Probability of fixation

and evolution of cooperation

Sabin Lessard
Université de Montréal

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Thanks

Collaborators

Véronique Ladret
Philippe Lahaie
Samuel Langevin
David Lasalle-Ialongo
John Wakeley

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Competitors

Martin Nowak
François Rousset
and many others

1. Examples of cooperation

Cooperation is widespread...

but emergence of cooperation is problematic!

- A game-theoretic framework based on pairwise interactions is a first step toward a better understanding of a complex phenomenon.

- This framework can provide clues about conditions that would favor the evolution of cooperation.

2. Prisoner's Dilemma (PD)

Payoff Matrix

*C*ooperate	*R*eward	*S*ucker's payoff
*D*efect	*T*emptation	*P*unishment
against	*C*ooperate	*D*efect

$T > R > P > S$

C	5	1
D	14	3
against	*C*	*D*

Iterated Prisoner's Dilemma (IPD)

▶ PD repeated n times between the same players with additive payoffs

Tit-for-Tat (A)	$a = Rn$	$b = S + P(n-1)$
Always-Defect (B)	$c = T + P(n-1)$	$d = Pn$
against	A	B

$$a > c > d > b \text{ for } n > \frac{T-P}{R-P}$$

A	50	28
B	41	30
against	A	B

for $n = 10$ in the previous example

Expected payoffs in an infinite population

► random pairwise interactions

► $x :$ frequency of A

$$w_A(x) = ax + b(1-x)$$

$$w_B(x) = cx + d(1-x)$$

$$\boxed{w_A(x) > w_B(x) \text{ if and only if } x > \frac{d-b}{a-b-c+d} = x^* \downarrow 0 \text{ as } n \uparrow \infty}$$

3. Evolutionary dynamics in an infinite population

- reproduction with discrete, non-overlapping generations

- $s \geq 0$: intensity of selection with expected payoff as coefficient

- $x(t)$: frequency of A in offspring in generation t before selection

$$x(t+1) = \frac{x(t)(1 + s w_A(x(t)))}{1 + s \bar{w}(x(t))}$$

$$x(t+1) - x(t) = \frac{s(a - b - c + d)x(t)(1 - x(t))(x(t) - x^*)}{1 + s \bar{w}(x(t))}$$

$$\boxed{x(t) \uparrow 1 \text{ if } x(0) > x^* \text{ and } x(t) \downarrow 0 \text{ if } x(0) < x^*}$$

4. Probability of fixation in a finite population

- N parents chosen at random to produce the next generation (assumed large)

- $(v_1, ..., v_N)$: proportions of offspring produced in large numbers (assumed exchangeable)

- $X(t)$: frequency of A in offspring in generation t before selection

- $X(0) = N^{-1}$

$$X(T) \to X(\infty) = X(0) + \sum_{t \geq 0}(X(t+1) - X(t))$$

$X(\infty) = 1$ with probability $u(s)$, and 0 otherwise

- $u(s) = E_s[X(\infty)]$: probability of ultimate fixation of A

- $u(0) = X(0)$

$$
\begin{aligned}
u(s) &= X(0) + \sum_{t \geq 0} E_s[X(t+1) - X(t)] \\
&= u(0) + s(a - b - c + d) \sum_{t \geq 0} E_s\left[\frac{X(t)(1 - X(t))(X(t) - x^*)}{1 + s\bar{w}(X(t))}\right] \\
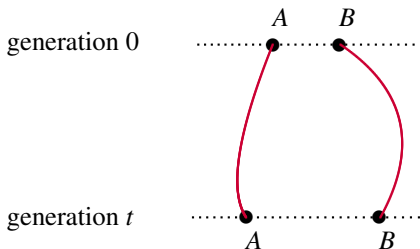&\approx u(0) + s(a - b - c + d) \sum_{t \geq 0} E_0[X(t)(1 - X(t))(X(t) - x^*)]
\end{aligned}
$$

