Spatial Evolutionary Games

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Archetti, Ferraro, and Christofori (2015)

Heterogeneity for IGF-II production maintained by public goods dynamics in neuroendocrine pancreatic cancer. PNAS 112, 1833–1838

	1	**2**
1	0	λ
2	1	1

2's produce Insulin-like growth factor-II while 1's free ride on that produced by other cells. Since they do not produce the growth factor $\lambda > 1$.

Homogeneously mixing environment

Frequencies of strategies follow the replicator equation

$$\frac{dx_i}{dt} = x_i(F_i - \bar{F})$$

$F_i = \sum_j G_{i,j} x_j$ is the fitness of strategy i, $\bar{F} = \sum_i x_i F_i$, average fitness

If we add a constant to a column of G then $F_i - \bar{F}$ is not changed.

Replicator equation for our example

Subtract a constant to make the diagonal 0.

$$\begin{array}{c|cc} & \mathbf{1} & \mathbf{2} \\ \mathbf{1} & 0 & b \\ \mathbf{2} & c & 0 \end{array}$$

$b = \lambda - 1$, $c = 1$. Let $u = u_1$. Replicator equation is

$$\frac{du}{dt} = u(1-u)[b - (b+c)u]$$

If $b, c > 0$, $u(t) \to b/(b+c) = (\lambda - 1)/\lambda$.

Spatial Model

Space is the d-dimensional integer lattice, $d \geq 3$. Interaction kernel $p(x) = 1/2d$ for the nearest neighbors $x \pm e_i$, e_i is the ith unit vector.

$\xi(x)$ is strategy used by x. Fitness is $\psi(x) = \sum_y p(y-x)G(\xi(x), \xi(y))$.

Birth-Death dynamics: Each individual gives birth at rate $\psi(x)$ and replaces the individual at y with probability $p(y-x)$.

Death-Birth dynamics: Each particle dies at rate 1. Is replaced by a copy of y with probability proportional to $p(y-x)\psi(y)$. In our special case we pick with a probability proportional to its fitness.

To reduce the number of formulas we will consider only Birth-Death updates.

Small selection

We are going to consider games with $\bar{G}_{i,j} = \mathbf{1} + wG_{i,j}$ where $\mathbf{1}$ is a matrix of all 1's, and w is small. Does not change the behavior of the replicator equation.

If $G_{i,j} \equiv 1$, B-D or D-B dynamics give the **voter model**. Remove an individual and replace it with a copy of a neighbor chosen at random (according to p).

With small selection this is a **voter model perturbation** in the sense of Cox, Durrett, Perkins (2013) *Astérisque* volume 349, 120 pages. Available on the arXiv and on my web page.

PDE limit for voter model perturbations

Theorem. Flip rates are those of the voter model $+\epsilon^2 h_{i,j}(0,\xi)$. If we rescale space to $\epsilon\mathbb{Z}^d$ and speed up time by ϵ^{-2} then in $d \geq 3$

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

converges to the solution of the system of PDE:

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

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.

Reaction term

Let $p(0|x|y)$ be the probability that the three random walks started from 0, x and y 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.

Let v_1, v_2 be independent with $P(v_i = x) = p(x)$.

$$p_1 = Ep(0|v_1|v_1 + v_2) \qquad p_2 = Ep(0|v_1, v_1 + v_2)$$

The reaction term is p_1 times the replicator equation for $H = G + A$ where

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

In the $d = 3$ nearest neighbor case $\theta = p_2/p_1 \approx 0.5$. Adding a constant to a column does not change A. (False for DB).

Back to our example

When the diagonal is 0, $H_{i,j} = (1+\theta)G_{i,j} - \theta G_{j,i}$.
In $d = 3$ nearest neighbor case $\theta = 1/2$.

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

When the diagonal is 0, $H_{i,j} = (1+\theta)G_{i,j} - \theta G_{j,i}$.

