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.

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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.

Two strategy games

Payoffs to player 1. C = cooperate, D = defect

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

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

3. Battle of the sexes
$$\begin{array}{ccc} & C & D \\ C & 0 & 1 \\ D & 2 & -1 \end{array}$$

4. Stag Hunt
$$\begin{array}{ccc} & C & D \\ C & 3 & 0 \\ D & 2 & 1 \end{array}$$

Only three cases in Replicator equation (next slide).
1. $D \gg C$; 2, 3. attracting fixed point; 4. bistable.

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.

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 microenvironment, and D = cancer cells that remain dependent on the microenvironment.

	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.

Three species chemical competition

First example Tomlinson (1997) and also Durrett and Levin (1997) three species colicin

$$\begin{array}{cccc}
 & 1 & 2 & 3 \\
1 = Producer & 1 - f + (g - e) & 1 - e & 1 + (g - e) \\
2 = Resistant & 1 - h & 1 - h & 1 - h \\
3 = Sensitive & 1 - f & 1 & 1
\end{array}$$

Here f is the cost of sensitivity to toxin, g is the advantage to producer, e is cost to produce, h is cost of resistance.

$S > R$; if $g > e$ then $P > S$; if $h < e$ and $h < e + f - g$ then $R > P$.
Backwards rock-paper-scissors: $R > P > S > R$

Rock-Paper Scissors for Lizards

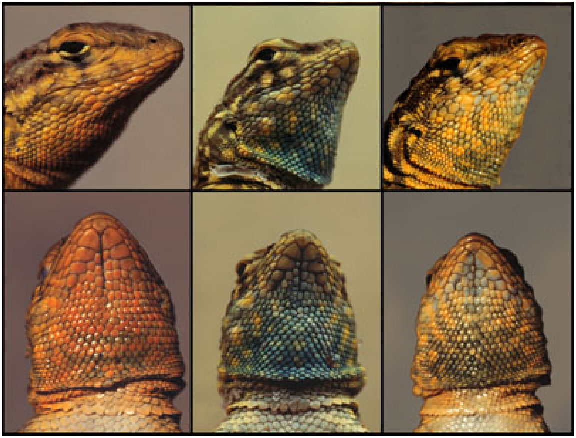


Figure: Orange = several mates > Blues = monagamous > Yellow = sneaky maters > Orange

Non-spatial Generalized Rock-Paper-Scissors

	R	**P**	**S**
R	0	α_3	β_2
P	β_3	0	α_1
S	α_2	β_1	0

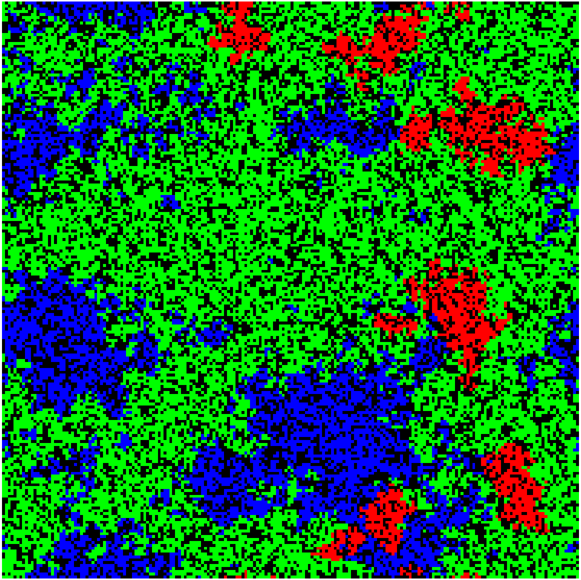
$\alpha_i < 0 < \beta_i$

Fixed point for replicator dynamics (all components > 0):

$$u_1 = (\beta_1\beta_2 + \alpha_1\alpha_3 - \alpha_1\beta_1)/D$$
$$u_2 = (\beta_2\beta_3 + \alpha_3\alpha_2 - \alpha_2\beta_2)/D$$
$$u_3 = (\beta_3\beta_1 + \alpha_2\alpha_1 - \alpha_3\beta_3)/D$$

Let $\Delta = \beta_1\beta_2\beta_3 + \alpha_1\alpha_2\alpha_3$. $\Delta > 0$ orbits spiral in. $\Delta < 0$ **spiral out.**
$\Delta = 0$ **one parameter family of periodic orbits.**

Spatial three species colicin



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. **Population size $= \infty$, so not weak selection.**

Does not change the behavior of the replicator equation.

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

If the game matrix is 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.
Durrett and Levin (1994) expected value w.r.t. product measure.

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.

Two big ideas

On the next two slides we will give some ugly formulas for the limiting PDE in our two cases.