$u(s) > u(0)$ for $s > 0$ small : weak selection favors A replacing B

$$
\boxed{x^* < \frac{\sum_{t \geq 0} E_0[X(t)^2(1 - X(t))]}{\sum_{t \geq 0} E_0[X(t)(1 - X(t))]} = \tilde{x}}
$$

5. Generalized one-third law

$$\sum_{t \geq 0} E_0[X(t)(1-X(t))] = \sum_{t \geq 0} P_0(A, B \text{ in generation } t)$$

$$= \sum_{t \geq 0} p_{22}(t) P_0(A, B \text{ in generation } 0)$$

$$= \frac{X(0)(1-X(0))}{1-p_{22}}$$

with $p_{22}(t) = p_{22}^t$ the probability that two offspring chosen at random in generation t descend from two distinct ancestors in generation 0

$$\sum_{t \geq 0} E_0[X(t)^2(1 - X(t))] = \sum_{t \geq 0} P_0(A, A, B \text{ in generation } t)$$

$$= \sum_{t \geq 0} p_{33}(t) P_0(A, A, B \text{ in generation } 0)$$

$$+ \sum_{t \geq 0} \frac{p_{32}(t)}{3} P_0(A, B \text{ in generation } 0)$$

with $p_{33}(t) = p_{33}^t$ the probability that three offspring chosen at random in generation t descend from three distinct ancestors in generation 0, and

$$p_{32}(t) = \sum_{r=0}^{t-1} p_{33}^{t-r-1} p_{32} p_{22}^r = p_{32} \left(\frac{p_{33}^t - p_{22}^t}{p_{33} - p_{22}} \right)$$

the probability that they descend from two distinct ancestors in generation 0.
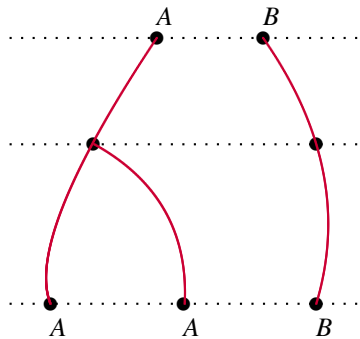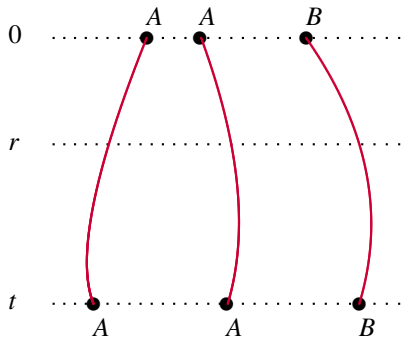
$$\sum_{t \geq 0} E_0[X(t)^2(1-X(t))] = \frac{X(0)^2(1-X(0))}{1-p_{33}} + \frac{p_{32}X(0)(1-X(0))}{3(1-p_{22})(1-p_{33})}$$

$$\approx \frac{p_{32}X(0)(1-X(0))}{3(1-p_{22})(1-p_{33})}$$

and therefore

$$\boxed{\tilde{x} \approx \frac{p_{32}}{3(1-p_{33})} \leq \frac{1}{3}}$$

with equality if and only if at most 2 lineages out of 3 coalesce at a time backward in time with probability 1, which characterizes the Kingman coalescent for a wide range of reproduction schemes as $N \to \infty$ with N generations as unit of time (Möhle 2000).

Λ-coalescent (e.g., Eldon and Wakeley 2006)

- $1 - N^{-\alpha}$: probability that every parent produces the same proportion N^{-1} of the offspring

- $N^{-\alpha}$: probability that a parent chosen at random produces a proportion ψ of offspring and every other parent a proportion $(1 - \psi)(N-1)^{-1}$

$$\tilde{x} \approx \frac{1-\psi}{3-2\psi} < \tfrac{1}{3} \text{ if } \alpha < 1$$

which means a more stringent condition for cooperation to be favored in the case of a highly skewed distribution for the contribution of parents in offspring.