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

Example continued

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

If $\lambda > 4$ we have $\bar{c} < 0$ so $1 \gg 2$ and 1's win.
If $\lambda < 4/3$ we have $\bar{b} < 0$ so $2 \gg 1$ and 2's win.
If $4/3 < \lambda < 4$ then coexistence occurs, equilibrium frequencies

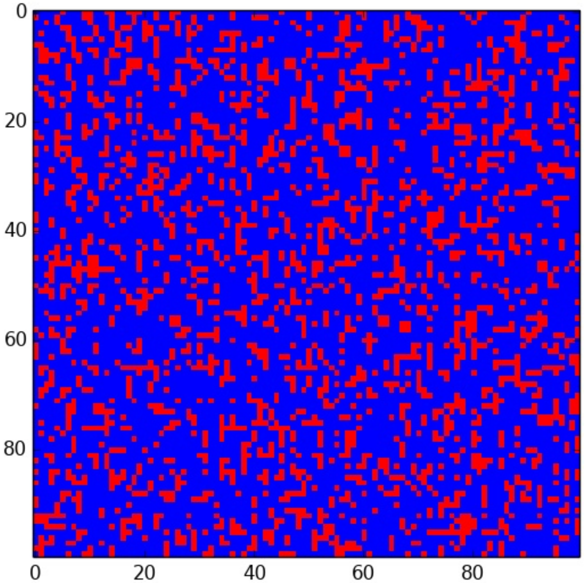
$$\approx (\bar{b}/(\bar{b} + \bar{c}), \bar{c}/(\bar{b} + \bar{c})$$

Homogeneously mixing case: coexistence for all $\lambda > 1$.

Simulation data

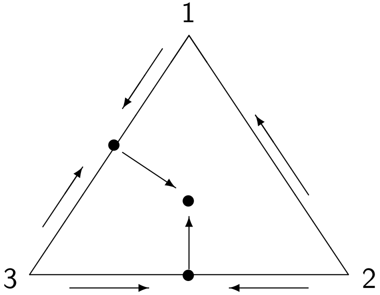
λ	4/3	3/2	3	3.5	4
Original game	0.11	0.25	0.75	0.83	0.89
w **= 1/2**	0.01	0.19	0.79	0.88	0.96
w **= 1/10**	0.00	0.16	0.82	0.92	0.98
w to 0 limit	0	0.17	0.83	0.93	1

3D Simulation $\lambda = 3$, w $= 1/2$, blue $= 1$



Three strategy games

If there are no unstable edge equilibria and 1, 2, or 3 edge equilibria that are attracting and can be invaded by the other strategy then results in Durrett (2014) EJP show that there is coexistence (all three strategies present in equilibrium) when w is small



Rock Paper Scissors

If the $\alpha_i > 0$, $\beta_i < 0$ then $1 \gg 2 \gg 3 \gg 1$

$$\begin{array}{cccc} & \mathbf{1} & \mathbf{2} & \mathbf{3} \\ \mathbf{1} & 0 & \alpha_3 & \beta_2 \\ \mathbf{2} & \beta_3 & 0 & \alpha_1 \\ \mathbf{3} & \alpha_2 & \beta_1 & 0 \end{array}$$

If the game G has an interior fixed point it must be:

$$\begin{aligned} \rho_1 &= (\beta_1\beta_2 + \alpha_1\alpha_3 - \alpha_1\beta_1)/D \\ \rho_2 &= (\beta_2\beta_3 + \alpha_2\alpha_1 - \alpha_2\beta_2)/D \\ \rho_3 &= (\beta_3\beta_1 + \alpha_3\alpha_2 - \alpha_3\beta_3)/D \end{aligned}$$

In RPS the three numerators are positive, so fixed point exists.

Almost constant sum games

The transformed game has $H_{i,j} = (1+\theta)G_{i,j} - \theta G_{j,i}$.
If G is RPS then so is H.

Thorem. *Suppose that the 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 $V(u) = \sum_i u_i - \rho_i \log u_i$ is a convex Lyapunov function. This implies that there is coexistence and that for any $\delta > 0$ if $w < w_0(\delta)$ and μ is any stationary distribution concentrating on configurations with infinitely many 1's, 2's and 3's we have*

