Evolution of staying together in structured and unstructured populations

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mulicellularity

- land plants
- charophycean algae
- (Chlamydomonas, Volvox)
- chlorophycean algae
- red algae
- rhizaria
- ciliates
- diatoms
- brown algae
- diatoms
- acrasid slime molds
- excavates
- fungi
- animals
- plasmodial slime molds
- dictyostelid slime molds
- choanoflagellates
- all members unicellular
- some members unicellular, some unicellular
- most members unicellular, rare multicellular species
- all members unicellular or colonial
- most members unicellular, rare colonial species
- all members unicellular
simple multicellular organisms

- Volvox
- Yeast
- Filamentous bacteria

*Saccharomyces cerevisiae*
multicellularity happens in all life forms

1. group formation potential (staying together, coming together)

2. evolution of altruistic and cooperative behavior

3. mechanism conflict resolution

4. division of labour

5. evolution of life cycles/ transfer of fitness to higher level
Staying together and group formation

**staying together**

1. staying together can be due to over production of an adhesive protein (in yeast or bacterial models)

2. In eusociality, can be staying together of parent and offspring

3. Is different, in evolutionary dynamics, from coming together

4. either increases the growth and individual fitness or reduces death rates.
evolution of staying together

we assume staying together is evolved due to a mutation

- we assume staying together is fully evolved in a mutant type

- question is how selection dynamics is affected by staying together potential

- how cooperation inside groups and increase in survival affects overall fitness advantage/disadvantage

- how spatial structure can influence the dynamics of selection between two units (complexes and singlets)
staying together

(a) mature complex

(a) singlet mutan

Life cycle of a complex

(type A) average no of offsprings after three divisions

(type B)
**Moran dynamics**

(a) Life cycle of a simple multicellular complex of maturation size \( n = 3 \). (b) Comparison between division events in a multicellular complex versus that of a singlet (for \( n = 3 \)). Each complex seeds a singlet that grows into a mature complex, during the same time (same number of divisions) a singlet cell can divide into the same number of springs. The sum of fitnesses of individuals inside a complex of size \( i \) is denoted by \( a_i \) and fitness of singlet wild type population is set to unity.

(a) death

birth

a singlet mutant is chosen to replicate with fitness \( h_2 \)

the offspring randomly replaces a wild-type singlet

(b) death

birth

a singlet mutant is chosen to replicate with fitness \( h_2 \)

the offspring replaces a neighboring wild-type singlet

Figure 2: Sequence of birth-death events describing competition between complexes and singlets in (a) well-mixed populations (b) a square lattice (degree-4 regular graph). In both cases, (i) an individual is chosen proportional to its fitness (inside or outside a complex). (ii) The offspring randomly stays together inside an immature complex and lead to growth of the complex. Otherwise it leaves the group and replaces an individual (complex or singlet) with the probability inversely proportional to the survival rate of the target individual. The (mutant) staying together strategy is denote with blue and wild type is shown with red.

Moran dynamics
The fixation probability of a complex mutant in a background of the above condition is equivalent to A(fixation probability of single mutant, n=2) complexes.

Fixation probability of sticky mutant

\[
\rho_A(a) = \frac{1 - \frac{a_1 + a_2 + 1}{a_2(a_1 + 1)}}{1 - \left(\frac{a_1 + 1}{a_1 a_2}\right)^N}
\]

\[
= \frac{a_1}{a_1 + 1} \cdot \frac{1 - \left(\frac{a_1 a_2}{a_1 + 1}\right)^{-1}}{1 - \left(\frac{a_1 a_2}{a_1 + 1}\right)^{-N}}
\]

For maximum size \(n=2\) the above result is straightforwardly generalized (see SI section for the derivation).

