think it will be instructive for readers not familiar with dulaity. Our assumptions imply that $p(y)$ has mean 0 and finite variance. Well known results for random walk imply that in $d \le 2$ the associated random walk is recurrent. This implies that two independent random walks will eventually and hence

$$P(\xi_t(x) \neq \xi_t(y)) \le P(\zeta_t^{x,t} \neq \zeta_t^{y,t}) \to 0$$

To prove the second result it suffices to show that ξ_t^u converges in distribution to a limit ξ_∞^u, for then standard results for Markov processes will imply that the distribution of ξ_∞^u is stationary. To do this, we use (32) to conclude

$$P(\xi_t^u(x) = 1 \text{ for all } x \in B) = E\left(u^{|\zeta_t^B|}\right)$$

$t \to |\zeta_t^B|$ is decreasing, and $u^{|\zeta_t^B|} \le 1$, so $P(\xi_t(x) = 1 \text{ for all } x \in B)$ converges to a limit $\phi(B)$ for all finite sets B. Since the probabilities $\phi(B)$ determine the distribution of ξ_∞^u, the proof is complete. □

7 Proofs of the coalescence identities

Let v_1, v_2, v_3 be independent and have distribution p. In this section we prove the coalescence identities stated in Section 3

Lemma 1. $p(0|v_1 + v_2) = p(0|v_1) = p(v_1|v_2)$

Proof. Let S_n be the discrete time random walk with has jumps distributed according to p and let

$$h(x) = P_x(S_n \neq 0 \text{ for all } n \ge 0)$$

be the probability the walk never returns to 0 starting from x. By considering what happens on the first step $h(v_1) = h(v_1+v_2)$. Since v_1 and $-v_1$ have the same distribution $h(v_1+v_2) = h(v_2 - v_1)$. The two results follow since $p(x|y) = h(y - x)$. □

Lemma 2. $p(v_1|v_2 + v_3) = (1 + 1/\kappa)p(0|v_1)$

Proof. Starting at $S_0 = -v_1$, $S_1 = v_2 - v_1$ and $S_2 = v_2 + v_3 - v_1$. Since $P_{-v_1}(S_1 = 0) = 1/\kappa$.

$$\begin{aligned} h(v_2 + v_3 - v_1) - h(v_1) &= P_{-v_1}(S_1 = 0, S_n \neq 0 \text{ for } n \ge 2) \\ &= (1/\kappa)P_0(S_n \neq 0 \text{ for } n \ge 1) = (1/\kappa)h(v_3) = (1/\kappa)p(0|v_1) \end{aligned}$$

which proves the desired result □

From the two particle identities we easily get some for three particles. The starting point is to note that considering the possibilities for y when x and z don't coalesce we have a result we earlier called (9)

$$p(x|z) = p(x|y|z) + p(x, y|z) + p(x|y, z)$$

Combining this identity with one for another pair that shares a site in common leads to identities that relate the three ways three particles can coalesce to give two.

Lemma 3. $p(0, v_1|v_1 + v_2) = p(0, v_1 + v_2|v_1) = p(v_1, v_1 + v_2|0)$ *and hence*

$$p(0|v_1) = 2p(x, y|z) + p(0|v_1|v_1 + v_2)$$

where x, y, z *is any ordering of* $0, v_1, v_1 + v_2$.

Proof. Using (9)

$$\begin{aligned} p(0|v_1) &= p(0|v_1|v_1 + v_2) + p(v_1, v_1 + v_2|0) + p(0, v_1 + v_2|v_1) \\ p(0|v_1 + v_2) &= p(0|v_1|v_1 + v_2) + p(v_1, v_1 + v_2|0) + p(0, v_1|v_1 + v_2) \\ p(v_1|v_1 + v_2) &= p(0|v_1|v_1 + v_2) + p(0, v_1 + v_2|v_1) + p(0, v_1|v_1 + v_2) \end{aligned}$$

