Spatial Evolutionary Games

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Prisoner's Dilemma / Alturism

$$\begin{array}{ccc} & C & D \\ C & b-c & -c \\ D & b & 0 \end{array}$$

A cooperator pays a cost c to give the other player a benefit b. The matrix gives the payoffs to player 1. If, for example, player 1 plays C and player 2 plays D then player 1 gets $-c$ and player 2 gets b.

Space is important. Strategy 1 dominates strategy 2. In a homogeneously mixing world, C's die out. Under "Death-Birth" updating on a graph in which each individual has k neighbors, C's take over if $b/c > k$.

Snowdrift game

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

Two individuals are trapped on either side of a snowdrift. C is shovel your way out, D is do nothing. If both play C they split the work. If you play C versus an opponent who plays D you do all of the work but at least you don't have to spend the night in your car. If $b > c$ then there is a mixed strategy equilibrium.

Facultative cheating in Yeast. Nature 459 (2009), 253–256. 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, cooperators can invade a population of cheaters.

Glycolytic phenotype

Cancer cells are initially characterized as having autonomous growth (AG), but could switch to glycolysis for energy production (GLY), or become increasing motile and invasive (INV).

$$\begin{array}{lccc} & 1 & 2 & 3 \\ 1 = AG & \frac{1}{2} & 1 & \frac{1}{2} - n \\ 2 = INV & 1 - c & 1 - \frac{c}{2} & 1 - c \\ 3 = GLY & \frac{1}{2} + n - k & 1 - k & \frac{1}{2} - k \end{array}$$

Here c is the cost of motility, k is the cost to switch to glycolysis, n is the detriment for nonglycolytic cell in glycolytic environment, which is equal to the bonus for a glycolytic cell.

Tumor-Stroma Interactions

Prostate cancer. $S =$ stromal cells, $I =$ cancer cells that have become independent of the micro-environment, and $D =$ cancer cells that remain dependent on the microenviornment.

	S	D	I
S	0	α	0
D	$1+\alpha-\beta$	$1-2\beta$	$1-\beta+\rho$
I	$1-\gamma$	$1-\gamma$	$1-\gamma$

Here γ is the cost of being environmentally independent,
β cost of extracting resources from the micro-environment,
α is the benefit derived from cooperation between S and D,
ρ benefit to D from paracrine growth factors produced by I.

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.

Spatial Model

Suppose space is the d-dimensional integer lattice. Interaction kernel $p(x)$ is a probability distribution with $p(x) = p(-x)$, finite range, covariance matrix $\sigma^2 I$. E.g., $p(x) = 1/2d$ for the nearest neighbors $x \pm e_i$, e_i is the ith unit vector.

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

Birth-Death dynamics: Each individual gives birth at rate $\Phi(x)$ 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 $p(y-x)\Phi(y)$. When $p(z) = 1/k$ for a set of k neighbors $\mathcal{N}$, we pick with a probability proportional to its fitness.

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.

Holley and Liggett (1975)

Consider the voter model on the d-dimensional integer lattice $\mathbb{Z}^d$ in which each vertex decides to change its opinion at rate 1, and when it does, it adopts the opinion of one of its $2d$ nearest neighbors chosen at random.

In $d \leq 2$, the system approaches complete consensus. That is if $x \neq y$ then $P(\xi_t(x) \neq \xi_t(y)) \to 0$.

In $d \geq 3$ if we start from ξ_0^p product measure with density p, i.e., $\xi_0^p(x)$ are independent and equal to 1 with probability then ξ_t^p **converges in distribution to a limit ν_p, which is a stationary distribution for the voter model.**

PDE limit

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.

More about ν_u

Voter model is dual to coalescing random walk = genealogies that give the origin of the opinion at x at time t.

Random walks jump at rate 1, and go from x to $x+y$ with probability $p(y) = p(-y)$. Random walks from different sites are independent until they hit and then coalesce to 1.

$\langle \xi(0) = 1, \xi(x) = 0 \rangle_u = p(0|x)u(1-u)$, where $p(0|x)$ is the probability the random walks never hit.

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

Sites separated by a bar do not coalesce. Those within the same group do.

Coalescence probabilities describe voter equilibrium.

