Emergence of cooperative behaviors.

fixation probability & chances of success of a mutant.

Bahram Houchmandzadeh

Laboratoire Interdisciplinaire de Physique, CNRS & Grenoble Universités.

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Outlines.

- The Fisher-Wright & Moran model, Genetic Drift and fixation probabilities.

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- The "*paradox*" of altruism and cooperative behaviors and current models.

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- The Fisher-Wright & Moran model, Genetic Drift and fixation probabilities.
- The "*paradox*" of altruism and cooperative behaviors and current models.
- An alternative model of "common good" production.

What is Evolution ?

We cannot run faster than him!

What is Evolution ?

I don't want to run faster than him; I want to run faster than *YOU* !

The deterministic formulation.

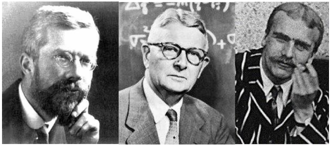
How a beneficial mutation does spread ?

Deterministic (mean field) answer :
If p is the proportion of mutants with relative excess fitness s , then

$$dp/dt = sp(1-p)$$

Corrolary (Adaptationism) : Every aspect of life we see around is beneficial in some way, we have only to discover how!

The New Synthesis.

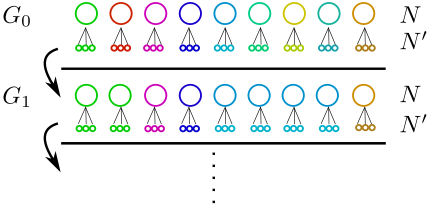


How a beneficial mutation does spread ?

Stochastic answer :
Evolutionary dynamics is a competition between deterministic selection pressure and stochastic events due to random sampling from one generation to the other.
An advantageous mutation has only a better *probability* of spreading to the whole population. The quantity that captures this interplay is *the fixation probability*.

The Fisher-Wright Model.

- The habitat sustains N individuals.
- Each Individual produces many progeny.
- N individuals are selected at random among the offspring to form the new generation.



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- Each Individual produces many progeny.
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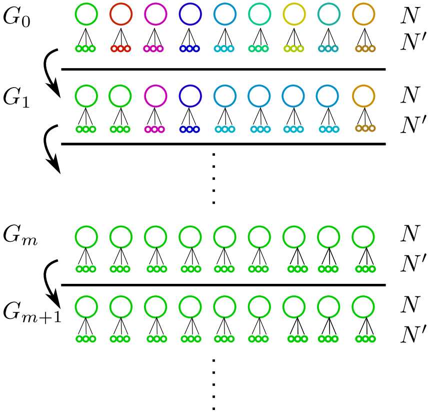
- After M generations , all individuals are from the same ancestor and an allele has been fixed.



Fixation probability of FW.

In the two alleles model (A and B), with s being the relative fitness of A, let $\pi_A(n)$ be the probability of fixation of A, beginning with n individuals at G_0. $\pi(n)$ can be computed from the diffusion approximation (Kimura 1962)

$$\pi_A(n) = \frac{1 - e^{-ns}}{1 - e^{-Ns}}$$

In particular, for $Ns \ll 1$

$$\begin{aligned} \pi_A(1) &\approx \frac{1}{N} + \frac{s}{2} \\ \pi_B(1) &= 1 - \pi_A(N-1) \approx \frac{1}{N} - \frac{s}{2} \end{aligned}$$

The Moran Model.

- Continuous time model.
- Death events occur at rate μ.
- When an individual dies, it is immediately replaced by the progeny of another one.

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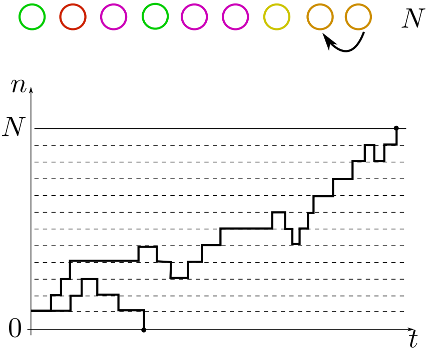

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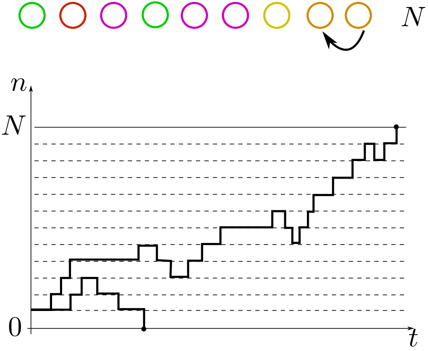
- The number of say, green individuals at time t is a random variable $n(t)$.
- **The carrying capacity N is fixed.**



The Master Equation.