Since $p(0|v_1 + v_2) = p(0|v_1)$ by Lemma 7 the first result follows. Translation invariance implies $p(0|v_1) = p(0|v_2) = p(v_1|v_1 + v_2)$ so comparing the first and third lines gives the second result. The displayed identity follows from the first two and first and third in the proof. □

Lemma 4. $p(v_1, v_2|v_2 + v_3) = p(v_2, v_2 + v_3|v_1) = p(v_1, v_2 + v_3|v_2) + (1/\kappa)p(0|v_1)$ *and hence*

$$\begin{aligned} p(v_1|v_2)(1 + 1/\kappa) &= 2p(v_2, v_2 + v_3|v_1) + p(v_1|v_2|v_2 + v_3) \\ &= 2p(v_1, v_2|v_2 + v_3) + p(v_1|v_2|v_2 + v_3) \\ p(v_1|v_2)(1 - 1/\kappa) &= 2p(v_1, v_2 + v_3|v_2) + p(v_1|v_2|v_2 + v_3) \end{aligned}$$

Proof. Using (9)

$$\begin{aligned} p(v_1|v_2) &= p(v_1|v_2|v_2 + v_3) + p(v_1, v_2 + v_3|v_2) + p(v_2, v_2 + v_3|v_1) \\ p(v_2|v_2 + v_3) &= p(v_1|v_2|v_2 + v_3) + p(v_1, v_2 + v_3|v_2) + p(v_1, v_2|v_2 + v_3) \\ p(v_1|v_2 + v_3) &= p(v_1|v_2|v_2 + v_3) + p(v_2, v_2 + v_3|v_1) + p(v_1, v_2|v_2 + v_3) \end{aligned}$$

Since $p(v_2|v_2 + v_3) = p(v_1|v_2)$ by Lemma 1, the first result follows. Noting that Lemma 2 implies $p(v_1|v_2 + v_3) = p(0|v_1)(1 + 1/\kappa)$ and subtracting the second equation in the proof from the third gives

$$(1/\kappa)p(0|v_1) = p(v_2, v_2 + v_3|v_1) - p(v_1, v_2 + v_3|v_2)$$

and the second result follows. To get the first displayed equation in the lemma, substitute $p(v_1, v_2 + v_3|v_2) = p(v_2, v_2 + v_3|v_1) - (1/\kappa)p(0|v_1)$ in the first equation in the proof. Since $p(v_1, v_2|v_2+v_3) = p(v_2, v_2+v_3|v_1)$ the second follows. For the third one, use $p(v_2, v_2+v_3|v_1) = p(v_1, v_2 + v_3|v_2) + (1/\kappa)p(0|v_1)$ in the first equation in the proof. □

8 Derivation of the limiting PDE

In this section we will compute the functions $\phi^i_B(u)$ and $\phi^i_D(u)$ that appear in the limiting PDE. To do this it is useful to note that since $\sum_j u_i = 1$ we can write the replicator equation (19) as

$$\frac{du_i}{dt} = \sum_{j \neq i,k} u_i u_j u_k (G_{i,k} - G_{j,k}) \tag{33}$$

where the restriction to $j \neq i$ comes from noting that the when $i = j$ the G's cancel.

8.1 Birth-Death dynamics

By (3) the perturbation is

$$h_{i,j}(0,\xi) = \sum_k f^{(2)}_{j,k}(0,\xi) G_{j,k}$$

In the multi-strategy case the rate of change of the frequency of strategy i in the voter model equilibrium is

$$\begin{aligned} \phi^i_B(u) &= \left\langle \sum_{j \neq i,k} -1(\xi(0)=i) h_{j,k}(0,\xi) + 1(\xi(0)=j) h_{i,k}(0,\xi) \right\rangle_u \\ &= \sum_{j \neq i,k} -q(i,j,k) G_{j,k} + q(j,i,k) G_{i,k} \end{aligned} \tag{34}$$

where $q(a,b,c) = P(\xi(0)=a, \xi(v_1)=b, \xi(v_1+v_2)=c)$ and v_1, v_2 are independent random choices from $\mathcal{N}$. If $a \neq b$ then

$$\begin{aligned} q(a,b,c) &= p(0|v_1|v_1+v_2) u_a u_b u_c \\ &\quad + 1_{(c=a)} p(0, v_1+v_2|v_1) u_a u_b + 1_{(c=b)} p(0|v_1, v_1+v_2) u_a u_b \end{aligned} \tag{35}$$

