Evolution of social behaviors in a growing habitat with vacancies

H-C Jeong (Sejong Univ.)

HJ Park, BJ Kim, C. Hilbe, M. Nowak

Game (e.g., Prisoner Dilemma (PD) game)

1. **Players**: A & B
2. **Actions**: Cooperation (C), Defection (D)
3. **Payoff**: depends on action profile

p_A		B: C	B: D
A	C	R	S
A	D	T	P

- Payoff of the player A
- PD game: $T > R > P > S$

4. **Strategy space**: $\mathcal{M}_0=\{C,D\}$, $\mathcal{M}_{\frac{1}{2}}=\{C,D,T,AT\}$,
   $\mathcal{S}_0=\{p\}$, $\mathcal{S}_{\frac{1}{2}}=\{(p_C,p_D)\}$, $\mathcal{S}_1=\{(p_{CC},p_{CD},p_{DC},p_{DD})\}$, $\cdots$

Evolutionary Game Theory

- Time evolution of game strategy
- Evolution of life: **population dynamics with game theory**

- **Why Game in Evolution?**
  - **Players**: Individuals
  - **Strategy**: gene (normal/mutant allele)
  - **Payoff**: fitness (number of offspring)
  - **Survival of the fittest** $\Longrightarrow$ payoff maxi. ("rational" gene)

why male:female = 1:1?

Elephant Seal

- **Harem: polygyny**
- $\mathbf{A}$=\{m:f=50:50\} vs. $\mathbf{B}$=\{m:f=20:80\}
- **population size ratio,** $\mathbf{A} : \mathbf{B}$

  100:100 $\rightarrow$ 100:160

  $\rightarrow$ 100:256 $\rightarrow$ 100:410 $\rightarrow$ $\cdots$

R. A. Fisher (1930)

- strategy: r_m = prob. to produce male offspring (gene)
- payoff: x_g = expected number of grandchildren

- Consider $r_m = 0.2$ population with $N_m = 20$ and $N_f = 80$ children.

  p_g: prob. that a baby in the grandchild generation is my grandchild.

$$p_g = \begin{cases} 1/20 & \text{If you have one male child.} \\ 1/80 & \text{If you have one female child.} \end{cases}$$

- mutation with $r'_m > 0.2$ has a higher fitness.

- for $r_m < 1/2$ population, $r'_m > r_m$ mutation is better.
- for $r_m > 1/2$ population, $r'_m < r_m$ mutation is better.
- ESS (Evolutionary Stable Strategy): $r_m = 1/2$

Social Dilemma and Social Behavior Puzzle

Social Dilemma game

- $\mathrm{m} : \mathrm{f} = 20 : 80$ population
  - social behavior: female offspring
  - selfish behavior: male offspring
- peacock train (tail)
  - social behavior: small & dim
  - selfish behavior: big & bright
- other social dilemma examples
  - bird song, small face, slim waist
  - elephant-seal size, stag antler
  - bird migration, egg incubation
  - air conditioning with door open

Prisoner's Dilemma game

- payoff of A

$$\begin{pmatrix} A\backslash B & C & D \\ C & R & S \\ D & T & P \end{pmatrix}$$

$$T > R > P > S$$

Evolution of cooperation

- cell→organ→indi.→soc.
  - cf: cancel cell
- eusociality
  - ants, bees, mole-rats
- super-cooperator: people

Five rules for the evolution of cooperation

- **direct reciprocity**: memory
  - TFT, WSLS, $\cdots$
  - next encounter: $w > c/b$
- **PD game**

$$\begin{pmatrix} A\backslash B & C & D \\ C & b-c & -c \\ D & b & 0 \end{pmatrix}$$

- **indirect reciprocity** : name and fame
  - asymmetric partner
  - Information (language, name)
  - reputation: $q > c/b$
  - optional game (CDL)
- **Kin selection** : relatedness
  - two brothers or eight cousins
  - selfish gene
  - relatedness: $r > c/b$
  - Gametocyte Malaria sex-ratio: inbreeding 62%
- **group selection**
  - multi-level selection
  - moral, norm, identity
  - group fecundity: $M/N > c/b$
- **Network reciprocity**
  - interaction and competition network
  - assortment
  - degree: $1/k > c/b$ (DB process)

Model

- **Population**: **growing** habitat (in 1D lattice)
- **Interaction**: **simplified PD** game (**donation** game)

  R, S, T, P: given in terms of benefit (b) and cost (c) of cooperation.