We first consider maximum size of a mutant of maximum size is given by (See SI section for the derivation)

\[
\frac{a_1 a_2}{a_1 + 1} \geq 1 \quad \text{invading complex}
\]

\[
\frac{a_1 a_2^{N/(N-1)}}{a_1 + 1} \geq 1 \quad \text{invading singlet}
\]
fixation probability (n=2)
Fixation probability of  a sticky complex

Fixation probability of  a sticky singlet

$A(\text{fixation of a mutant complex vs effective fitness})$

$\rho_A(a) = \frac{f_n}{a_n} \times \frac{1 - \left(\frac{1}{f_n}\right)}{1 - \left(\frac{1}{f_n}\right)^N}$

$A(\text{fixation probability vs inter-complex fitness})$

$\rho_A = \frac{f_n}{a_n} \times \frac{1 - \left(\frac{1}{f_n}\right)}{1 - \left(\frac{1}{f_n}\right)^N}$

$A(\text{fixation probability for various complex sizes})$

$\rho_A(a) = \frac{f_n}{a_n} \times \frac{1 - \left(\frac{1}{f_n}\right)}{1 - \left(\frac{1}{f_n}\right)^N}$

$A(\text{neutral condition})$

$A(\text{fitness inside the mature complex})$

$A(\text{approximation for the fixation probability on a cycle})$

$A(\text{mutant unicellular fitness})$

$A(\text{reasoning (see Appendix)})$

$A(\text{one would expect the condition for the mutant type})$

$A(\text{to be advantageous can be given from a condition regarding})$

$A(\text{We should expect to see that for both the line and the cycle, the condition for})$

$A(\text{then mature fully to a type})$

$A(\text{matured individuals. However, it now takes more than one step to increase the})$

$A(\text{in this case, an initial invading mutant will eventually produce a cluster of fully})$

$A(\text{is not dependent on the size of the cluster.})$

$A(\text{of the cluster and the probability that the cluster increases or decreases in size})$

$A(\text{represented as a birth death process, where the quantity of interest is the size})$

$A(\text{that can only be decreased in size from the point at which it meets the wild type})$

$A(\text{the above condition is equivalent to})$

$A(\text{structures such as a line or a cycle. We derive here an exact expression for the})$

$A(\text{The simplest population structures to investigate are those that are one-dimensional})$

$A(\text{for various complex sizes})$

$A(\text{for maximum size})$

$A(\text{the results are plotted in Fig. Fig.})$

$A(\text{shows the fixation probability ... The results are in very good})$

$A(\text{match with the simulation results.})$

$A(\text{in the Figs. Fig.})$

$A(\text{Section 5})$

$A(\text{SI section). The fixation probability of a complex mutant in a background of})$

$A(\text{For maximum size})

$A(\text{complex. The survival probability can be easily calculated and the overall result})$

$A(\text{mutant survives and grows into a complex times the fixation probability of the})$

$A(\text{the fixation probability is that of standard Moran process})$

$A(\text{and the fixation probability is that of standard Moran process})$

$A(\text{we can look at the neutrality condition in the standard sense when})$
The probability of having a single group of two mutants and where $n = 3$ the system of equations A.9 becomes

$$
N \frac{\partial F(z_1, z_2; t)}{\partial t} = (z_1 - 1)W_1^+(\hat{n}_1, \hat{n}_2) + (z_1^{-1} - 1)W_1^-(\hat{n}_1, \hat{n}_2)
+ (z_2^{-1} - 1)W_2^-(\hat{n}_1, \hat{n}_2) + (z_2z_1^{-1} - 1)W_{12}^+(\hat{n}_1, \hat{n}_2)
$$

The probability generating function, $F(z_1, z_2; t) = \sum_{n_1, n_2} z_1^{n_1} z_2^{n_2} p(n_1, n_2; t)$,

$$a_2(z_1 - 1) + (z_2^{-1} - 1) = 0$$
$$a_1(z_1^{-1} - 1) + a_1(z_1^{-1} z_2 - 1) = 0$$

$$z_1^* = \frac{a_1 + a_2 + 1}{a_2(a_1 + 1)}$$
$$z_2^* = \frac{a_1 + 1}{a_2 a_1}$$

$$\rho = \frac{1 - z_1^*}{1 - (z_2^*)^N}$$
$$\rho = \frac{a_1}{a_1 + 1} \cdot \frac{1 - \left(\frac{a_1 + 1}{a_1 a_2}\right)}{1 - \left(\frac{a_1 + 1}{a_1 a_2}\right)^N}$$
fixation probability (invasion analysis)