6. Projected average allelic effect

For any number of types $A_1, ..., A_n$ and any coefficient of selection w_{ij} for A_i in interaction with A_j, the first order effect of selection on the probability of fixation of A_i is

$$u'_i(0) = X_i(0)a_i(0)$$

where $a_i(0)$ is a projected average allelic effect on the selection coefficient given by

$$
\begin{aligned}
a_i(0) &= E_0(S_3)\left[\sum_k w_{ik}X_k(0) - \sum_j\sum_k w_{jk}X_j(0)X_k(0)\right] \\
&+ \left(\frac{E_0(S_2) - E_0(S_3)}{2}\right)\left[w_{ii} - \sum_j w_{ji}X_j(0)\right] \\
&+ \left(\frac{E_0(S_2) - E_0(S_3)}{2}\right)\left[\sum_j w_{ij}X_j(0) - \sum_j w_{jj}X_j(0)\right]
\end{aligned}
$$

with $E_0(S_j)$ being the expected number of generations with j lineages.
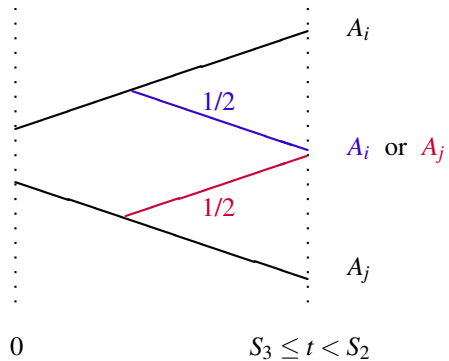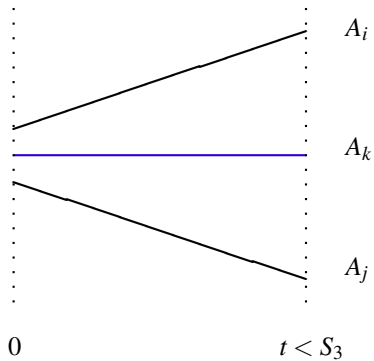
Symmetric case $w_{ij} = w_{ji}$

$$
\begin{aligned}
a_i(0) &= E_0(S_3)\left[\sum_k w_{ik}X_k(0) - \sum_j\sum_k w_{jk}X_j(0)X_k(0)\right] \\
&+ \left(\frac{E_0(S_2) - E_0(S_3)}{2}\right)\left[w_{ii} - \sum_j w_{jj}X_j(0)\right]
\end{aligned}
$$

with autozygous pairs having the same weight as allozygous pairs, leading to the one-third law of evolution, in the domain of application of the Kingman coalescent, and a lighter weight than allozygous pairs otherwise.

7. Effect of population structure

- D groups of N parents producing equal proportions of offspring (D assumed large)

- m : proportion of offspring that disperse uniformly before selection (Wright island model)

- $X_i(t)$: frequency of A in group i after dispersal in generation t

- $\overline{X(t)} = D^{-1} \sum_{i=1}^{D} X_i(t)$: frequency of A in the population in generation t

- $\overline{X(0)} = (ND)^{-1}$

- selection: within groups after dispersal

$$\tilde{x} \quad = \quad \frac{\sum_{t \geq 0} E_0 \left[\overline{X(t)^2(1 - X(t))} \right]}{\sum_{t \geq 0} E_0 \left[\overline{X(t)(1 - X(t))} \right]}$$

$$= \quad \frac{\sum_{t \geq 0} P_0(A, A, B \text{ in the same group in generation } t)}{\sum_{t \geq 0} P_0(A, B \text{ in the same group in generation } t)}$$

States for the ancestors of 3 offspring
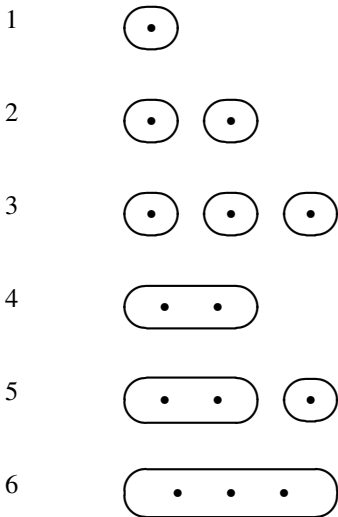
Transition matrix backward in time

