Some directions of research

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First-order effect of selection on fixation probability based on the neutral ancestral process

- Not limited to the Prisoner's Dilemma or its iterated version: the approach does not depend on special relationships between the payoffs a, b, c and d when the fitnesses of A and B are given in the form

$$\begin{aligned} f_A(x) &= 1 + s w_A(x) \\ f_B(x) &= 1 + s w_B(x) \end{aligned}$$

where $w_A(x) = ax + b(1-x)$ and $w_B(x) = cx + d(1-x)$.

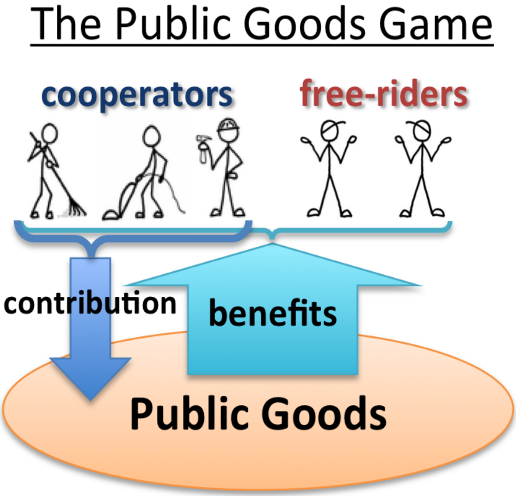
- Not even limited to matrix games: the approach can be extended to more general cases of frequency-dependence with

$$w_A(x) - w_B(x) = \sum_{k=0}^{N-1} c_k x^k$$

Then weak selection favors A replacing B if

$$\sum_{k=0}^{N-1} c_k \sum_{t\geq 0} E_0[X(t)^{k+1}(1-X(t))] > 0$$

It suffices to consider up to $N+1$ lineages backwards in time. This can be used to get an approximation in the case where the difference $w_A(x) - w_B(x)$ is a continuous function of x. (L. & Ladret *JMB* 2007)


The Public Goods Game
cooperators
free-riders
contribution
benefits
Public Goods

- Applicable to Public Goods games:

A	$a_{k-1} = \frac{kcr}{N} - c$
B	$b_k = \frac{kcr}{N}$

Payoffs in a group of k cooperators among N players

- N-person Snowdrift games:

	$k < M$	$k \geq M$
A	$a_{k-1} = -\frac{c}{M}$	$a_{k-1} = b - \frac{c}{k}$
B	$b_k = 0$	$b_k = b$

Payoffs in a group of k cooperators among N players

- N-person Stag Hunt games:

	$k < M$	$k \geq M$
A	$a_{k-1} = -c$	$a_{k-1} = \frac{kcr}{N} - c$
B	$b_k = 0$	$b_k = \frac{kcr}{N}$

Payoffs in a group of k cooperators among N players

or their iterated versions, with payoffs to A and B in the form

$$w_A(x) = \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} a_k$$

$$w_B(x) = \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} b_k$$

Then weak selection favors a rare A replacing B in the domain of the Kingman coalescent in the limit of a large population size if

$$\sum_{k=0}^{N-1} (N-k)(a_k - b_k) > 0$$

(Gokhale & Traulsen *PNAS* 2010, L. *DGAA* 2011).

The corresponding condition outside this domain is unknown!

- Consistent with diffusion approximations but in the same domain: with the intensity of selection s of the same order of magnitude as the inverse of the population size and time scaled so that the rate of coalescence of two lineages is 1, the probability of fixation of A is

$$\int_0^{x_0} \exp\left\{-2\int_0^y \frac{m(x)}{v(x)}dx\right\}dy$$

with

$$\frac{m(x)}{v(x)} \propto w_A(x) - w_B(x)$$

where $m(x)$ and $v(x)$ are the infinitesimal mean and variance, respectively, and x_0 is the initial frequency. This can be extended to group-structured populations (L. *JMB* 2009).

The corresponding formula for jump processes outside this domain is unknown!

- Not limited to two strategies with one being a rare mutant strategy: in the case of n strategies with the fitness of A_i given in the form

$$f_{A_i}(\mathbf{x}) \quad = \quad 1 + s(A\mathbf{x})_i$$

for some payoff matrix $A = [a_{ij}]_{i,j=1}^{n}$, where $\mathbf{x} = (x_1, \ldots, x_n)$ is the strategy frequency vector in the population, the probability of fixation of A_i depends on the initial strategy frequency vector $\mathbf{x}(0)$.