Combining the last two equations, and comparing with (33) we see that

$$\begin{aligned} \phi^i_B(u) = \phi^i_R(u) p(0|v_1|v_1+v_2) &+ \sum_{j \neq i} p(0, v_1+v_2|v_1) u_i u_j (-G_{j,i} + G_{i,j}) \\ + \sum_{j \neq i} p(0|v_1, v_1+v_2) u_i u_j (-G_{j,j} + G_{i,i}) \end{aligned}$$

Lemma 10 implies that $p(0, v_1+v_2|v_1) = p(0|v_1, v_1+v_2)$ so the last two terms can be combined into one.

$$\phi^i_B(u) = \phi^i_R(u) p(0|v_1|v_1+v_2) + \sum_{j \neq i} p(0|v_1, v_1+v_2) u_i u_j (G_{i,i} - G_{j,i} + G_{i,j} - G_{j,j}) \tag{36}$$

which is the formula given in (20)

8.2 Death-Birth Dynamics

In this case (5) implies that the perturbation is

$$\bar{h}_{i,j}(0,\xi) = h_{i,j}(0,\xi) - f_j \sum_k h_{i,k}(0,\xi) + O(\varepsilon^2)$$

From this we see that $\phi^i_D = \phi^i_B + \psi^i_D$ where

$$\psi^i_D = \left\langle \sum_{j \neq i} 1(\xi(0)=i) f_j(0,\xi) \sum_k h_{i,k}(0,\xi) - \sum_{j \neq i} 1(\xi(0)=j) f_i(0,\xi) \sum_k h_{j,k}(0,\xi) \right\rangle_u .$$

Let v_1, v_2 and v_3 be independent random picks from $\mathcal{N}$ and let

$$q(a,b,c,d) = P(\xi(v_1) = a, \xi(0) = b, \xi(v_2) = c, \xi(v_2 + v_3) = d)$$

we can write the new term in ϕ^i_D as

$$\psi^i_D = \sum_{j \neq i,k,\ell} [-q(j,i,k,\ell) + q(i,j,k,\ell)] G_{k,\ell} \tag{37}$$

Adding and subtracting $q(i,i,k,\ell)$ we can do the sum over j to get

$$\psi^i_D = \sum_{k,\ell} [q(i,k,\ell) - q(i,\cdot,k,\ell)] G_{k,\ell} \tag{38}$$

where $q(a,b,c)$ is as defined above and

$$q(a,\cdot,b,c) = P(\xi(v_1) = a, \xi(v_2) = b, \xi(v_2 + v_3) = c)$$

If we let $q(b,c) = P(\xi(v_2) = b, \xi(v_2 + v_3) = c)$ and write the sum in (38) as $\sum_{k \neq i,\ell}$ plus

$$\begin{aligned} \sum_{\ell} [q(i,i,\ell) - q(i,\cdot,i,\ell)] G(i,\ell) &= [q(i,\ell) - q(i,\ell)] G_{i,\ell} \\ &\quad + \sum_{k \neq i,\ell} [-q(k,i,\ell) + q(k,\cdot,i,\ell)] G_{i,\ell} \end{aligned}$$

To see this move the second sum on the right to the left.