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

Replicator Equation for RPS

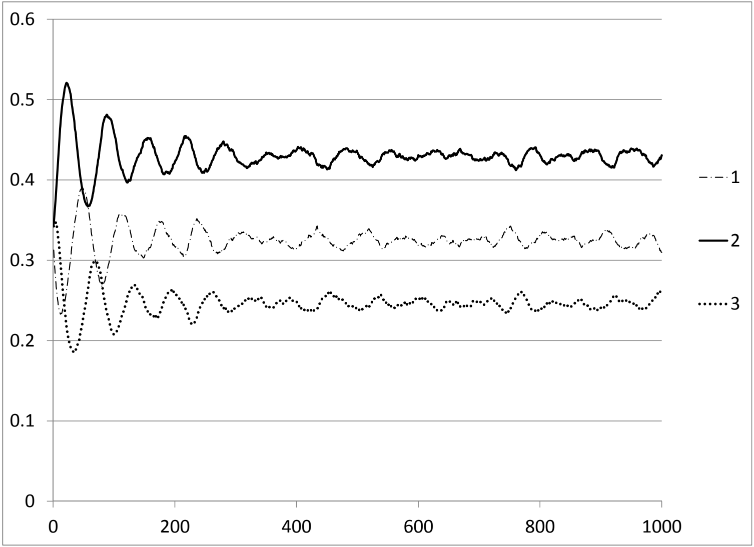
Theorem. Hofbauer and Sigmund. *Let* $\Delta = \beta_1\beta_2\beta_3 + \alpha_1\alpha_2\alpha_3$. *If* $\Delta > 0$ *solutions converge to the fixed point. If* $\Delta < 0$ *their distance from the boundary tends to 0. If* $\Delta = 0$ *there is a one-parameter family of periodic orbits.*

G_1	**0**	**1**	**2**
0	0	4	-3
1	-1	0	5
2	6	-2	0

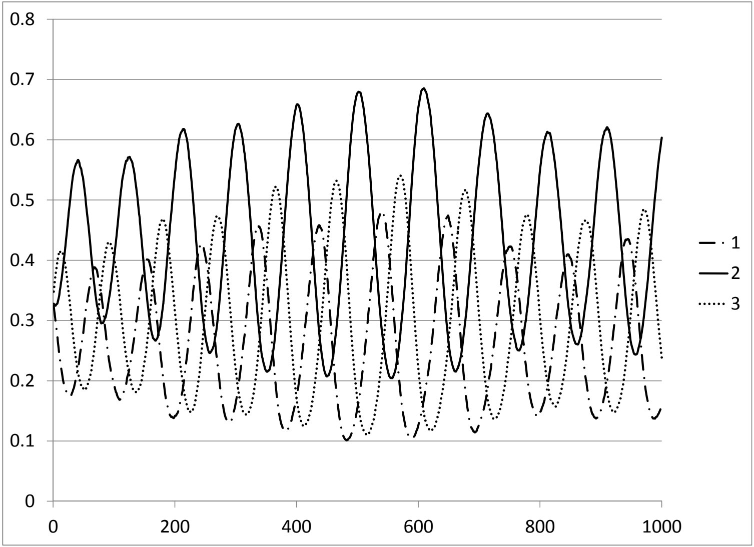
G_2	**0**	**1**	**2**
0	0	1	-2
1	-3	0	2
2	3	-2	0

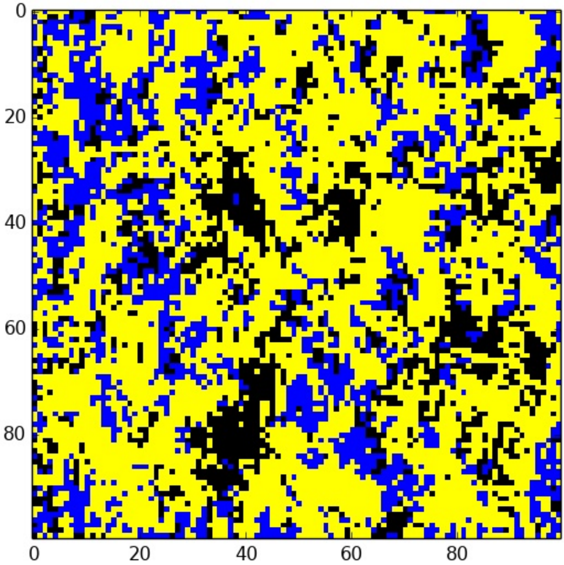
G_1 is constant sum and has $\Delta > 0$. G_2 has $\Delta < 0$.