\[
\begin{align*}
\frac{dx_0}{dt} &= \frac{x_0(x_1 + x_1)}{x_0 + a_1x_1 + x_2a_2} - \frac{a_2x_2}{x_0 + a_1x_1 + a_2x_2} \\
\frac{dx_1}{dt} &= \frac{a_2x_2 \cdot x_0}{x_0 + a_1x_1 + a_2x_2} - \frac{a_1x_1}{x_0 + a_1x_1 + a_2x_2} - \frac{x_0x_1}{x_0 + a_1x_1 + a_2x_2} \\
\frac{dx_2}{dt} &= \frac{a_1x_1 - x_0x_2}{x_0 + a_1x_1 + a_2x_2}
\end{align*}
\]

\[
\lambda_1 = -1 - \frac{a_1}{2} + \frac{1}{2} \sqrt{a_1^2 + 4a_1a_2} \\
\lambda_2 = -1 - \frac{a_1}{2} - \frac{1}{2} \sqrt{a_1^2 + 4a_1a_2}
\]

\[
\sqrt{a_1^2 + 4a_1a_2} > 2 + a_1 \\
\frac{a_1a_2}{a_1 + 1} > 1
\]
Fixation probability of a sticky complex

Fixation probability vs inter-complex fitness

\[ f_n = a_n \prod_{k=1}^{n-1} \frac{a_k}{a_k + 1} \]

effective fitness

\[ \rho_A(a) = \frac{f_n}{a_n} \times \frac{1 - \left( \frac{1}{f_n} \right)}{1 - \left( \frac{1}{f_n} \right)^N} \]

\[ f_n \geq a_n \]

invading singlet

\[ f_n \geq 1 \]

invading complex

Fixation probability of a singlet vs individual fitness for various complex sizes

In one-dimension, a single invading mutant will produce a cluster of mutants. In models where there are only two types, this can then be immediately represented as a birth death process, where the quantity of interest is the size of the mutant cluster. Working along this line, the mutant type to be advantageous can be given from a condition regarding the expected change in the boundary of the mutant cluster. We should expect to see that for both the line and the cycle, the condition for the fixation probability is that of standard Moran process (see SI section). The fixation probability of a complex mutant in a background of wild type singlets for general value of \( n \) is in fact expressed in terms of an analytic expression for the fixation probability of single mutant, \( \rho_{AB}(a) \)

\[ \rho_{AB}(a) = \left( \frac{1}{f_n} \right)^{\frac{1}{N}} \]

\[ f_n \geq a_n \]

\[ f_n \geq 1 \]
inter-complex cooperation

Fixation probability of a singlet mutant vs benefit production inside a complex

$\rho_A(a)$

$\begin{align*}
  a_1 &= 1 \\
  a_i &= i \times \{1 + w(b \cdot (i - 1))\}
\end{align*}$
The fixation probability of a singlet mutant is the probability that the singlet mutant survives and grows into a complex times the fixation probability of the complex. The survival probability can be easily calculated and the overall result is

$$\rho_A(a, d) = \frac{f_n}{a_n} \times \frac{1 - \left(\frac{1}{f_n}\right)}{1 - \left(\frac{1}{f_n}\right)^N}$$

We compared our results for the fixation probability of a mutant complex with stochastic simulations for $n = 2, 3, 4, 5, 6$. The results are plotted as a function of $f_n$. The results are plotted in Fig. ??

Similar to $n = 2$ case the condition for neutrality between two levels of selection, $\hat{\rho}_A = \hat{\rho}_B$ lead to $f_n = 1$. This means that the chance of selection of a invading higher unit of selection equal that of a lower units in the opposite types background. The condition for selection that the fixation probability of the opposing singlet genotypes equals each other is more complicated as is given by

$$f_n = \frac{(a_1/d_1) \cdots (a_n/d_n)}{(a_1/d_1 + 1) \cdots (a_{n-1}/d_{n-1} + 1)}$$
Moran dynamics on a spatial structure

Proliferation events for mutants in a linear structure

(a) A singlet mutant is chosen to replicate with fitness $h_1$.
(b) A mutant inside a complex is chosen to replicate with fitness $h_2$.

At the offspring replaces the neighboring wild-type cell.

WT mutant

birth stay-together death
Moran dynamics on a spatial structure

\[ f = \frac{a_1 \cdots a_n}{(a_1 + 1/2) \cdots (a_{n-1} + 1/2)} \]

\[ \rho = \frac{1 - \frac{1}{f}}{1 - \left(\frac{1}{f}\right)^N} \]