Putting things together we have

$$\psi^i_D = \sum_{k \neq i,\ell} [q(i,k,\ell) - q(i,\cdot,k,\ell)] G_{k,\ell} + \sum_{k \neq i,\ell} [-q(k,i,\ell) + q(k,\cdot,i,\ell)] G_{k,\ell}$$

One half of the sum is

$$\sum_{k,\ell} q(i,k,\ell) G_{k,\ell} - q(i,k,\ell) G_{k,\ell} = -\phi^i_B$$

Since $\phi^i_D = \phi^i_B + \psi^i_D$ we have

$$\phi^i_D = \sum_{k,\ell} -q(i,\cdot,k,\ell) G(k,\ell) + q(i,\cdot,k,\ell) G_{k,\ell} \tag{39}$$

Note the similarity to (34). If $a \neq b$ then

$$\begin{aligned} q(a,\cdot,b,c) &= p(v_1|v_2|v_2+v_3) u_a u_b u_c \\ &\quad + 1_{(c=a)} p(v_1, v_2+v_3|v_2) u_a u_b + 1_{(c=b)} p(v_1|v_2, v_2+v_3) u_a u_b \end{aligned} \tag{40}$$

As in the birth-death case it follows that

$$\begin{aligned} \phi^i_D(u) &= \phi^i_R(u) p(v_1|v_2|v_2+v_3) + \sum_{j \neq i} p(v_1, v_2+v_3|v_2) u_i u_j (-G_{j,i} + G_{i,j}) \\ &\quad + \sum_{j \neq i} p(v_1|v_2, v_2+v_3) u_i u_j (-G_{j,j} + G_{i,i}) \end{aligned}$$

By (11) $p(v_1, v_2+v_3|v_2) = p(v_1|v_2, v_2+v_3) - (1/\kappa)p(v_1|v_2)$, so we can rewrite this as

$$\begin{aligned}\phi_D^i(u) = \phi_R^i(u)p(v_1|v_2|v_2+v_3) + \sum_{j\neq i} p(v_1|v_2, v_2+v_3)u_i u_j (G_{i,i} - G_{j,i} + G_{i,j} - G_{j,j}) \\ - (1/\kappa)p(v_1|v_2)\sum_{j\neq i} u_i u_j(-G_{j,i} + G_{i,j}) \qquad (41)\end{aligned}$$

9 Two strategy games with Death-Birth updating

We give the details behind the conclusions drawn in Figure 2. In the Death-Birth case

$$\theta = \bar{\Delta} = \frac{\bar{p}_2}{\bar{p}_1}(R+S-T+P) - \frac{p(v_1|v_2)}{\kappa\bar{p}_1}(S-T)$$

To find the boundaries between the four cases using (25), we let $\mu = \bar{p}_2/\bar{p}_1 \in (0,1)$ and $\nu = p(v_1|v_2)/\kappa\bar{p}_1$. We have $\alpha = \gamma$ when

$$\begin{aligned}R - T = -\theta &= -\mu(R+S-T-P) + \nu(S-T) \\ &= -(\mu-\nu)(R+S-T-P) - \nu(R-P)\end{aligned}$$

Clearly $\nu > 0$. The fact that $\mu - \nu > 0$ follows from (18). Rearranging gives

$$(\mu-\nu)(S-P) + \nu(R-P) = (1+\mu-\nu)(T-R)$$

and hence

$$T - R = \frac{\mu-\nu}{1+\mu-\nu}(S-P) + \frac{\nu}{1+\mu-\nu}(R-P) \qquad (42)$$

Repeating the last calculation shows that $\beta = \delta$ when

$$S - P = -\theta = -(\mu-\nu)(R+S-T-P) - \nu(R-P) < 0$$

Rearranging gives $(1+\mu-\nu)(S-P) + \nu(R-P) = (\mu-\nu)(T-R)$, and we have

$$T - R = \frac{1+\mu-\nu}{\mu-\nu}(S-P) + \frac{\nu}{\mu-\nu}(R-P) \qquad (43)$$