Game G_1, Replicator eq converges to fixed point



Game G_2, Replicator eq spirals out to boundary



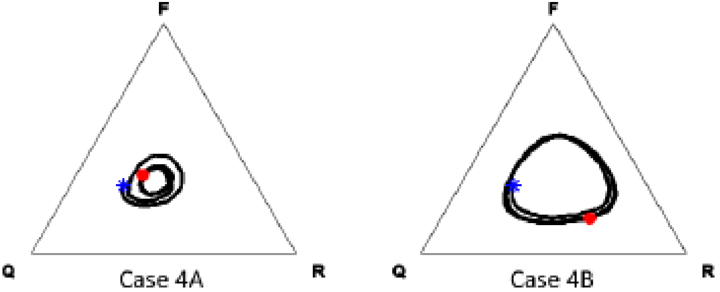

0
20
40
60
80
0
20
40
60
80

Marc Ryser and Kevin Murgas (2016) arXiv

Bone remodeling R = resorption, F = formation, Q = quiescent.

$$\begin{array}{cccc} & R & F & Q \\ R & 0 & \alpha_3 & \beta_2 \\ F & \beta_3 & 0 & \alpha_1 \\ Q & \alpha_2 & \beta_1 & 0 \end{array}$$

$\alpha_1, \alpha_2 < 0$, $\beta_1, \beta_2 > 0$, $\alpha_3, \beta_3 \in \mathbb{R}$. If $\alpha_3 < 0$, $\beta_3 > 0$ they have a RPS system. Case 4A stable, Case 4B unstable.



Stag Hunt

Mentioned in Rousseau's 1755 *A Discourse on Inequality*

	Stag	*Hare*
Stag	4	0
Hare	2	1

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 does also then you split the kill

$(1/3, 2/3)$ unstable equilibrium

Stag Hunt

Modify so that 0's on diagonal

G	$Stag$	$Hare$
$Stag$	0	-1
$Hare$	-2	0

$(1/3, 2/3)$ unstable equilibrium

$H_{ij} = (3/2)G_{i,j} - (1/2)G_{j,i}$

H	$Stag$	$Hare$
$Stag$	0	$-1/2$
$Hare$	$-5/2$	0

$(1/6, 5/6)$ unstable equilibrium

Bistable 2x2 games

Bistable $= b, c < 0$. Replicator equation is

$$\frac{du}{dt} = \phi(u) = u(1-u)[b-(b+c)u]$$

$\bar{u} = b/b+c$. If $\bar{u} < 1/2$, 1's take over, $\bar{u} > 1/2$ 2's take over.

Why?. PDE $\frac{du}{dt} = \sigma^2 u''/2 + u(1-u)[b-(b+c)u]$ has traveling wave solution

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

1's take over iff $c > 0$ iff $\int_0^1 \phi(x)\,dx > 0$ iff $\bar{u} < 1/2$.

Multiple Myeloma

Dingli et al (2009) British J. Cancer

Normal bone remodeling is a consequence of a dynamic balance between osteoclast (OC) mediated bone resorption and bone formation due to osteoblast (OB) activity.

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

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

OC cells produce osteoclast activating factors that stimulate the growth of MM cells where as MM cells are not effected by the presence of OB cells. These considerations lead to the following game matrix.

Transformed game

$$A = (1+\theta)a - \theta e, \ldots D = (1+\theta)d, F = \theta d$$

G	OC	OB	MM
OC	0	a	b
OB	e	0	$-d$
MM	c	0	0

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

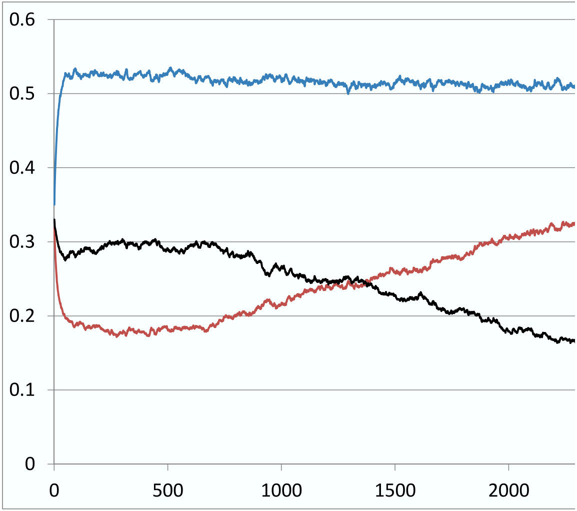
$a, b, c, d, e > 0$. D and $F > 0$ so $3 \gg 2$. (A, E), (B, C) can have any sign combination except $-, -$.