$$\begin{pmatrix} A\backslash B & C & D \\ C & R & S \\ D & T & P \end{pmatrix} \Longrightarrow \begin{pmatrix} A\backslash B & C & D \\ C & b-c & -c \\ D & b & 0 \end{pmatrix}$$

$$T > R > P > S \qquad\qquad b > c > 0$$

- **fitness**: interpreted as longevity.
  - **death rate**: $d = \dfrac{1}{1 + A\exp(wp)}$
  - p: total payoff, w: selection strength A: environment parameter
  - $A \uparrow \Longrightarrow d \downarrow$ (Large A : good environment)

1D lattice

		D	C				D		C	C	C		C	C		
-8	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7	8

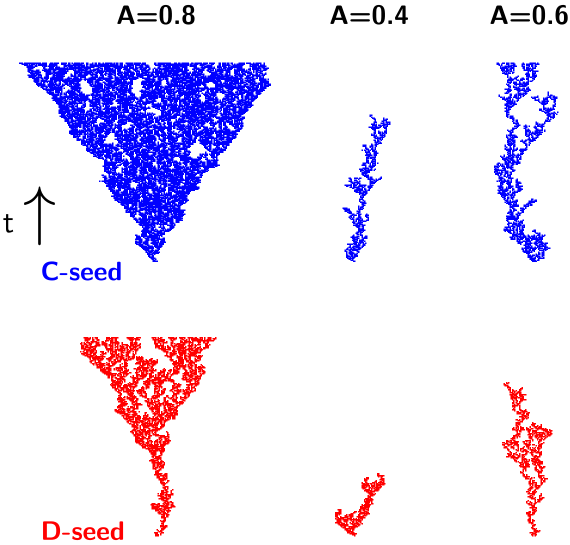
$$\begin{pmatrix} A\backslash B & C & D & E \\ C & b-c & -c & 0 \\ D & b & 0 & 0 \end{pmatrix}$$

- **start from one seed**: C or D
- **Habitat**: **From** $L=-6$ **to** $R=6$
- **choose a site**: $k \in \{L-1, \cdots, R+1\} = \{-7, -6, \cdots, 6, 7\}$
- **occupied site**: **death process** with prob. $d = \dfrac{1}{1 + A\, e^{wp}}$
- **empty site**: **birth process**
  - **both empty** neighbors ($k=-3$): remain empty ($E \to E$)
  - **one occupied** neighbor ($k=7$): neighbor's offspring ($E \to C$)
  - **both occupied** neighbors ($k=0$): random neighbor's offspring ($E \to C$ or $E \to D$)

Configurations

$$\begin{pmatrix} A\backslash B & C & D & E \\ C & b-c & -c & 0 \\ D & b & 0 & 0 \end{pmatrix}$$

- $b = 1$
- $c = 0.7$
- $d = \dfrac{1}{1 + A\,e^{wp}}$
- $w = 1$



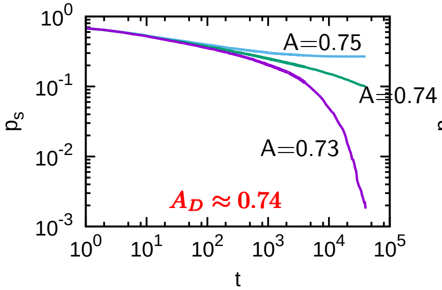
Survival function

$$p_s(t) = \frac{\text{\# of survival samples at } t}{\text{total \# of seeds}}$$