Death-Birth dynamics

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

Limiting PDE is $\partial u_i/\partial t = (1/2d)\Delta u + \phi_D^i(u)$ where

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

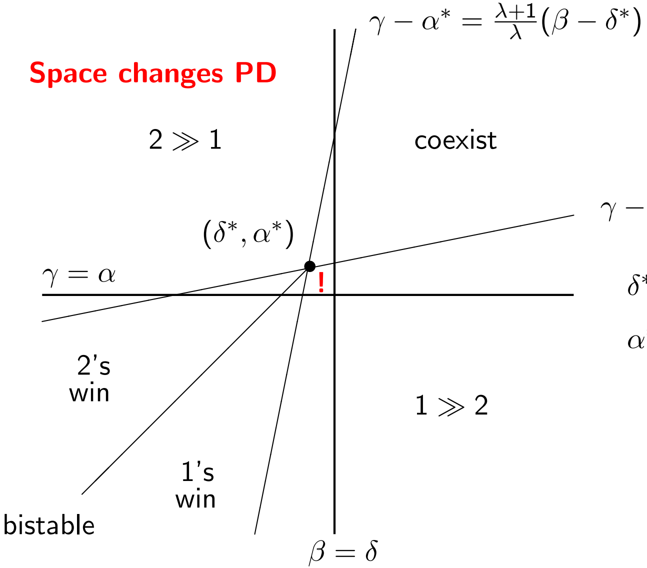
is $\bar{p}_1$ **times the RHS of the replicator equation for** $G + \bar{A}$

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

$\kappa = 1/P(v_1 + v_2 = 0)$ is the "effective number of neighbors."

Death-Birth updating ($\alpha > \delta$ fixed)

Space changes PD



$$\mu = \bar{p}_2 / \bar{p}_1$$

$$\nu = \frac{p(v_1|v_2)}{\kappa \bar{p}_1}$$

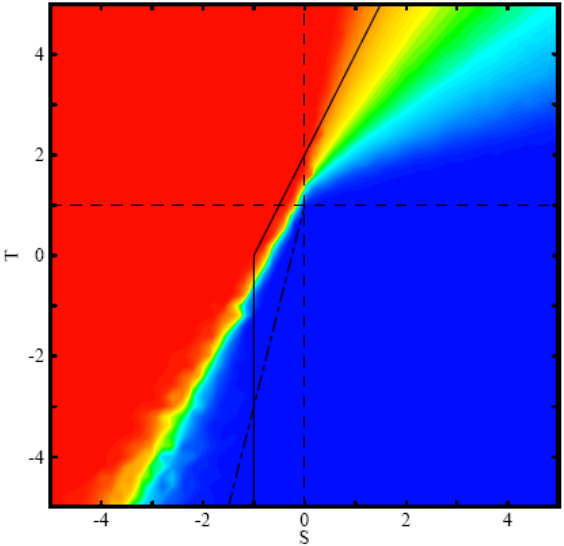
$$\lambda = \mu - \nu > 0$$

$$\delta^* = \delta - \frac{\nu(\alpha-\delta)}{1+2(\mu-\nu)}$$

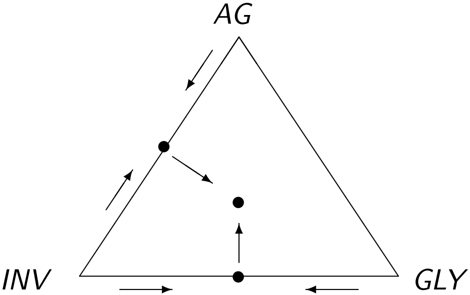
$$\alpha^* = \alpha + \frac{\nu(\alpha-\delta)}{1+(\mu-\nu)}$$

	1	2
1	α	β
2	γ	δ

Hauert's one dimensional simulations

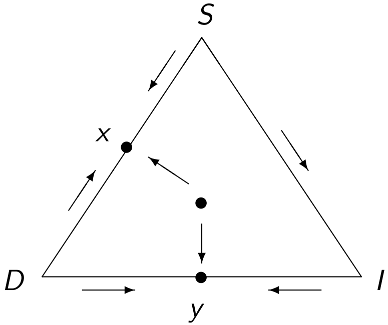


Two attracting boundary fixed points in H



We can construct a convex Lyapunov function that is nontrivial near the boundary, and conclude that there is coexistence in the spatial model. Spatial evolutionary games with small selection coefficients. *Electronic J. Probability.* 19 (2014), paper 121

Bistability in H



Prove existence of traveling wave w with $w(-\infty) = x$, $w(\infty) = y$.
Prove convergence theorem for PDE.
Sign of speed dictates the true equilibrium of spatial model.