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.

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

$b = \lambda - 1$, $c = 1$. 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). In $d \leq 2$, $P(\xi_t(x) \neq \xi_t(y)) \to 0$. In $d \geq 3$ if sites in ξ_0^p are independently $= 1$ then $\xi_t^p \Rightarrow \nu_p$ a one parameter family of stationary distributions.

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 $d \geq 3$

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

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 $\theta = 1/2$.

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

which simplifies to

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

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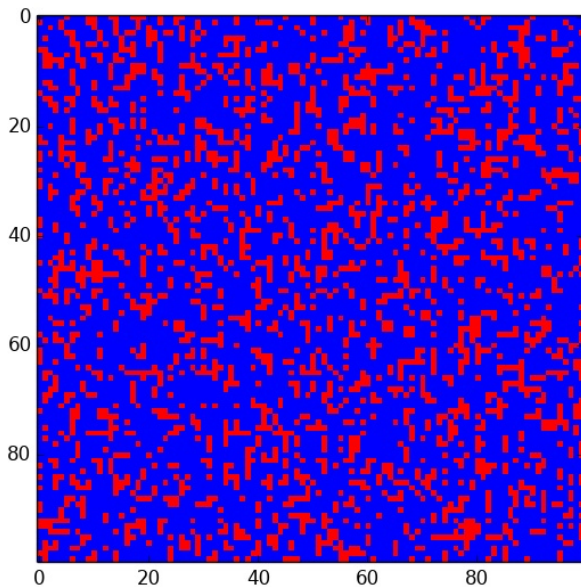
$$
\approx (\bar{b}/(\bar{b} + \bar{c}), \bar{c}/(\bar{b} + \bar{c})
$$

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
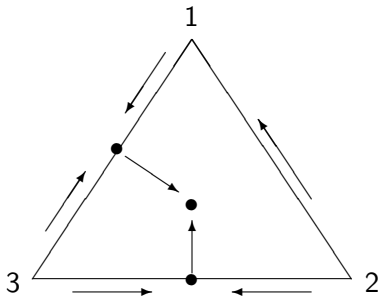
Rock Paper Scissors

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

	1	**2**	**3**
1	0	α_3	β_2
2	β_3	0	α_1
3	α_2	β_1	0

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

$$\rho_1 = (\beta_1\beta_2 + \alpha_1\alpha_3 - \alpha_1\beta_1)/D$$
$$\rho_2 = (\beta_2\beta_3 + \alpha_2\alpha_1 - \alpha_2\beta_2)/D$$
$$\rho_3 = (\beta_3\beta_1 + \alpha_3\alpha_2 - \alpha_3\beta_3)/D$$

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.

Theorem. *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*

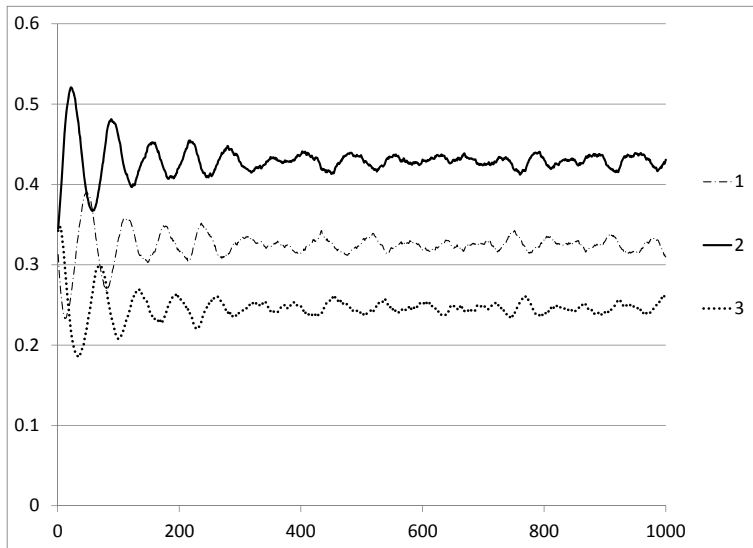$$\sup_x |\mu(\xi(x) = i) - \rho_i| < \delta$$