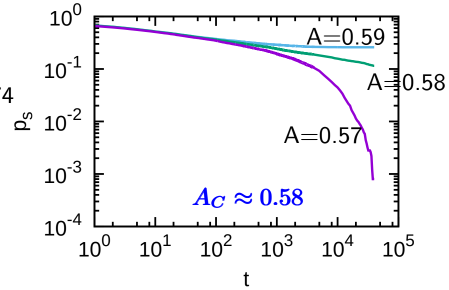
$$d = \frac{1}{1 + A\exp(wp)}$$

$$w = 1,\ b = 1,\ c = 0.7$$

D seed



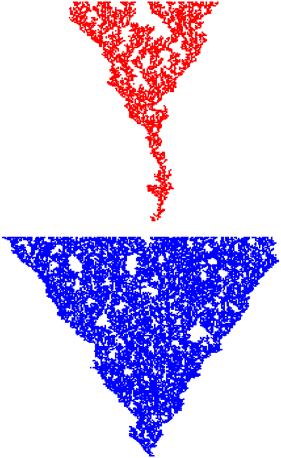
C seed

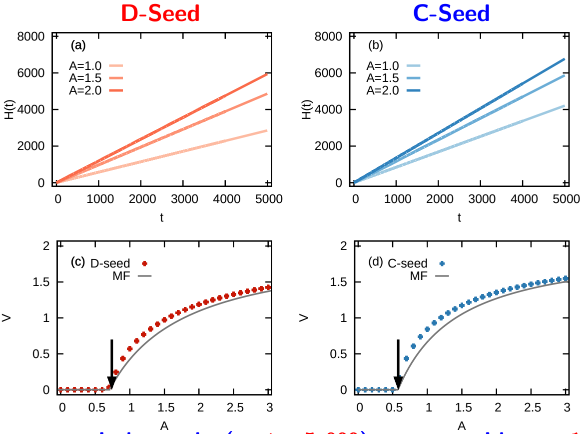


- $A_D < A$: Both cooperators and defectors survive
- $A_C < A < A_D$: Only cooperators survive
- $A < A_C$: Extinction for both C and D

Growth speed

- **Habitat size $H(t)$ & Habitat growth speed V_H**

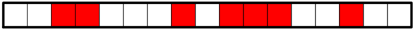




survival sample (at $t = 5,000$) average with $w = 1$, $b = 1$ and $c = 0.7$

$$\left[d = \frac{1}{1 + A \exp(wp)} \right]$$

- D-seed



$$\begin{pmatrix} A \backslash B & C & D & E \\ C & b-c & -c & 0 \\ D & b & 0 & 0 \end{pmatrix}$$

- death prob. is indep. of the configuration.

  $d = 1/\left[1 + Ae^{wp}\right] = 1/\left(1+A\right)$

$$V_D^{\mathrm{MF}} = 2\left(1 - d\left[1 + 2(1-\rho) + 3(1-\rho)^2 + \cdots\right]\rho\right) = 2\left(1 - \frac{d}{\rho}\right)$$

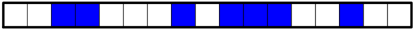
$$\rho_{\mathrm{MF}} = \frac{3 - \sqrt{1 + 4d}}{2} \qquad \left[\frac{\partial \rho}{\partial t} = (1-\rho)(2\rho - \rho^2) - \rho d = 0\right]$$

$$V_D^{\mathrm{MF}} = 2 - \frac{4d}{3 - \sqrt{1+4d}} = 2 - \frac{4}{3(A+1) - \sqrt{(A+1)(A+5)}}$$

$$A_{c\ \mathrm{MF}}^{D} = 1/\sqrt{2} \approx 0.71 \sim 0.74 = A_c^D \qquad \left[V_D^{\mathrm{MF}} = 0\right]$$

Growth speed in Mean-Field

- C-seed

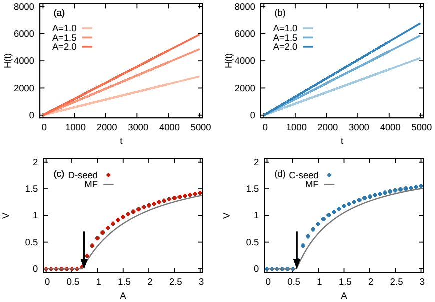


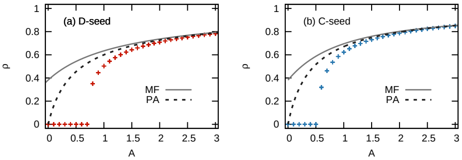
$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{ccc} C & D & E \end{array} \\ \begin{pmatrix} b-c & -c & 0 \\ b & 0 & 0 \end{pmatrix} \end{array}$$

- death prob. depends on the config.: d_0, d_1, d_2

$$\begin{aligned}
V_C^{\text{MF}} &= 2\Big(1 - d_1\rho - d_0\rho\left[2(1-\rho) + 3(1-\rho)^2 + \cdots\right]\Big) \\
&= 2\left(1 - (d_1 - d_0)\rho - \frac{d_0}{\rho}\right) \\
\frac{\partial \rho}{\partial t} &= (1-\rho)(2\rho - \rho^2) - \left[d_0\,(1-\rho)^2 + 2d_1\,(1-\rho)\,\rho + d_2\rho^2\right]\rho \\
\frac{\partial \rho_{\text{MF}}}{\partial t} &= 0 \qquad \Longrightarrow \quad \rho_{\text{MF}} \\
V_C^{\text{MF}} &= V_C^{\text{MF}}(\rho_{\text{MF}}) = V_C^{\text{MF}}(A, w, c/b) \\
A^C_{c\ \text{MF}} &= A^C_{c\ \text{MF}}(w, c/b) \qquad \left[V_C^{\text{MF}} = 0\right]
\end{aligned}$$