Applying Möhle (1998) lemma

$$P^{\lfloor NDf_{22}^{-1}\tau \rfloor} \rightarrow \begin{pmatrix} I & 0 \\ F & 0 \end{pmatrix} \begin{pmatrix} e^{\tau A} & 0 \\ Be^{\tau A} & 0 \end{pmatrix}$$

as $D \rightarrow \infty$, where

$$F = \begin{pmatrix} f_{21} & f_{22} & 0 \\ 0 & f_{21} & f_{22} \\ f_{31} & f_{32} & f_{33} \end{pmatrix}$$

with f_{nk} the probability for n offspring in the same group to have k ancestors in different groups in the case of an infinite number of groups, and

$$A = \begin{pmatrix} 0 & 0 & 0 \\ 1 & -1 & 0 \\ 0 & 3 & -3 \end{pmatrix}$$

the infinitesimal generator for the Kingman coalescent.

Two-time-scale argument for large D

- ▶ Fast scattering of lineages in the same group; slow collecting of lineages in different groups.

- ▶ Times spent with lineages in the same group can be neglected compared to times spent with lineages in different groups.

- ▶ The expected time spent with 2 lineages in different groups in number of generations is approximately NDf_{22}^{-1}, the effective population size.

- ▶ Moreover, the probability for two ancestors chosen at random in different groups in generation 0 to be of type A can be neglected.
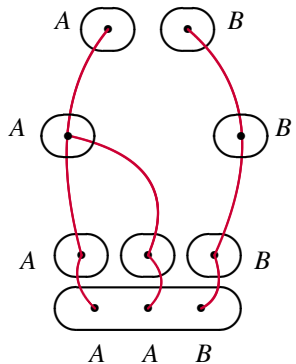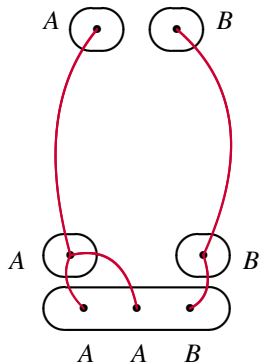
$$\sum_{t \geq 0} P_0(A, B \text{ in the same group in generation } t)$$

$$\approx \sum_{t \geq 0} P_{42}(t) P_0(A, B \text{ in different groups in generation } 0)$$

$$\approx f_{22} \times N D f_{22}^{-1} \times \overline{X(0)}(1 - \overline{X(0)})$$

state 2 in generation 0
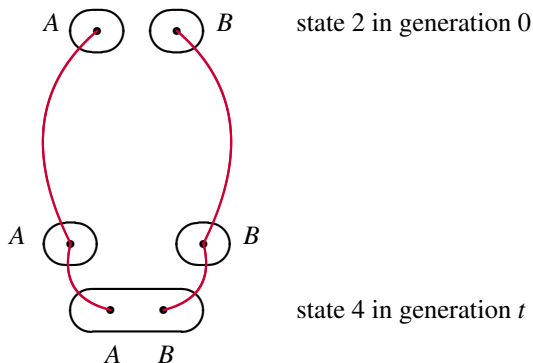
state 4 in generation t

$$\sum_{t \geq 0} P_0(A, A, B \text{ in the same group in generation } t)$$

$$\approx \frac{1}{3} \sum_{t \geq 0} P_{62}(t) P_0(A, B \text{ in different groups in generation } 0)$$

$$\approx \frac{1}{3} \times (f_{32} + f_{33}) \times ND f_{22}^{-1} \times \overline{X(0)}(1 - \overline{X(0)})$$

state 2 in generation 0

state 6 in generation t

$$\tilde{x} \approx \frac{1-f_{31}}{3(1-f_{21})} > \frac{1}{3}$$

with

$$
\begin{aligned}
f_{21} &= \frac{(1-m)^2}{Nm(2-m)+(1-m)^2} \\
f_{31} &= f_{21}\left[\frac{N(1-m)+2(N-1)(1-m)^3}{N^2m(3-3m+m^2)+(3N-2)(1-m)^3}\right]
\end{aligned}
$$

which means a less stringent condition for cooperation to be favored in the case of a group-structured population.