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.*
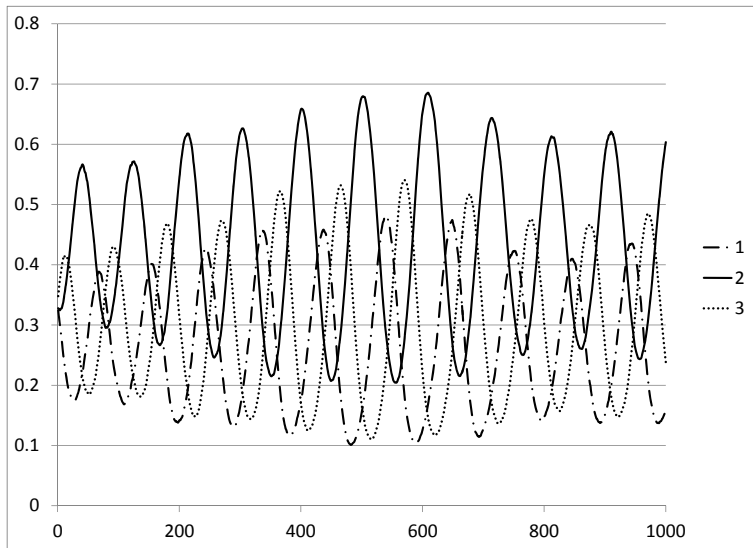
G_1	**0**	**1**	**2**		G_2	**0**	**1**	**2**
0	0	4	−3		**0**	0	1	−2
1	−1	0	5		**1**	−3	0	2
2	6	−2	0		**2**	3	−2	0

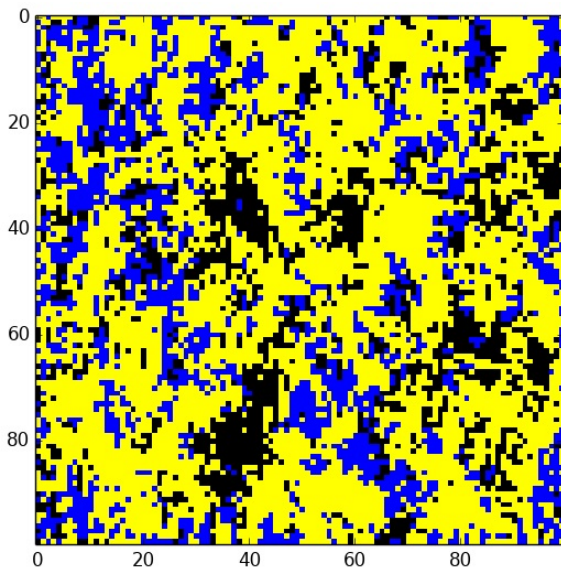G_1 is constant sum and has $\Delta > 0$. G_2 has $\Delta < 0$.

Game G_1, Replicator eq converges to fixed point

Game G_2, Replicator eq spirals out to boundary

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

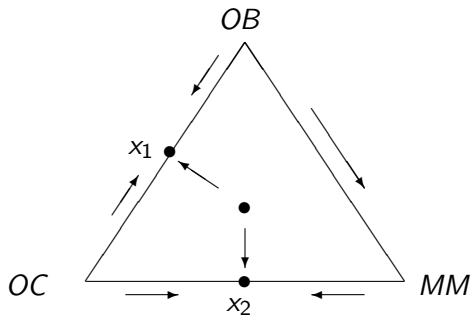$A = (1 + \theta)a - \theta e, \dots D = (1 + \theta)d, F = \theta d$

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

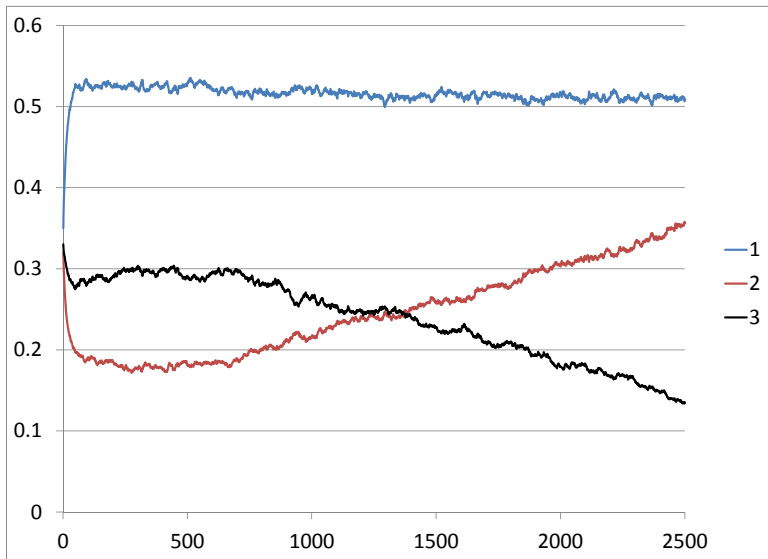$a, b, c, d, e > 0$. D and $F > 0$ so $3 \gg 2$. (A, E), (B, C) can have any sign combination except $-, -$.