Mean field growth speed and density





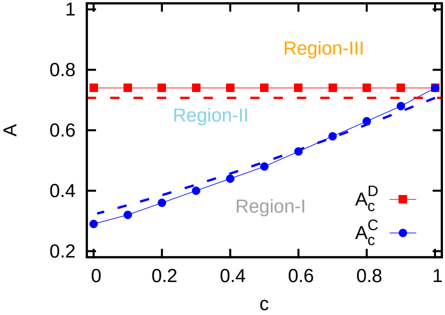
$$\frac{\partial \rho}{\partial t} = (1-\rho)(2\rho-\rho^2) - d\rho \implies \rho_s^{\mathrm{MF}} = \frac{3\sqrt{1+A}-\sqrt{5+A}}{2\sqrt{1+A}}$$

- **whole habitat**: (locally absorbing state) + (locally active state)
- **boundary**: locally active state

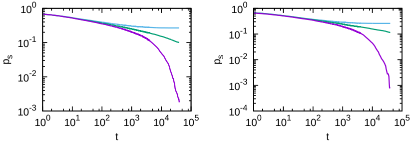
$$V_D^{MF} = 2\Big(1 - d\rho\,[1+2(1-\rho)+3(1-\rho)^2+\cdots]\Big)$$

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

$$d = \frac{1}{1 + A\exp(wp)}, \qquad w = 1, \qquad b = 1$$



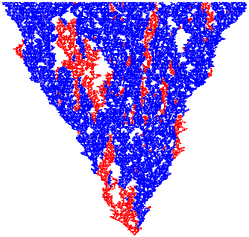
- **Region-I**: **Extinction**
- **Region-II**: **Only Cooperators**
- **Region-III**: **Both C and D**

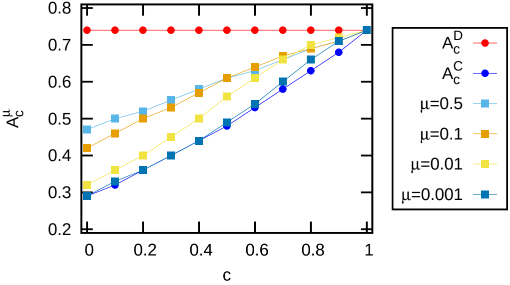


- **Mean-field**: $V^{\mathbf{MF}} = 0 \implies A_c^{\mathbf{MF}}$

Mutation

- **Steady state**: **independent of the seed type**
- **Small mutation limit** ($\mu \ll 1$): $A_c^\mu \to A_c^C$

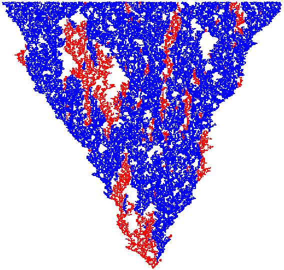


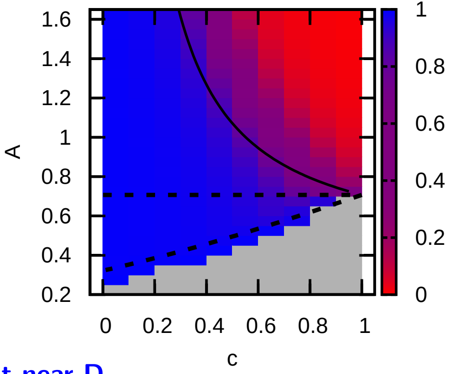


- $A_c^\mu < A < A_c^\nu$ ($\mu < \nu$): species with smaller mutation(μ) exist.
- **selection of copying-fidelity**

Cooperator frequency

$$x_c = \frac{N_C}{N_C + N_D}$$





- empty sites are abundant near D
- empty sites protect C from invasion of D

Concluding Remarks

Fitness: longevity (cf. fecundity)

- **Death rate**: $d = 1/\left[1 + A\exp(wp)\right]$
- **Moderately harsh environment** ($A_C < A < A_D$)
  only C can exist.
- **Mutation**: empty sites protect C from D even for $A_D < A$
- **Marginal state**: $A \gtrsim A_C$ due to human - environment interaction

Network reciprocity

- **conventional wisdom**
  - **assortments**: **interaction network $\neq$ competition network**
  - **cooperator's success** $\rightarrow$ **defectors follow the success**
- **our model**
  - **isolation** $\rightarrow$ **local group selection.**

Collaborators

- Hye Jin Park (SKKU)
- Beom Jun Kim (SKKU)
- Christian Hilbe (IST Austria)
- Martin Nowak (Harvard)