To find the intersections of the lines in (42) and (43), we set

$$\frac{\mu-\nu}{1+\mu-\nu}(S-P) + \frac{\nu}{1+\mu-\nu}(R-P) = \frac{1+\mu-\nu}{\mu-\nu}(S-P) + \frac{\nu}{\mu-\nu}(R-P)$$

which holds if

$$(\mu-\nu)^2(S-P) + \nu(\mu-\nu)(R-P) = (1+\mu-\nu)^2(S-P) + \nu(1+\mu-\nu)(R-P)$$

Solving gives

$$S - P = \frac{-\nu(R-P)}{1+2(\mu-\nu)} < 0$$

Using (43) we see that at this value of S

$$T - R = -\frac{\nu(R-P)}{\mu-\nu}\left[\frac{1+\mu-\nu}{1+2(\mu-\nu)} - 1\right] = \frac{\nu(R-P)}{1+2(\mu-\nu)} > 0$$

To simplify the formulas for (42) and (43) let

$$P^* = P - \frac{\nu(R-P)}{1+2(\mu-\nu)} \qquad R^* = R + \frac{\nu(R-P)}{1+2(\mu-\nu)} \tag{44}$$

From this and (42) we see that

$$\begin{aligned}
T - R^* &= T - R - \frac{\nu(R-P)}{1+2(\mu-\nu)} \\
&= \frac{\mu-\nu}{1+\mu-\nu}(S-P) + \frac{\nu}{1+\mu-\nu}(R-P) - \frac{\nu(R-P)}{1+2(\mu-\nu)} \\
&= \frac{\mu-\nu}{1+\mu-\nu}(S-P) - \frac{\mu-\nu}{1+\mu-\nu}\cdot\frac{\nu(R-P)}{1+2(\mu-\nu)} = \frac{\mu-\nu}{1+\mu-\nu}(S-P^*)
\end{aligned}$$

A similar calculation using (43) shows that

$$\begin{aligned}
T - R^* &= T - R - \frac{\nu(R-P)}{1+2(\mu-\nu)} \\
&= \frac{1+\mu-\nu}{\mu-\nu}(S-P) + \frac{\nu}{\mu-\nu}(R-P) - \frac{\nu(R-P)}{1+2(\mu-\nu)} \\
&= \frac{1+\mu-\nu}{\mu-\nu}(S-P) + \frac{1+\mu-\nu}{\mu-\nu}\cdot\frac{\nu(R-P)}{1+2(\mu-\nu)} = \frac{1+\mu-\nu}{\mu-\nu}(S-P^*)
\end{aligned}$$

so the two lines can be written as

$$T - R^* = \frac{\mu-\nu}{1+\mu-\nu}(S-P^*) \qquad T - R^* = \frac{1+\mu-\nu}{\mu-\nu}(S-P^*)$$

This leads to the four regions drawn in Figure 2. In the lower left region where there is bistability, 1's win if $\bar{u} > 1/2$ or what is the same if strategy 1 is better than strategy 2 when $u = 1/2$ or

$$R + S - T - P > -2\theta$$

Plugging in the value of θ this becomes

$$(1+2(\mu-\nu))(R+S-T-P) > -2\nu(R-P) \tag{45}$$

Dividing each side by $1+2(\mu-\nu)$ and recalling (44) this can be written as $R^* - T > P^* - S$. For the proof of Theorem 3 it is useful to write this as

$$\frac{1+2\mu}{1+2(\mu-\nu)}R + S > T + \frac{1+2\mu}{1+2(\mu-\nu)} \tag{46}$$

In the coexistence region, the equilibrium is

$$\bar{u} = \frac{S - P + \theta}{S - P + T - R} \tag{47}$$

Plugging in the value of θ, we see that $\bar{u}$ is constant on lines through $(S, T) = (R^*, P^*)$. Again for the proof of Tehorem 3 a less compact form is more desirable. Recalling the defintion of θ we see that $\bar{u} > 1/2$ when

$$2(S - P) + 2\mu(R + S - T - P) - 2\nu(S - T) > S - P + T - R$$

which rearranges to become

$$(1 + 2\mu)R + [1 + 2(\mu - \nu)]S > [1 + 2(\mu - \nu)]T + (1 + 2\mu)P$$

Dividing by $1 + 2(\mu - \nu)$ this becomes (46). To prove Theorem 3 now, we note that