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.

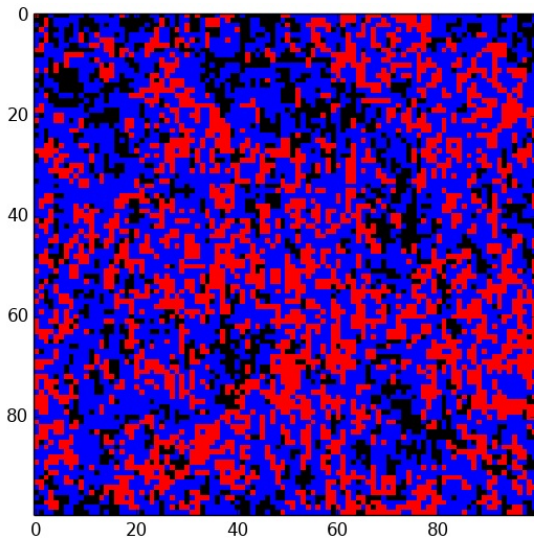$3 \to (1, 2)$ if $\frac{C}{E} > 1 - \frac{F}{A}$ \qquad Only one condition can hold if $F = 0$

$2 \to (1.3)$ if $1 - \frac{DC}{BE} > \frac{C}{E}$ \qquad 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 $c = 1.25$.

Figure: Caption for this slide NN.

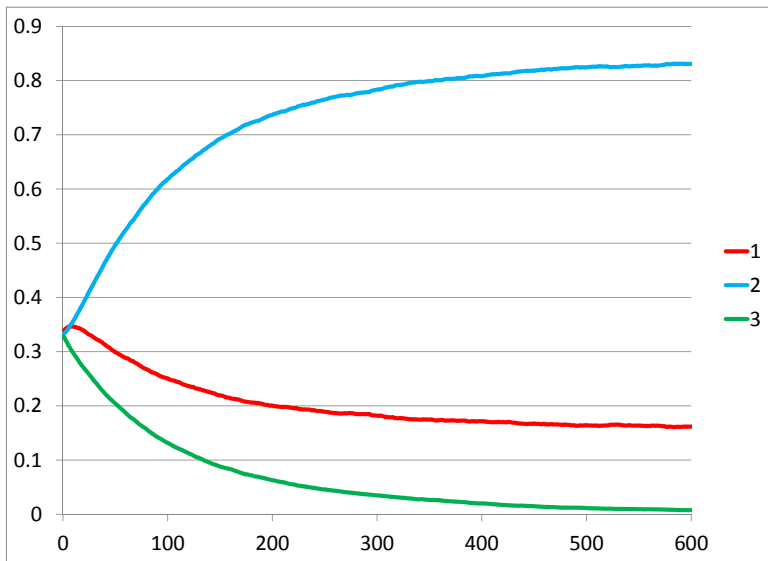# c = 1.25 at time 500. 1=blue, 2=red, 3=black

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**		H	**0**	**1**	**2**
0	0	2	3		**0**	0	2/3	3
1	4.667	0	−1		**1**	6	0	−1.5
2	3	0	0		**2**	3	0.5	0

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

Simulation with $w = 1/7$, Theorem: coexistence

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 (e.g. bistable games or unstable RPS) the behavior is not the same (stronger strategy always wins or there is coexistence). The last two conclusions ave not been proved mathematically.

References

R. Durrett and S. Levin. (1994) The importance of being discrete (and spatial). *Theoret. Pop. Biol.* 46, 363-394 [1085 citations]

J.T. Cox, R. Durrtt and E.A. Perkins. Voter model perturbations and reaction diffusion equations. Astérisque, volume 349 (113 pages) arXiv:1103.1676

R. Durrett. (2014) Spatial evolutionary games with small selection coefficients. *Electronic J. Probability.* 19, paper 121

Mridu Nanda and Rick Durrett (2017) Spatial evolutionary games with weak selection. *Proceedings of the National Academy of Science.* 114, 6046–6051