Probability density that A individuals decrease their number from n to $n-1$:

$$W^{-}(n)=\mu n\frac{N-n}{N}$$

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Let $P(n,t)$ be the probability of observing n A-individual at time t. Then

$$\begin{aligned} \frac{\partial P(n,t)}{\partial t} &= W^{+}(n-1)P(n-1) - W^{+}(n)P(n) \\ &+ W^{-}(n+1)P(n+1) - W^{-}(n)P(n) \end{aligned}$$

Mean field approximation.

Let $\langle n\rangle$ be the (ensemble) mean of number of A individuals :

$$\begin{aligned}\frac{d}{dt}\langle n\rangle &= \left\langle W^{+}(n) - W^{-}(n)\right\rangle \\ &= \frac{\mu s}{N}\langle n(N-n)\rangle\end{aligned}$$

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Mean field approximation :

$$\left\langle n^2 \right\rangle = \langle n \rangle^2$$

Let $p = \langle n \rangle / N$ the proportion of A mutants. Then

$$\dot{p} = \mu s p(1-p)$$

Fixation probability of Moran.

Fixation probability π_k: The probability for a given genotype, present at time 0 at k copies, to invade the community and reach N copies.

fixation probabilities can be extracted from the M.E. through a linear system of equation (Backward Kolmogorov):

$$\begin{aligned}-W^-(k)\pi_{k-1} + \big(W^-(k) + (W^+(k)\big)\,\pi_k - W^+(k)\pi_{k+1} &= 0 \\ \pi_0 = 0\ ;\ \pi_N = 1\end{aligned}$$

Fixation probability.

In this simplest case, fixation probabilities can be solved exactly. Set $r = (1 + s)$:

$$\pi_A(n) = \frac{1 - r^{-n}}{1 - r^{-N}}$$

And for $n = 1$, $Ns \ll 1$,

$$\pi_1 \approx \frac{1}{N} + \frac{s}{2}$$

s is the drift term and $1/N$ is the noise term.

Is Altruism compatible with Evolution ?

I don't want to run faster than him; I want to run faster than *YOU* !

Is Altruism compatible with Evolution ?

OK, I'll try to divert him.
And you'll see, my genes can
spread better than yours!

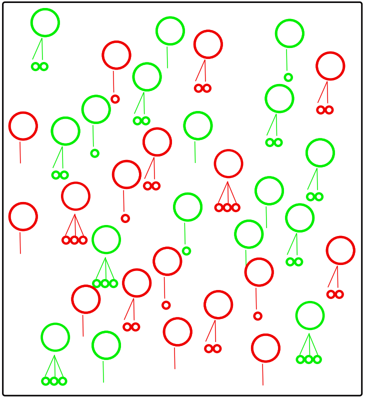
How to define altruism ?

An altruistic individual produces a *common good* which benefits everybody in the community at his own cost :

- The *fitness* of everybody is increased because of the availability of the common good.
- The fitness of the altruistic individual is decreased.

How to define fitness ?

The only measurable fitness is the **average number of progeny** passed into the next generation.



⟨🔴⟩ $= 0.98$

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Examples of altruism/cooperation in microbial world.

Dictoystelium Discoïdum : When the solitary amoebae aggregate, some cells will “die” in order to let others survive.

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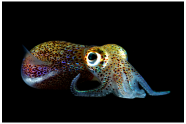

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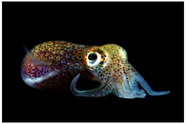
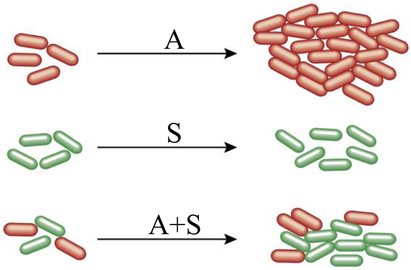


Pseudomonas aeruginosa : Siderophore production for iron uptake ; Quorum sensing for coordinated pathogenic infection.