$$1 + 2\mu = \frac{\bar{p}_1 + 2\bar{p}_2}{\bar{p}_1} = (1 + 1/\kappa)\frac{p(v_1|v_2)}{\bar{p}_1}$$

$$1 + 2(\mu - \nu) = (1 + 1/\kappa)\frac{p(v_1|v_2)}{\bar{p}_1} - 2\frac{p(v_1|v_2)}{\kappa\bar{p}_1}$$

so we have

$$\frac{1 + 2\mu}{1 + 2(\mu - \nu)} = \frac{\kappa + 1}{\kappa - 1}$$

9.1 Direct proof of Tarnita's formula

Lemma 5. *Suppose the ϕ in the limiting PDE is cubic. The limiting frequency of 1's in the PDE is $> 1/2$ (and hence also in the particle system with small ε) if and only if $\phi(1/2) > 0$.*

Proof. As explained in the proof of Theorem 2 given in [42] the behavior of the PDE is related to the shape of ϕ in the following way.

$\phi'(0) > 0$, $\phi'(1) > 0$. There is an interior fixed point $\bar{u}$, which is the limiting frequency. If $\phi(1/2) > 0$ then $\bar{u} > 1/2$.

$\phi'(0) > 0$, $\phi'(1) < 0$. $\phi > 0$ on $(0, 1)$ so the system converges to 1.

$\phi'(0) < 0$, $\phi'(1) > 0$. $\phi < 0$ on $(0, 1)$ so the system converges to 0.

$\phi'(0) < 0$, $\phi'(1) < 0$. There is an unstable fixed point $\bar{u}$. If $\bar{u} < 1/2$ which in this case is equivalent to $\phi(1/2) > 0$ the system converges to 1, otherwise it converges to 0.

Combining our observations proves the desired result. □

Death-Birth updating. In this case, we have $\phi(1/2) > 0$ if

$$a + b + \bar{\Delta} > c + d - \bar{\Delta}$$

where $\Delta = (p_2/p_1)(a + b - c - d) - p(v_1|v_2)/\kappa p_1$. Rearranging we see that the last inequality holds if

$$\kappa(\bar{p}_1 + 2\bar{p}_2)(a + b - c - d) - 2p(v_1|v_2)(b - c)$$

Using (14) $\bar{p}_1 + 2\bar{p}_2 = p(v_1|v_2)(1 + 1/\kappa)$ this becomes

$$p(v_1|v_2)[(\kappa + 1)(a - d) + (\kappa - 1)(b - c)$$

which is the condition in Tarnita's formula with $\sigma = (\kappa + 1)/(\kappa - 1)$.

References

[1] von Neumann, J., and Morgenstern, O. (1944) *The Theory of Games and Economic Behavior.* Princeton U. Press

[2] Maynard Smith, J., and Price, G.R. (1973) The logic of animal conflict. *Nature.* 401, 268–371

[3] Axelrod, R., and Hamilton, W.D. (1981) The evolution of cooperation. *Science.* 211, 1390–1396

[4] Maynard Smith, J. (1982) *Evolution and the Theory of Games.* Cambridge U. Press

[5] Axelrod, R. 91984) *The Evolution of Cooperation.* Basic Books, New York

[6] Harsanyi, J., and Selten, R. (1988) *General Theory of Equilibrium in Games.* MIT Press, Cambridge MA

[7] Hofbauer, J., and Sigmund, K. (1998) *Evolutionary Games and Population Dynamics.* Cambridge U. Press

[8] Hofbauer, J., and Sigmund, K. (2003) Evolutionary game dynamics. *Bull. Amer. Math. Soc.* 40, 479–519

[9] Nowak, M.A., and Sigmund, K. (2004) Evolutionary dynamics of biological games. *Science.* 303, 793–799

[10] Nowak, M.A. (2006) *Evolutionary Dynamics.* Belknap Press, Harvard University.