Idea 1. Ohtsuki and Nowak. The reaction term is the replicator equation for a modification of the game.

Idea 2. Tarnita et al. The effect of the dispersal kernel can be encapsulated in two numbers. One number in the two strategy case.

Caveat. Let v_1 and v_2 be independent and have distribution $p(x)$. We will also need

$$\kappa = 1/P(v_1 + v_2 = 0)$$

is the "effective number of neighbors." If p is unform on a set of size k, $\kappa = k$.

Birth-Death dynamics

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

Let v_1, v_2 be independent with distribution p

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

PDE is $\partial u_i/\partial_t = (1/2d)\Delta u + \phi_B^i(u)$ where

$$\phi_B^i(u) = p_1 \phi_R^i(u) + p_2 \sum_{j \neq i} u_i u_j (G_{i,i} - G_{j,i} + G_{i,j} - G_{j,j})$$

This is p_1 times the RHS of the replicator equation for $G + A$:

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

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 $\partial u_i/\partial t = (1/2d)\Delta u + \phi^i_D(u)$ where

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

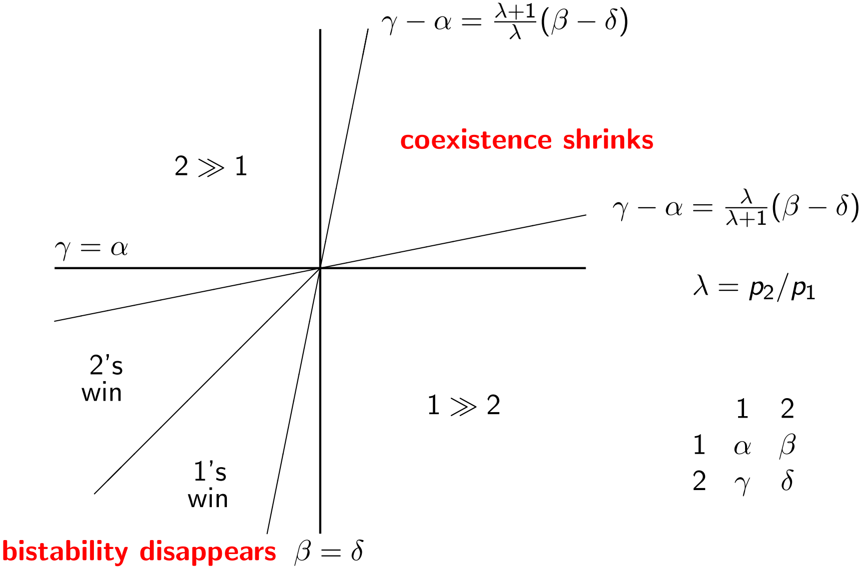
is $\bar{p}_1$ **times the RHS of the replicator equation for** $G + \bar{A}$

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

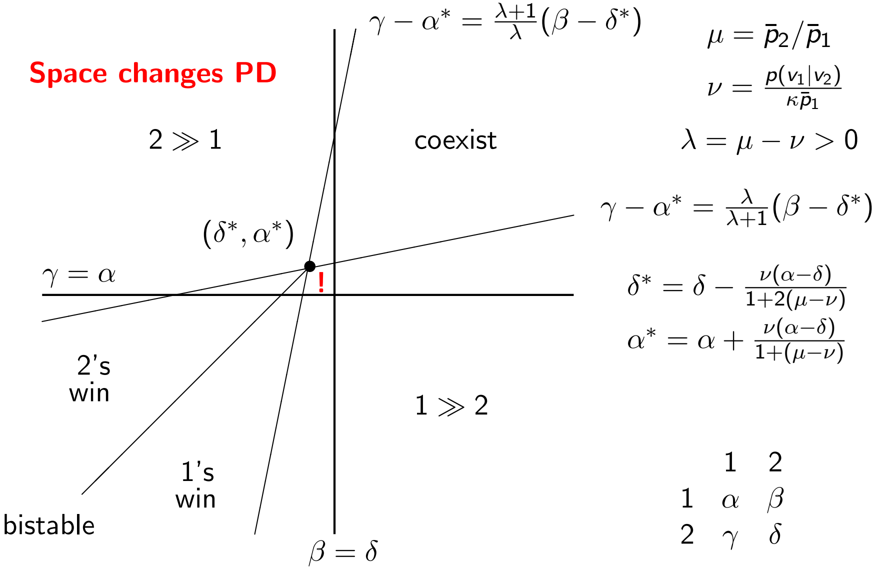
$\kappa = 1/P(v_1 + v_2 = 0)$ is the "effective number of neighbors."