8. Variants and extensions

▶ Dispersal after selection:

$$
\begin{aligned}
u'(0) &= (b-d) \sum_{t \geq 0} E_0 \left[\overline{X(t)(1-X(t))} \right] \\
&+ (a-b-c+d) \sum_{t \geq 0} E_0 \left[\overline{X(t)^2(1-X(t))} \right] \\
&+ m(2-m)(b+c-2d) \sum_{t \geq 0} E_0 \left[\overline{X(t)^2} - \overline{X(t)}^2 \right] \\
&+ m(2-m)(a-b-c+d) \sum_{t \geq 0} E_0 \left[\overline{X(t)^3} - \overline{X(t)} \; \overline{X(t)^2} \right]
\end{aligned}
$$

$$E_0\left[\overline{X(t)^2} - \overline{X(t)}^2\right] \approx P_0(A, B \text{ in different groups})$$
$$- P_0(A, B \text{ in the same group})$$
$$E_0\left[\overline{X(t)^3} - \overline{X(t)}\ \overline{X(t)^2}\right] \approx P_0(A, A, B \text{ with } B \text{ in a different group})$$
$$- P_0(A, A, B \text{ in the same group})$$

$$\boxed{\tilde{x} \approx \frac{(1-f_{31})(1-m)^2}{3(1-f_{21})} + \frac{2m(2-m)}{3} + \frac{(a-d)(N-1)^{-1}}{(a-b-c+d)} > \frac{1-f_{31}}{3(1-f_{21})}}$$

which means an even less stringent condition for cooperation to be favored.

- Dispersal before selection with exchangeable contributions of groups: $D^{-\beta}$ the probability that a group at random provides a fraction ϕ of the migrants and every other a fraction $(1-\phi)(D-1)^{-1}$ in the case $\beta < 1$

$$
\begin{aligned}
u'(0) &\approx \left[(b-d)f_{22} + \left(\frac{a-b-c+d}{3}\right)\left(f_{32} + f_{33}\frac{\mu_{32}}{\mu_{32}+\mu_{33}}\right)\right] \\
&\times \mu_{21}^{-1}ND^{\beta} \times \overline{X(0)}(1-\overline{X(0)})
\end{aligned}
$$

where μ_{lk} is the rate of transition from l to k lineages in different groups backwards in time with ND^{β} generations as unit of time as $D \to \infty$

$$
\boxed{\tilde{x} \approx \frac{1-f_{31}-f_{33}\frac{\mu_{33}}{\mu_{32}+\mu_{33}}}{3(1-f_{21})} < \frac{1-f_{31}}{3(1-f_{21})}}
$$

which means a more stringent condition for cooperation to be favored.

Rates of transition for lineages in different groups

$$\mu_{lk} = \sum_{l \geq j \geq n \geq k} \lambda_{lj} p_{jn} f_{nk}$$

where

$$\lambda_{lj} = \binom{l}{j} (\phi m)^j (1 - \phi m)^l$$

$$p_{jn} = \frac{N^{[n]} S_j^{(n)}}{N^j}$$

with

$$N^{[n]} = N(N-1)...(N-n+1)$$

$$S_j^{(n)} = \frac{1}{n!} \sum_{\substack{j_1, ..., j_n \geq 1 \\ j_1 + ... + j_n = j}} \binom{j}{j_1, ..., j_n}$$

f_{nk} is the probability of *k* types among *n* genes in an exact Wright-Fisher model with probability of mutation to a novel type *m* per gene per generation

$$f_{nk} = \sum_{j=0}^{k} \sum_{l=k-j}^{(n-1)\wedge(n-j)} \binom{n}{j} \frac{(Nm)^j (1-m)^{n-j} N^{[l]} S_{n-j}^{(l)}}{N^n - (1-m)^n N^{[n]}} f_{l,k-j}$$

where $|S_n^k| =$ coefficient of x^k in $x(x+1)...(x+n-1)$, in agreement with the approximation from the Ewens sampling formula for *m* small and *N* large

$$f_{nk} \approx \frac{M^k |S_n^k|}{M(M+1)...(M+n-1)}$$

where $M = 2Nm$.