Weak selection favors A_i to go to fixation if

$$\left(\frac{E(S_2)-E(S_3)}{2}\right)\left[a_{ii}-\sum_{j=1}^{n}a_{ji}x_j(0)+\sum_{j=1}^{n}a_{ij}x_j(0)-\sum_{j=1}^{n}a_{jj}x_j(0)\right]$$
$$+E(S_3)\left[\sum_{k=1}^{n}a_{ik}x_k(0)-\sum_{j=1}^{n}\sum_{k=1}^{n}a_{jk}x_j(0)x_k(0)\right]>0$$

where S_2 and S_3 are backward times with 2 and 3 lineages, respectively.
(L. & Lahaie *TPB* 2009)

Related to the effect of selection on average abundance of A_i in the stationary distribution in the limit of weak selection and low mutation, which is greater than $1/n$ if

$$a_{ii} - \sum_{j=1}^{n} a_{ji} + \sum_{j=1}^{n} a_{ij} - \sum_{j=1}^{n} a_{jj} > 0$$

(Antal et al. *JTB* 2009a) In the case of two strategies, A_1 and A_2, this gives

$$a_{11} + a_{12} > a_{21} + a_{22}$$

which is also the condition for the probability of fixation of a rare A_1 to exceeds the probability of fixation of a rare A_2. This is the condition for risk dominance in the case of two strategies that are the best replies to themselves, that is, $a_{11} > a_{21}$ and $a_{22} > a_{12}$.

The corresponding conditions for non-linear payoffs are unknown!

- Allows for interactions among adults: a matrix game among N adults in a well-mixed population with payoff matrix A is equivalent to a matrix game among an infinite number of offspring in a well-mixed population with payoff matrix

$$A^\circ = A - \left(\frac{A + A^T}{N}\right)$$

(L. *TPB* 2005, Hilbe *BMB* 2011)

This is an effect of competition between an individual and itself!

- Revealed by the effective game matrix: a matrix game in a group-structured population with uniform dispersal of a fraction of offspring, or probability of local extinction and uniform recolonization, and payoff matrix $A = [a_{ij}]_{i,j=1}^{n}$ within groups is equivalent to a matrix game among offspring in a well-mixed population with effective payoff matrix $A^{\circ} = [a_{ij}^{\circ}]_{i,j=1}^{n}$ given by

$$a_{ij}^{\circ} = a_{ii}\phi_{IJ} + a_{ij}\phi_{I/J} - a_{ii}\phi_{I_cIJ} - a_{ij}\phi_{I_cI/J} - a_{ji}\phi_{J_cI/J}$$

for some coefficients of relatedness involving up to three offspring in the same group. (L. *DGAA* 2011)

I_c $\qquad\qquad$ J_c

competing with $\qquad\qquad$ competing with

I of type A_i interacting with J of type A_j

$$
\begin{aligned}
a_{ii}\phi_{IJ} &= a_{ii}P(I \equiv J) \\
+a_{ij}\phi_{I/J} & \quad +a_{ij}P(I \not\equiv J) \\
-a_{ii}\phi_{I_cIJ} & \quad -a_{ii}P(I_c \equiv I \equiv J) \\
-a_{ij}\phi_{I_cI/J} & \quad -a_{ij}P(I_c \equiv I \not\equiv J) \\
-a_{ji}\phi_{J_cI/J} & \quad -a_{ji}P(J_c \equiv I \not\equiv J)
\end{aligned}
$$

with $\equiv$ for identity-by-descent in a population with infinite groups.

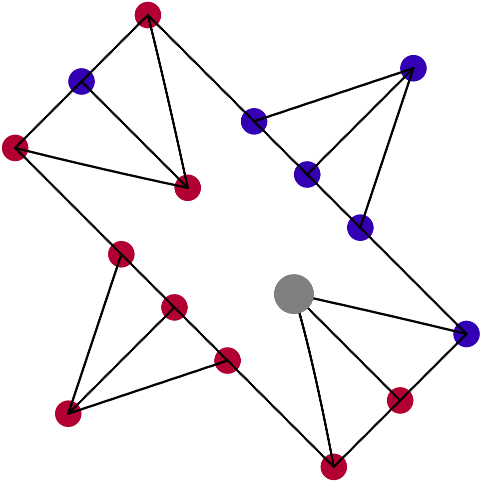
In the additive case $a_{ij} = -c_i + b_j$, the marginal effective payoff to A_i is equivalent to a personal inclusive payoff

$$a_i^{\circ\circ} = -c_i(1 - \phi_{I_cI}) + b_i(\phi_{IJ} - \phi_{I_cIJ} - \phi_{J_cI/J})$$

whose mean in the population increases over time.