Only 2 constants: $2\bar{p}_1 + \bar{p}_2 = (1 + 1/\kappa)p(0|v_1)$

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



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



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

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

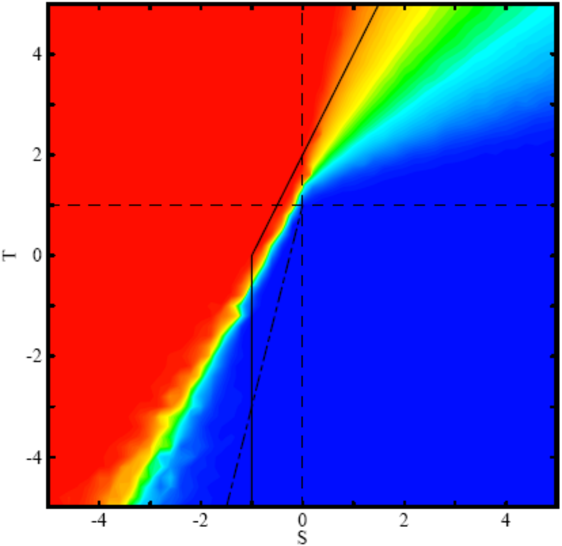
$$\lambda = \mu - \nu > 0$$

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

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

	1	2
1	α	β
2	γ	δ

Hauert's one dimensional simulations



Spatial Generalized Rock-Paper-Scissors

	R	**P**	**S**
R	0	α_3	β_2
P	β_3	0	α_1
S	α_2	β_1	0

$\alpha_i < 0 < \beta_i$

In this game the diagonal entries $G_{i,i} = 0$ the reaction terms for both updates have the form $p(\phi^i_R(u) + \theta \sum_j u_i u_j (G_{i,j} - G_{j,i}))$.
The reaction term is the RHS of the replicator equation for

$$H = \begin{pmatrix} 0 & \alpha_3 + \theta(\alpha_3 - \beta_3) & \beta_2 + \theta(\beta_2 - \alpha_2) \\ \beta_3 + \theta(\beta_3 - \alpha_3) & 0 & \alpha_1 + \theta(\alpha_1 - \beta_1) \\ \alpha_2 + \theta(\alpha_2 - \beta_2) & \beta_1 + \theta(\beta_1 - \alpha_1) & 0 \end{pmatrix}$$

also a rock-paper-scissors game since $\beta_i > \alpha_i$.

PDE result

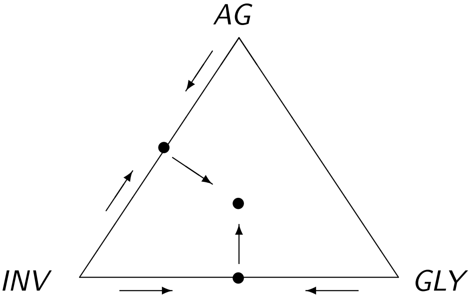
Lemma. Consider PDE with reaction term = RHS of the replicator equation for H. Suppose that the game H has (i) zeros on the diagonal, (ii) an interior equilibrium ρ, and that H is almost constant sum: $H_{ij} + H_{ji} = c + \eta_{ij}$ where $\max_{i,j} |\eta_{i,j}| < c/2$. In this case, if we start the from a continuous initial configuration in which $\{u_i > 0 \text{ for all } i\}$ is a nonempty open set, then **PDE converges to ρ on a linearly growing set**.

Proof. $\phi(u) = \sum_i u_i - \rho_i \log u_i$ **is a convex Lyapunov function.** If $h(t,x) = \phi(u(t,x))$, and Φ is the Hessian of ϕ

$$\frac{\partial h}{\partial t} = \frac{\sigma^2}{2}\Delta h + \phi^*(u(t,x)) - \nabla u \cdot \Phi(u(t,x))\nabla u$$

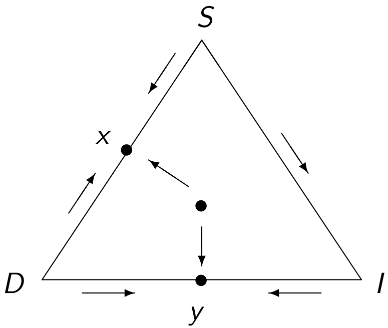
Lemma and CDP implies existence of stationary distribution with densities $\approx \rho_i$

Two attracting boundary fixed points in H



Using results from R. Durrett (2002) Mutual Invadability Implies Coexistence. *Memoirs of the AMS.* Volume 156, Number 740, we can construct a convex Lyapunov function that is nontrivial near the boundary, and conclude that there is coexistence in the spatial model.

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.

Spatial Evolutionary Games with Small Selection Coefficients

Electronic J. Probability or my web page

Contains an extensive analysis of 3×3 games