Spatial games

[11] Nowak, M.A., and May, R.M. (1992) Evolutionary games and spatial chaos. *Nature.* 359, 826–829

[12] Huberman, B., and Glance, N. (1993) Evolutionary games and computer simulation. *Proc. Natl. Acad. Sci., IUSA.* 90, 7716–7718

[13] Nowak, M.A., and May, R.M. (1993) The spatial dilemmas of evolution. *Int. J. Bifurcat. Chaos.* 3, 35–78

[14] Nowak, M.A., Bonhoeffer, S., and and May, R.M. (1994) More spatial games. *Int. J. Bifurcat. Chaos.* 4, 33–56

[15] Nowak, M.A., Bonhoeffer, S., and and May, R.M. (1994) Spatial games and the maintenance of cooperation. *Proc. Natl. Acad. Sci. USA.* 91, 4877–4881

[16] Durrett, R., and Levin, S. (1994) The importance of being discrete (and spatial). *Theor. Pop. Biol.* 46, 363–394

[17] Killingback, T., and Doebli, M. (1996) Spatial evolutionary game theory: Hawks and Doves revisited. *Proc. Roy. Soc. London, B.* 263, 1135–1144

[18] Killingback, T., and Doebli, M. (1998) Self-oraganized criticality in spatial evolutionary game theory. *J. Theoretical Biology.* 191, 335–340

[19] Szabó, G., and Töke, C. (1998) Evolutionary prisoner's dliemma game on a square lattice. *Phys. Rev., E.* 58, 69–73

[20] van Baalen, M., and Rand, D.A. (1998) The unit of selection in viscous populations and the evolution of altruism. *J. Theor. Biol.* 193, 631-648

[21] Hauert, C. (2001) Fundamental clusters in spatial 2×2 games. *Proc. Roy. Soc. London, B.* 268, 761–769

[22] Hauert, C. (2002) Effects of space on 2×2 games. *International Journal of Biifurcation and Chaos.* 12, 1531–1548

[23] Hauert, C., and Doebeli, M. (2004) Spatial structure often inhibits the evolution of cooperation in the snowdrift game. *Nature.* 428, 643–646

[24] Hauert, C., and Szabó, G. (2005) Game theory and physics. *Am. J. Physics.* 73, 405-414

[25] Szabo, G., Vukov, J., and Szolnoki, A. (2005) Phase diagrams for an evolutionary Prisoner's dilemma game on two-deimnsional lattices. *Phys. Rev. E.* 72, paper 047107

[26] Doebeli, M., and Hauert, C. (2005) Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. *Ecology Letters.* 8, 748–766

[27] Gore, J., Youk, H., and van Oudenaarden, A. (2009) Snowdrift game dynamics and facultative cheating in yeast. *Nature.* 459, 253–256.

[28] Roca, C.P., Cuesta, J.A., and Sanchez, A. (2009) Effect of spatial structure on the evolution of cooperation. *Phys. Rev. E.* 80, paper 046106

[29] Roca, C.P., Cuesta, J.A., and Sanchez, A. (2009) Evolutionary game theory: temporal and spatial effects beyond replicator dynamics. *Phys. Life Rev.* 6, 208–249

[30] Tarnita, C.E., Ohtsuki, H., Antal, T., Feng, F., and Nowak, M.A. (2009) Strategy selection in structured populations. *J. Theoretical Biology* 259, 570–581

[31] Tarnita, C.E., Wage, N., and Nowak, M. (2011) Multiple strategies in structured populations. *Proc. Natl. Acad. Sci.* 108, 2334–2337

[32] Lanchier, N. (2013) Evolutionary games on the lattice: payoffs affecting birth and death rates. Preprint.