Problem with altruism.

Altruism is unstable against *cheaters*!

Selection operates at level of individuals : If a cheater individual benefits from the common good, but does not produce any, then this mutant fitness is bigger than the Altruistic ones.



M.Nowak, Nature 2006.

Problem with altruism.

A non-cooperator mutant has a higher fitness. If the cost to altruist is s, then in average, altruists decrease their proportions (mean field) as

$$\dot{p} = -sp(1-p)$$

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Conclusion: Altruism does not exist. Altruistic behaviors have hidden benefits. If these benefits are taken into account, the fitness of an altruist is higher than those of a selfish.

Altruism: kin selection/inclusive fitness.

Hamilton(~1960): Altruism can exist *if* help is restricted to kins (kin selection, nepotism) and

$$c/b < r$$

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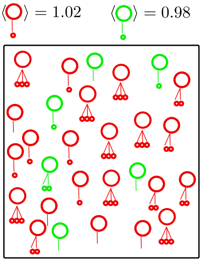
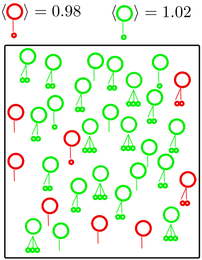
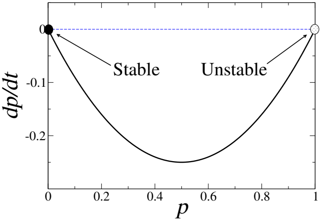
The effective cost is "**frequency dependent**" : if there are enough kin around, then the effective fitness (inclusive fitness) can be higher than one.





kin selection : frequency dependence.



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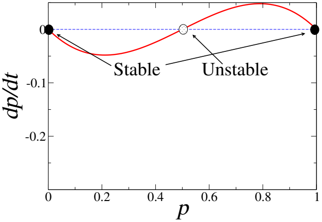

$$\dot{p} = f(p)p(1-p)$$

Kin Selection : Stochastic dynamics.

Probability density that A individuals decrease their number from n to $n-1$ (cost $c>1$):

$$W^{-}(n) = cn\frac{N-n}{N}$$

Probability density that A individuals increase their number from n to $n+1$:

$$W^{+}(n) = (N-n)\frac{n}{N}f(n)$$

Fixation probability of altruists can become

$$\pi > 1/N$$

Problems with kin selection.

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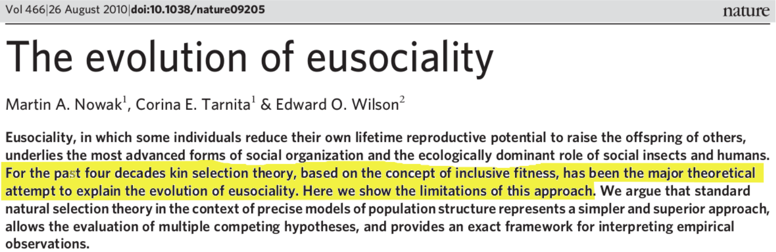

Vol 466|26 August 2010|**doi:10.1038/nature09205** nature

The evolution of eusociality

Martin A. Nowak[1], Corina E. Tarnita[1] & Edward O. Wilson[2]

Eusociality, in which some individuals reduce their own lifetime reproductive potential to raise the offspring of others, underlies the most advanced forms of social organization and the ecologically dominant role of social insects and humans. For the past four decades kin selection theory, based on the concept of inclusive fitness, has been the major theoretical attempt to explain the evolution of eusociality. Here we show the limitations of this approach. We argue that standard natural selection theory in the context of precise models of population structure represents a simpler and superior approach, allows the evaluation of multiple competing hypotheses, and provides an exact framework for interpreting empirical observations.

Group Selection theory.

- Dobzhanski/Mayr (1940-1960): a cost at the individual level can benefit the population as a whole. Altruistic behavior can be selected if *populations* are competing.
- G.C Williams (1965-2000): Selection is at the individual levels. Group selection does not exist (G.S. excommunicated).
- Lewontin,Price, Maynard-Smith(1975-present): Group selection may exist (multilevel selection).

