# Evolutionary Games on the Torus

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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 $D$ dominates strategy $C$. 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 $b/c > k$. $D$'s always win under Birth-Death.

# 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.

# 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 microenviornmnet.

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

Here $\gamma$ is the cost of being environmentally independent,
$\beta$ cost of extracting resources from the micro-environment,
$\alpha$ is the benefit derived from cooperation between $S$ and $D$,
$\rho$ benefit to $D$ from paracrine growth factors produced by $I$.

# Three Species Colicin

Durrett and Levin (1997) = Tomlinson (1997)

| | 1 | 2 | 3 |
|---|---|---|---|
| $1 = Producer$ | $1 - f + (g - e)$ | $1 - e$ | $1 + (g - e)$ |
| $2 = Resistant$ | $1 - h$ | $1 - h$ | $1 - h$ |
| $3 = Sensitive$ | $1 - f$ | $1$ | $1$ |

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.

$S > R$ in $2 \times 2$ subgame; if $g > e$ then $P > S$; if $h < e$, $h < e + f - g$ then $R > P$. **Backwards rock-paper-scissors:** $R > P > S > R$

# Rock-Paper Scissors for Lizards

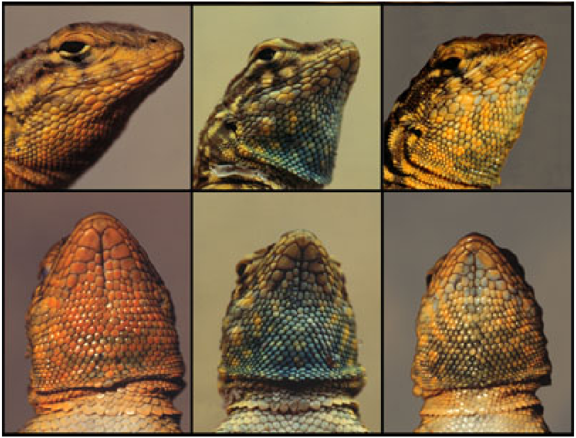


Figure: Orange = several mates > Blues = monagamous > Yellow = sneaky maters > Orange

# 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 multiply the matrix by a constant only the time scale changes.

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 torus. 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 $i$th 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.

# Weak 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.

**$G$ and $\bar{G}$ have the same the behavior under the replicator equation.**

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

# Holley and Liggett (1975)

Consider the voter model on the $d$-dimensional integer lattice $\mathbb{Z}^d$ in which each individual decides to change its opinion at rate 1, and when she does, she 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 $\xi_0^p$ product measure with density $p$, i.e., $\xi_0^p(x)$ are independent and equal to 1 with probability then $\xi_t^p$ **converges in distribution to a limit $\nu_p$, 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 $\epsilon^{-2}$ 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 $\nu_u$ in which the densities are given by the vector $u$.

# More about $\nu_u$

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 slide we will give an ugly formulas for the limiting PDE in the Death-Birth Case.

**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 uniform on a set of size $k$, $\kappa = k$.

# 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

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

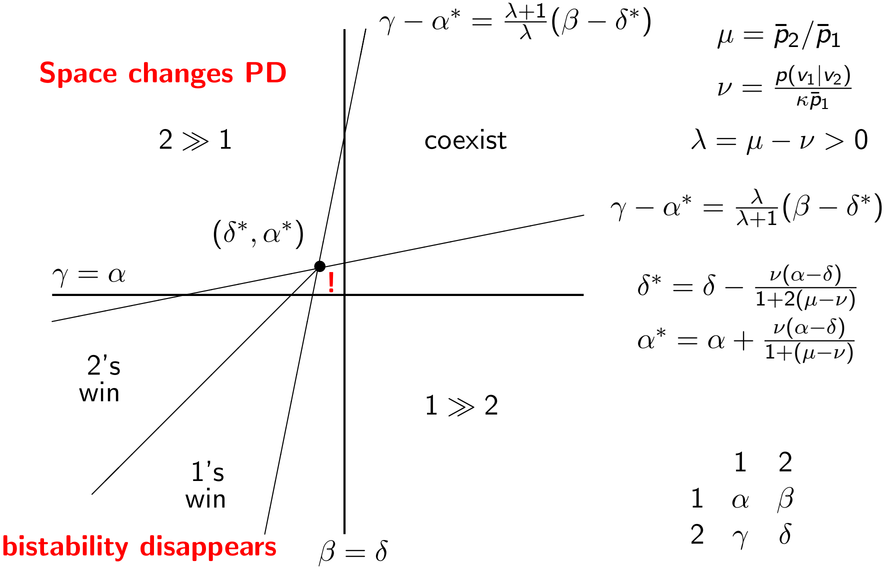
$$- (1/\kappa) p(v_1|v_2) \sum_{j \neq i} u_i u_j (G_{i,j} - G_{j,i}) \qquad 0 \text{ in B-D}$$