Games on graphs

[33] Lieberman, E., Hauert, C., and Nowak, M.A. (2005) Evolutionary dyanmics on graphs. *Nature.* 433, 312–316

[34] Ohtsuki, H., and Nowak, M.A. (2006) Evolutionary games on graphs. *J. Theoretical Biology.* 243, 86–97

[35] Ohtsuki, H., Hauert, C., Lieberman, E., and Nowak, M.A. (2006) A simple rule for the evolution of cooperation on graphs and social networks. *Nature.* 441, 502–505

[36] Ohtsuki, H., and Nowak, M.A. (2006) The replicator equation on graphs. *J. Theor. Biol.* 243, 86–97

[37] Szabó, G., and Fáth, G. (2007) Evolutionary games on graphs. *Physics Reports.* 46, 97–216

Other references

[38] Aronson, D.G. and Weinberger, H.F. (1975) Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation. Pages 5–49 in *Partial Differential Equations and Related Topics.* Springer Lecture Notes in Math 446, Springer, New York.

[39] Aronson, D.G. and Weinberger, J.F. (1978) Multidimensional nonlinear diffusion arising in population genetics. *Adv. in Math.* 30, 33–76.

[40] Blume, L.E. (1993) The statistical mechanics of strategic interaction. *Games and Economic Behavior.* 5, 387-424

[41] Clifford, P. and Sudbury, A. (1973) A model for spatial conflict. *Biometrika.* **60**, 581–588

[42] Cox, T., Durrett, R., and Perkins, E. (2011) Voter model perturbations and reaction diffusion equations. *Astérisque*, to appear. arXiv:1103.1676

[43] Durrett, R. (1992) Predator-prey systems. Pages 37-58 in *Asymptotic problems in probability theory: stochastic models and diffusions on fractals.* (1992) Edited by K.D. Elworthy and N. Ikeda. Pitman Research Notes 283. Longman, Essex, England

[44] Durrett, R. (2002) Mutual invadability implies coexistence in spatial models. *Memoirs of the AMS.* Volume 156, Number 740

[45] Durrett, R. (2009) Coexistence in Stochastic Spatial Models. *Ann. Appl. Prob.* 19, 477–496

[46] Durrett, R. (2010) *Probability: Theory and Examples.* 4th Edition. Cambridge U. Press

[47] Durrett, R., and Neuhauser, C. (1994) Particle systems and reaction diffusion equations. *Ann. Prob.* 22 (1994), 289–333

[48] Durrett, R., and Swindle, G. (1994) Coexistence results for catalysts. *Prob. Th. Rel. Fields*, 98 (1994), 489–515

[49] Ellison, G. (1993) Learning, local interaction, and coordination. *Econometrica.* 61, 1047–1071

[50] Fife, P.C. and McLeod, J.B. (1977) The approach of solutions of nonlinear diffusion equations to traveling front solutions. *Arch. Rat. mech. Anal.* 65, 335–361

[51] Fife, P.C. and McLeod, J.B. (1981) A phase plane discussion of convergence to traveling fronts for nonlinear diffusion. *Arch. Rat. mech. Anal.* 75, 281–314

[52] Gore, J., Youk, H., and van Oudenaarden, A. (2009) Snowdrift game dynamics and facultative cheating in yeast. *Nature.* 459, 253–256

[53] Griffeath, D.S. (1978) *Additive and Cancellative Interacting Particle Systems.* Springer Lecture Notes in Math.

[54] Harris, T.E. (1976) On a class of set-valued Markov processes. *Ann. Prob.* 4, 175–194

[55] Holley, R., and Liggett, T. (1975) Ergodic theorems for weakly interacting systems and the voter model. *Ann. Probab.* 4, 195–228

[56] Kandori, M., Mailath, G., and Rob, R. (1993) Learning, mutation, and long run equilibria. *Econometrica.* 61, 29–56

[57] Licht, A.M. (1999) Games commissions play" 2×2 games of international securities regulation. *Yale Journal of International Law.* 24, 61–128

[58] Liggett, T.M. (1999) *Stochastic Interacting Systems: Contact, Voter and Exclusion Processes.* Springer, New York.