The Price Equation.

$$\Delta \langle p \rangle = \mathsf{Cov}(f, p) + \langle f \, \delta p \rangle$$

Even if $\langle f \, \delta p \rangle < 0$ (the proportion in each group decrease), if $\mathrm{Cov}(f, p) > 0$, then the total proportion of altruist in the population can increase.

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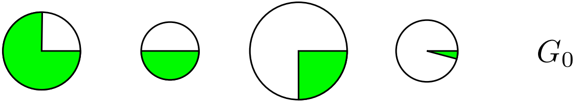

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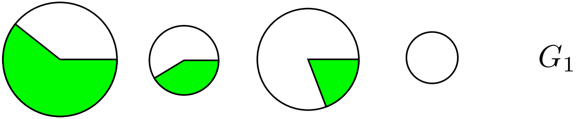

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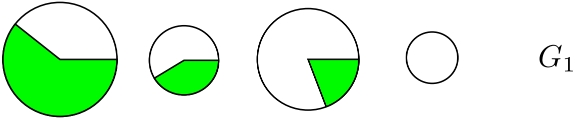


Simpson's Paradox in a Synthetic Microbial System, John S. Chuang, Olivier Rivoire, Stanislas Leibler, Science, 323:272 (2009).

Problems with group selection.

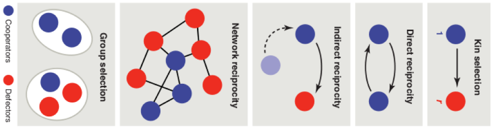
- Need mixing step (Haystack model).
- How did group emerged ?
- Cheaters are never eliminated, but reach an equilibrium.
- Other models can be written, by most of them involve putting multilevel selection by hand.

Summary.

Five Rules for the Evolution of Cooperation

Martin A. Nowak

8 DECEMBER 2006 VOL 314 SCIENCE www.sciencemag.org



- In all these model, the deterministic (mean field) equation possess multiple stable point.
- One stable points corresponds to the dominance of altruists.

Can altruism be much simpler ?
(Can it be good to be just good ?)

Altruism has emerged and is widespread in microbial word. Its emergence should be explained in a simple framework which:

- Keep the simplicity of the original FW model and include very few key ingredient.
- DOES NOT involve a recognition mechanism.
- DOES NOT involve group (multilevel) selection.
- Conform to selection at the level of individuals.

Noise Driven Evolution.

FW: Evolutionary dynamics is stochastic.

Fluctuations can fix a deleterious mutations :

$$\pi_A(1) \neq 0$$

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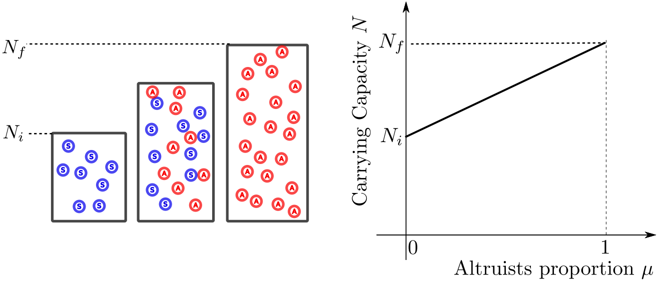
Key Ingredient: Relax the constraint of fixed size habitat.

Stochastic dynamic of Variable size populations.

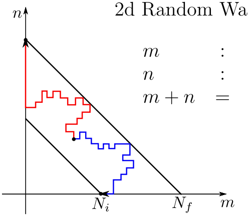
Key Ingredient: Production of Common Good increases the carrying capacity of the habitat.

Moran Model with variable size population: The number of individuals living on a patch (carrying capacity N) increases with the number of Altruists.



Generalized Moran Model.

- Stochastic process : $N \to N \pm 1$, $N_i < N < N_f$.
- The probability $N \to N + 1$ depends on the number of A.
- An A individual has fitness $-s$, a S one fitness $+s$: When population increases, the new individual has a larger chance ($\propto s$) of being S.
- Analog process for $N \to N - 1$.

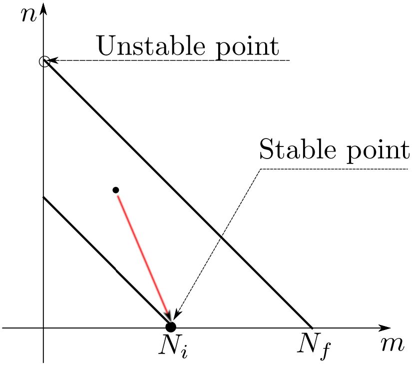


2d Random Walk

m : number of selfish
n : number of altruists
$m + n = N$

Deterministic (mean field) approach.