In general, the marginal effective payoff corresponds to a personal inclusive payoff which is frequency-dependent, so that the mean inclusive payoff does not generally increase!

- To be further studied on graph structures: regular graph of degree $k = 3$



With death-birth updating, the entries of the effective payoff matrix are

$$a_{ij}^{\circ} = a_{ij} + \frac{(k+1)a_{ii} + a_{ij} - a_{ji} - (k+1)a_{jj}}{(k+1)(k-2)}$$

Moreover, in a large population in the limit of weak selection and low strategy mutation, A_1 is more abundant on average than A_2 if

$$\sigma a_{11} + a_{12} > \sigma a_{22} + a_{21}$$

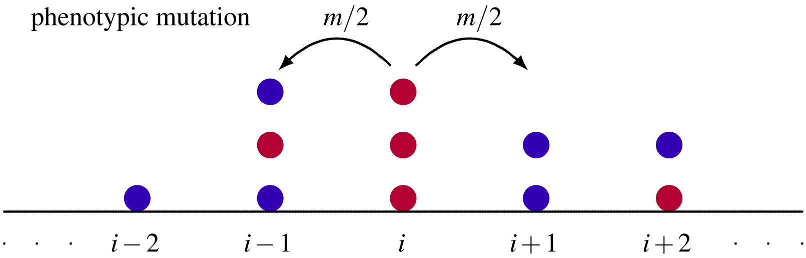
where

$$\sigma = \frac{k+1}{k-1} > 1$$

is increasing as k decreases (Ohtsuki & Nowak *JTB* 2006), which favors A_1 against A_2 if $a_{11} > a_{22}$.

The interpretation in terms of coefficients of relatedness remains to be made!

- In phenotype spaces:



With updating according to a Wright-Fisher process in a large population in the limit of weak selection and low strategy mutation, A_1 is more abundant on average than A_2 if

$$\sigma a_{11} + a_{12} > \sigma a_{22} + a_{21}$$

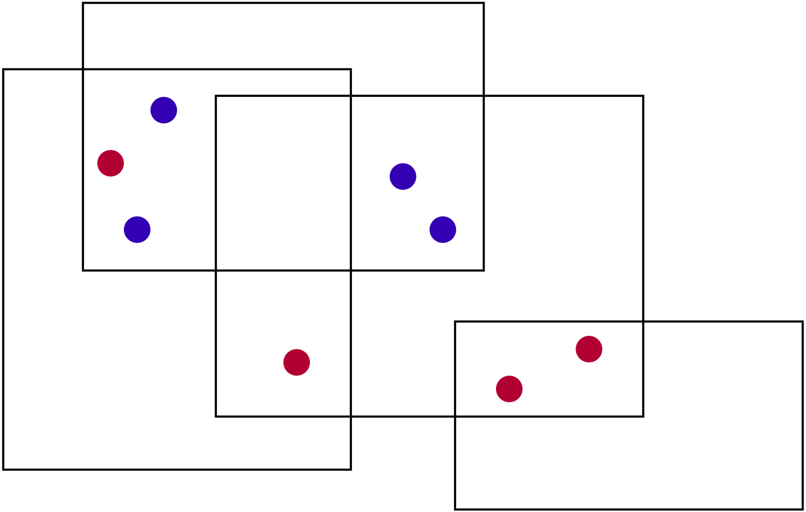
where

$$\sigma = \frac{1+4Nm}{2+4Nm}\left(1+\sqrt{\frac{3+12Nm}{3+4Nm}}\right) > 1$$

is increasing as Nm increases (Antal et al. *PNAS* 2009b), which favors which favors A_1 against A_2 if $a_{11} > a_{22}$.

The effective payoff matrix and its interpretation remain to be given!

- In collections of sets: membership mutation m among all $2 = 4r$ sets



With updating according to a Wright-Fisher process in a large population in the limit of weak selection and low strategy mutation, A_1 is more abundant on average than A_2 if

$$\sigma a_{11} + a_{12} > \sigma a_{22} + a_{21}$$

where

$$\sigma = \frac{3 + 4Nm + 4rNm(1 + Nm)}{1 + 4rNm(1 + Nm)} \frac{1 + 2Nm}{3 + 2Nm}$$

is maximum when $Nm \approx 1/(2\sqrt{r})$ (Tarnita et al. *PNAS* 2009), which favors A_1 against A_2 if $a_{11} > a_{22}$.

Other group structures remain to be studied!

In summary, there is need to go beyond:

- pairwise interactions
- two strategies at a time
- simple updating procedures
- well-mixed populations

and place for:

- robust qualitative results
- general conditions for the evolution of cooperation

Good luck!