Remark. The recursion equation can be extended to the Cannings model.

9. Summary and comments

- IPD in an infinite population can explain the spread of cooperation but only from a frequency $x > x^*$.

- IPD in a finite population can explain that cooperation is favored to go to fixation from a low frequency under the condition $x^* < \tilde{x}$.

- In a large population, $\tilde{x} \leq 1/3$ with a strict inequality leading to a more stringent condition if the contribution of parents in offspring is highly skewed.

- In a group-structured population with a large number of groups, the condition is less stringent with $\tilde{x} > 1/3$ unless the contribution of groups in offspring is skewed enough.

- The first-order effect of selection on the probability of fixation of an allele is given by the projected average allelic effect on the selection coefficient.

- This effect can be obtained under more complex population assumptions: interactions between any number of individuals, diploid populations with sex differences and overlapping generations, different timings for selection, mating and dispersal or local extinction in group-structured populations, etc.

- The effect of selection of any order on the probability of fixation in a multiallele multilocus setting can be obtained in a similar way in terms of expected sojourn times.

- ▶ The approximations given by the first-order effect of selection are valid under very weak selection, actually as long as the intensity of selection is small compared to the intensity of the other evolutionary forces, but without constraints on the reproduction scheme.

- ▶ An alternative approach under the assumption that the intensity of selection is of the same order of magnitude as the other evolutionary forces is a diffusion approximation, but then the contributions of parents and groups in offspring cannot be too highly skewed.

References

- Lasalle-Ialongo D., M.Sc. Thesis, Université de Montréal 2008

- Ladret V., Lessard S., *Theor. Pop. Biol.* 2007

- Lessard S., *Proc. Roy. Soc. B* 2007

- Lessard S., *Genetics* 2007

- Lessard S., *J. Math. Biol.* 2009

- Lessard S., Ladret V., *J. Math. Biol.* 2007

- Lessard S., Lahaie P., *Theor. Pop. Biol.* 2009

Diffusion approximation for the Wright island model

- ▸ $s = \sigma(ND)^{-1}$ and dispersal before selection

- ▸ ND generations as unit of time as $D \to \infty$

Applying Ethier and Nagylaki (1980) conditions, the infinitesimal mean and variance of the limiting diffusion are

$$
\begin{aligned}
m(x) &= \sigma(a-b-c+d)x(1-x)(xf_{33} - x^*f_{22} + f_{21} - f_{31}) \\
v(x) &= x(1-x)f_{22}
\end{aligned}
$$

and the probability of fixation of A from a small initial frequency x_0 is

$$
\int_0^{x_0} \exp\left\{-2\int_0^y \frac{m(x)}{v(x)}dx\right\} dy \approx x_0 + \sigma(a-b-c+d)x_0(1-x_0)f_{22}\left(\frac{1-f_{31}}{3f_{22}} - x^*\right)
$$

Recursion equation for the Cannings model

$$f_{n,k} = \sum_{j=0}^{k} \sum_{l=k-j}^{(n-1)\wedge(n-j)} \sum_{\mathbf{r}} \frac{n! N^{[l]} m^j (1-m)^{n-j} E\left(\prod_{i=1}^{l} \nu_i^{[r_i]}\right)}{j! l! \left(\prod_{i=1}^{l} r_i!\right) N^{[n-j]} \left[1 - (1-m)^n E\left(\prod_{i=1}^{n} \nu_i\right)\right]} f_{l,k-j}$$

where $\mathbf{r} = (r_1, ..., r_l)$ satisfy $r_1, ..., r_l \geq 1$ with $r_1 + ... + r_l = n - j$.