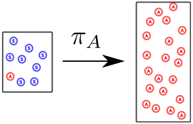
As altruists have constant, negative fitness, a mean field approximation of the above idea leads to their eventual extinction.



Stochastic approach : "Back of the envelop" estimation.

The relevant quantity if the fixation probability π.

$$\pi_A = \frac{1}{N_i} - \frac{s}{2}$$



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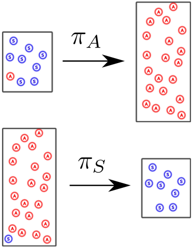

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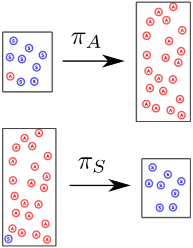

$$\pi_A > \pi_S \quad \text{if} \quad s < \frac{1}{N_i} - \frac{1}{N_f}$$

$$\bar{N}s < \frac{\Delta N}{\bar{N}}$$

Why ?

Pure stochastic effect :

In order to win, a mutant has to overcome the Genetic Drift.
By making the population larger, Altruists increase the random noise which the Selfish have to fight.

Transition rates.

2d Moran model for (n, m). n : number of Altruists ; m: number of Selfish.

- Uncoupling $n \to n \pm 1$ and $m \to m \mp 1$
- Keeping $N = n + m \in [N_i, N_f]$
- $N \to N + 1$ favored by n ; $N \to N - 1$ favored by m
- Cost of altruism $c > 1$.

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- Cost of altruism $c > 1$.

$$\begin{aligned}
W(n, m \to n, m+1) &= (N_f - (n+m))\,(\alpha n)m \\
W(n, m \to n+1, m) &= (N_f - (n+m))\,(\alpha n)n \\
W(n, m \to n, m-1) &= (m + n - N_i)\,(\alpha m)m \\
W(n, m \to n-1, m) &= c\,(m + n - N_i)\,(\alpha m)n
\end{aligned}$$

Fixation probabilities.

$\pi(\mathbf{k})$ the probability of fixation of altruists, beginning with $\mathbf{k} = (m_0, n_0)$ individual :

$$\sum_{\mathbf{q}} (\pi(\mathbf{k}) - \pi(\mathbf{q}))\, W(\mathbf{k} \to \mathbf{q}) \;=\; 0$$

$$\pi(\mathbf{k_0}) = 0 \;\; ; \;\; \pi(\mathbf{k}_1) = 1$$

Mean field approximation.

Setting the proportion μ and relative number of individuals η

$$\begin{aligned}\mu &= \frac{n}{m+n} \\ \eta &= (m+n)/N_f\end{aligned}$$

the mean field equation for the proportion reads

$$\frac{1}{N_f^2\alpha}\frac{d\mu}{dt} = -(c-1)\eta(\eta - \frac{N_i}{N_f})\mu(1-\mu)^2 < 0$$

Stochastic computations: diffusion approximation for π.

Setting $x = m/N_f$, $y = n/N_f$, $k = N_i/N_f$, and denoting $\pi(x,y)$ the fixation probability for the initial composition (x,y), the diffusion equation reads :

$$\begin{aligned} F\left(x\partial_x\pi + y\partial_y\pi\right) &+ \\ (1/2N_f)G\left(x\partial^2_{xx}\pi + y\partial^2_{yy}\pi\right) &+ \\ (c-1)H\left(-\partial_y\pi + (1/2N_f)\partial^2_{yy}\pi\right) &= 0 \end{aligned}$$

where

$$\begin{aligned} F &= y + kx - (x+y)^2 \\ G &= y - kx + (x^2 - y^2) \\ H &= xy(x+y-k) \end{aligned}$$