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

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

**Only 2 constants [not counting $\kappa$]:** $2\bar{p}_1 + \bar{p}_2 = (1 + 1/\kappa) p(0|v_1)$

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




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

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

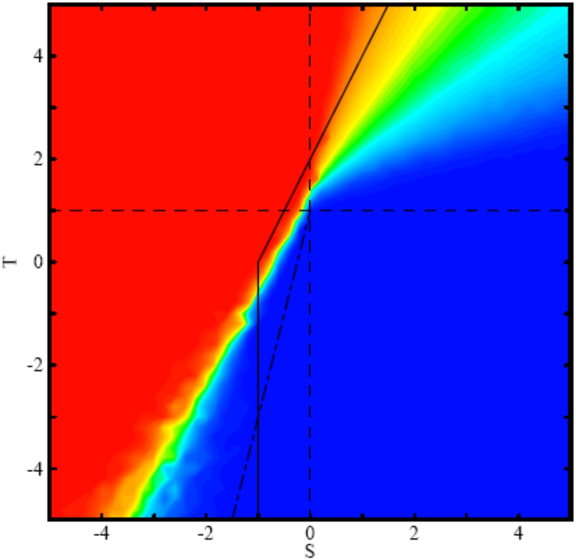
$$\lambda = \mu - \nu > 0$$

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

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

| | 1 | 2 |
|---|---|---|
| 1 | $\alpha$ | $\beta$ |
| 2 | $\gamma$ | $\delta$ |

# Hauert's one dimensional simulations



# Where does this come from?

There are four cases for the modified game:

(i) stable mixed strategy equilibrium (coexist)

(ii) $1 \gg 2$

(iii) $2 \gg 1$

(iv) unstable mixed strategy equilibrium (bistable)

Reaction term is a cubic: $\phi(u) = cu(1-u)(u-\rho)$. PDE converges to (i) $\rho$, (ii) 1, (iii) 0, (iv) 1 or 0 depending on the sign of the speed of the traveling wave.

# Tarnita's formula $m = 2$ strategies

Tarnita et al (J, Theor. Biol. 2009) say that a strategy in a $m$ strategy game is "favored by selection" if its frequency in equilibrium is $> 1/m$ when $w$ is small. Under some general assumptions on the spatial evolution, they argued that this holds for strategy 1 in a 2 by 2 game if and only if

$$\sigma G_{1,1} + G_{1,2} > G_{2,1} + \sigma G_{2,2}$$

where $\sigma$ is a constant that depends only on the dynamics.

Using the machinery of voter model perturbations one can show that this hold with $\sigma = 1$ for Birth-Death dynamics and $\sigma = (\kappa + 1)/(\kappa - 1)$ for Death-Birth dynamics.

**Key to proof: 1 is favored by selection if and only if $\phi(1/2) > 0$.**

# Tarnita's formula, $m > 2$ strategies. PNAS 2011

To state their result we need some notation.

$$\hat{G}_{*,*} = \frac{1}{m}\sum_{i=1}^{m} G_{i,i} \qquad \hat{G}_{k,*} = \frac{1}{m}\sum_{i=1}^{m} G_{k,i}$$

$$\hat{G}_{*,j} = \frac{1}{m}\sum_{i=1}^{m} G_{i,j} \qquad \hat{G} = \frac{1}{m^2}\sum_{i=1}^{m}\sum_{j=1}^{m} G_{i,j}$$

where $*$'s indicate values that have been summed over. The condition for strategy $k$ to be favored as

$$\sigma_1(\hat{G}_{k,*} - \hat{G}) + \sigma_2(G_{k,k} - \hat{G}_{*,*}) + (\hat{G}_{k,*} - \hat{G}_{*,k}) > 0$$