If $A, B, C, E > 0$. $(\frac{A}{A+E}, \frac{E}{A+E}, 0)$ "normal" and $(\frac{B}{B+C}, 0, \frac{C}{C+B})$ "cancer" are stable equilibria on their edges.

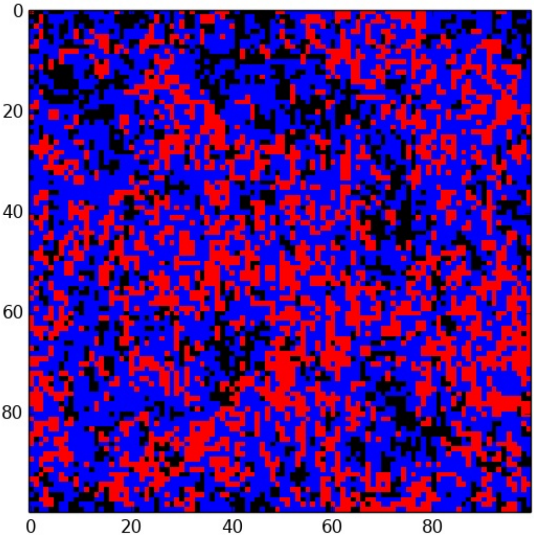
$3 \to (1,2)$ if $\frac{C}{E} > 1 - \frac{F}{A}$ Only one condition can hold if $F = 0$

$2 \to (1.3)$ if $1 - \frac{DC}{BE} > \frac{C}{E}$ so no three species coexistence.

$a = e = 2$, $b = c$, $d = 1$. Bistable for $c \in [0.5, 1.5]$. 1,2 wins $c = 1.5$, 1,3 wins $c = 1$. Simulation is for $c = 1.25$.



c = 1.25 at time 500. 1=blue, 2=red, 3=black



Coexistence in Spatial MM game

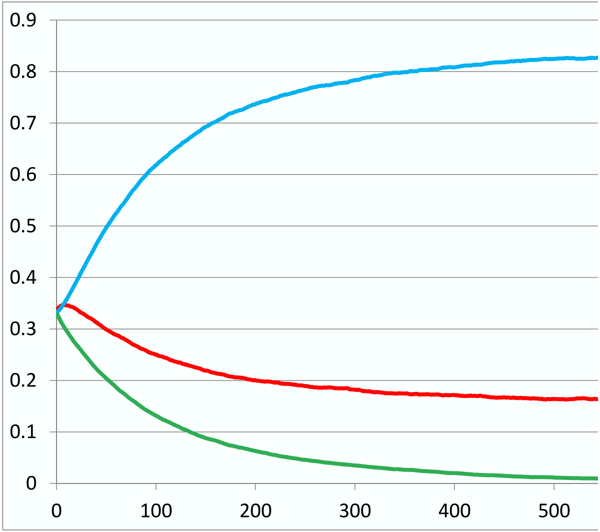
If $1 - \frac{DC}{BE} > \frac{C}{E} > 1 - \frac{F}{A}$ then both boundary equilibria can be invaded and there is coexistence for small w. (Theorem)

G	**0**	**1**	**2**
0	0	2	3
1	4.667	0	-1
2	3	0	0

H	**0**	**1**	**2**
0	0	2/3	3
1	6	0	-1.5
2	3	0.5	0

The stationary distribution for H is $(0.19, 0.67, 0.15)$

Simulation with $w = 1/7$



Summary

The main contribution is to describe a procedure for determining the behavior of spatial three strategy games with weak selection, 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 three 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 Durrett (2014) EJP

2. As first observed by Durrett and Levin (1994), 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 suggest 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 point. This was proved in Durrett (2014) EJP hen 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 result has also been found recently by Ryser and Murgas (2017).

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 even 0.25.

References

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