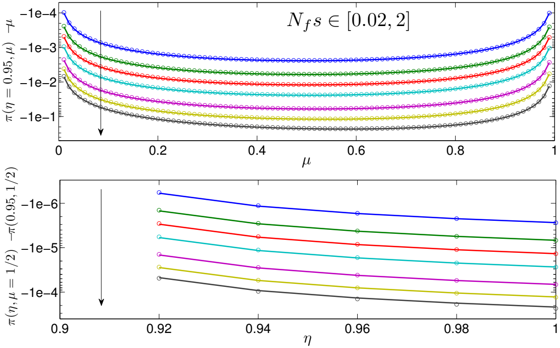
Fixation probability solution.

$$\mu = y/(x+y)\ ,\ \eta = x+y,\ s = c-1$$

$$\pi(\mu,\eta) = \frac{e^{N_f s \mu g(\eta)} - 1}{e^{N_f s g(\eta)} - 1}$$

where

$$g(\eta) = \gamma(1 - 1/\eta N_f)$$



Fixation probability for one mutant.

$$\begin{aligned}\pi_A &= \pi(m = N_i - 1, n = 1)\\ &= \frac{1}{N_i} - \frac{\gamma}{2}\frac{(N_i - 1)(N_f N_i - 1)}{N_i^3}s\end{aligned}$$

$$\begin{aligned}\pi_S &= 1 - \pi(m = 1, n = N_f - 1)\\ &= \frac{1}{N_f} + \frac{\gamma}{2}\frac{(N_f - 1)^2(N_f + 1)}{N_f^3}s\end{aligned}$$

Criterion for altruists domination.

$\pi_A > \pi_S$ if :

$$N_f s < N_f s^* = \frac{1}{\gamma}\frac{\Delta N}{\bar{N}}$$

Altruists are favored if the *selection pressure* against them is smaller than the relative increase in population size!

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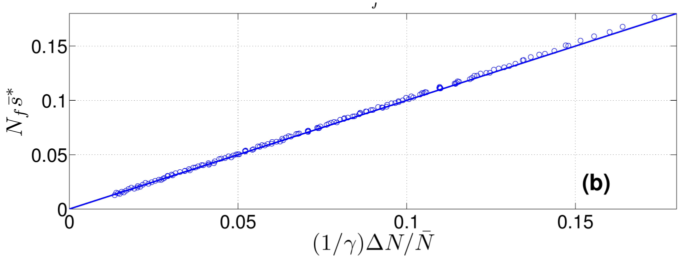

Geographically structured populations.

- The Altruists advantage disappears for large $\bar{N}$:

$$\Delta = \pi_A - \pi_S = \frac{\Delta N}{\bar{N}} - \bar{N}s$$

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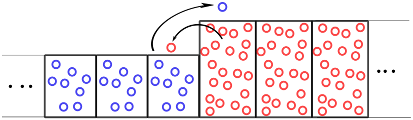
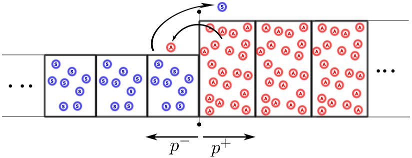
- 1d space divided into patches, neighboring patches exchange individuals with a migration coefficient D:



Low migration limit $\tau_{\text{mig}} \gg \tau_{\text{fix}}$



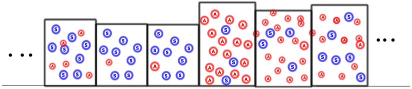
The frontier performs a biased (p^-, p^+) random walk.

Altruism's advantage amplified by demographic effect :

$$\frac{p^-}{p^+} = \frac{\pi_A}{\pi_S} \times \frac{N_f}{N_i}$$

$\Pi_s \approx 0$: The probability for a cheater to invade the community is 0.

High migration limit $\tau_{\text{mig}} \ll \tau_{\text{fix}}$



- At extremely high migration, the system is non-structured and can be considered as 1 big population of size $N_T = MN$
- $N_T s$, the *selection pressure* against altruists, would always be too high : Genetic drifts cannot compensate the cost of producing "common good".
- $\Pi_A \approx 0$: The probability for an altruist to invade the community is 0.

Summary.

- A new theoretical framework to help explain the emergence of altruism.
- A simple model, with 3 ingredients (Population size N, cost of altruism s and relative population increase due to common good production $\Delta N/N$).
- No hidden benefits of altruism, only based on known phenomena of genetic drift.
- Future advance:
    - Deriving a 1d Markov chain.
    - Exact computation for intermediate migration rate.
    - Laboratory experiment with microorganism.

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