**Linear in matrix entries.** Condition is equivalent to

$$\phi_k(1/m, \ldots, 1/m) > 0$$

# Non-spatial Generalized Rock-Paper-Scissors

$$\begin{array}{cccc} & \mathbf{R} & \mathbf{P} & \mathbf{S} \\ \mathbf{R} & 0 & \alpha_3 & \beta_2 \\ \mathbf{P} & \beta_3 & 0 & \alpha_1 \\ \mathbf{S} & \alpha_2 & \beta_1 & 0 \end{array} \qquad \alpha_i < 0 < \beta_i$$

**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.**

The modified game for Birth-Death or Death-Birth dynamics

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

where

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

This is also a rock-paper-scissors game since $\beta_i > 0 > \alpha_i$.

# 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 $\rho$, 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 $\rho$ on a linearly growing set**.

Using CDP now the spatial model has a nontrivial stationary distribution with densities close the $\rho_i$. So 1 is favored by selection if

$$(\beta_1\beta_2 + \alpha_1\alpha_3 - \alpha_1\beta_1)/D > 1/3$$

**Quadratic in the matrix entries.**

## Regime 1. $\epsilon_L^{-1} \ll L$, or $w \gg N^{-2/d}$

In this case when we rescale space by multiplying by $\epsilon_L$ then the limit of the torus is all of $\mathbb{R}^d$ and the PDE limit holds.

**Theorem.** *Consider a two strategy evolutionary game with an attracting fixed point, so* $\phi(u) = \lambda u(1-u)(\rho - u)$. *Suppose that* $\epsilon_L^{-1} \sim CL^\alpha$ *where* $0 < \alpha < 1$ *and that for each* $L$ *we start from a product measure in which each type has a fixed positive density. Let* $N_1(t)$ *be the number of sites occupied by 1's at time* $t$. *There is a* $c > 0$ *so that for any* $\delta > 0$ *if* $L$ *is large and* $\log L \le t \le \exp(cL^{(1-\alpha)d})$ *then* $N_1(t)/N \in (\rho - \delta, \rho + \delta)$ *with high probability.*

For contact process on finite set have survival for time $\exp(cL^d)$. For contact process with fast voting (a VM perturbation) only have survival for $\le \exp(cL^{d-\alpha})$.

## Regime 2. $L \ll \epsilon_L^{-1} \ll L^{d/2}$ or $N^{-2/d} \gg w \gg N^{-1}$.

Time scale for the perturbation to have an effect, $\epsilon_L^{-2}$ is $\gg$ the time $O(L^2)$ needed for a random walk to come to equilibrium, but $\ll O(L^d)$, the time it takes for two random walks to hit.

$$U_i(t) = \frac{1}{N} \sum_{x \in \mathcal{T}_L} 1\left( \xi^{\epsilon}_{t\epsilon_L^{-2}}(x) = i \right)$$

**Theorem.** *If $U_i(0) \to u_i$ then $U_i(t)$ converges uniformly on compact sets to $u_i(t)$, the solution of*

$$\frac{du_i}{dt} = \phi_i(u) \qquad u_i(0) = u_i$$

*where $\phi_i$ is the reaction term in the PDE limit.*

# Tarnita's formula.

Introduce mutations are rate $\mu$ that set the strategy to one chosen at random from the $m$ possibilities. If $\mu \gg w$ then dominant contribution comes from one selection event.

**Theorem.** Suppose we are regime 2, $N^{-2/d} \gg w \gg N^{-1}$. If $\mu/w \to \infty$ slowly enough then strategy $k$ is favored by mutation if and only if

$$\phi_k(1/m, \ldots, 1/m) > 0.$$

**This is Tarnita's formula.**

# References

Slides are on my web page.

R. Durrett (2014) Spatial evolutionary gamees with small selection. *Electron. J. Probab.* 19, paper 121.

J.T. Cox and R. Durrett (2016) Evolutionary games on the torus withe weak selection. *Stoch. Proc. Appl.* Available on line but not yet assigned to an issue

Currently working with a student Ran Hou on the latent voter model on random graphs generated by the configuration model. We prove convergence to an ODE limit and use it to show that if voters have even a very short latent period at their switch opinions in which they won't change their minds then the density in the voter model $\to 1/2$ and stay close to that value for time $\ll N^p$ any $p < \infty$.