Replicator Equation + Direct reciprocity

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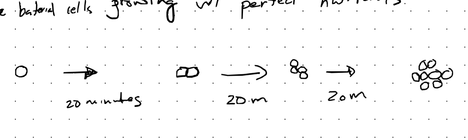
We will discuss the basic building blocks of evolution!

Imagine bacterial cells growing w/ perfect nutrients.



After t generations (= 20 mins in this example), # cells is 2^t.

Can write a discrete-time formula for this.

$$\underbrace{X_{t+1}}_{\text{\# cells at time } t+1} = \overbrace{2}^{\text{splitting / doubling}} \cdot \underbrace{X_t}_{\text{\# cells at time } t}$$

$$\Rightarrow \boxed{X_t = X_0 \cdot 2^t} \quad \text{initial \# of cells}$$

Can also write continuous time version.

Suppose cells divide at rate r. $(\sim Exp(1/r))$ avg # splits per time period per cell

PDF $\lambda e^{-\lambda t}$, λ = rate

$$\dot{X} = \frac{dx}{dt} = r \cdot x \quad \text{\# cells at time } t$$

$$\Rightarrow \boxed{X(t) = X_0 e^{rt}}$$

If t has units of days, then

r = 1 split per 20 mins = 3 splits per hour
= $(3 \cdot 24 =)$ 72 splits per day
= 72

After 3 days, one cell will generate $x(3) = e^{3 \cdot 72} = e^{216}$
$\approx 6 \times 10^9$ cells!!

Now, lets say cells die at rate d.

Then $\dot{x} = rx - dx = (r-d)x$

$$\Rightarrow \boxed{x(t) = x_0 e^{(r-d)t}}$$

- If $r > d$, $x(t) \to \infty$
- If $r < d$, $x(t) \to 0$
- If $r = d$, $x(t)$ is constant but unstable

r/d is known as reproductive ratio. Need $r/d > 1$ for population growth.

Now, say that there is some upper limit to the # of individuals in a population.

$\dot{x} = rx(1 - x/K)$ K is carrying capacity

Logistic Equation $\dot{x} = \alpha x$ where $\alpha = \beta r$, $\beta = 1 - x/K$ damping factor

- As x gets larger, β gets smaller, so α gets closer to 0
- As x gets smaller, β gets larger so α gets closer to r

Soln
$$\boxed{x(t) = \frac{K x_0 e^{rt}}{K + x_0(e^{rt} - 1)}}$$

Equilibrium of $x(t) \to K$ as $t \to \infty$ assuming $x_0 > 0$.

Above, we studied reproduction. Now we study selection.

Selection occurs when there are different reproduction rates.

Two types: A & B (rate a, rate b)

$\dot{x} = ax$ # A individuals
$\dot{y} = by$ # B individuals

Soln $x(t) = x_0 e^{at}$
$y(t) = y_0 e^{bt}$

Now, suppose population size is held constant.

We will use $x(t)$, $y(t)$ to be the relative freq. of A, B at time t.

So $x(t) + y(t) = 1 \quad \forall t$.

A proportional amount of A and B are continuosly removed from the population. "flux" / "flush" rate

So,
$$\dot{x} = ax - \phi x$$
$$\dot{y} = by - \phi y \qquad (*)$$

What is ϕ?

We know $x + y = 1$, thus $\dot{x} + \dot{y} = \frac{d}{dt}[x+y] = \frac{d}{dt}[1] = 0$

$\Rightarrow \underbrace{(ax - \phi x)}_{\dot{x}} + \underbrace{(by - \phi y)}_{\dot{y}} = 0$

$\Rightarrow \phi \cdot \underbrace{(x+y)}_{=1} = ax + by$

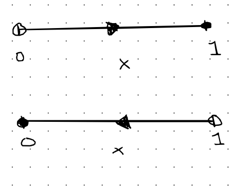
$\Rightarrow \boxed{\phi = ax + by} \quad (**)$

Also, we know $y = 1 - x$, thus Eqn $(*)$ becomes:

$$\begin{aligned}
\dot{x} &= ax - (ax + by)x \\
&= ax - (ax + b(1-x))x \\
&= ax - ax^2 - bx(1-x) \\
&= ax - ax^2 - bx + bx^2 \\
&= ax - bx - (ax^2 - bx^2) \\
&= (a-b)x - (a-b)x^2 \\
&= (a-b)(x - x^2)
\end{aligned}$$

$$\boxed{\dot{x} = (a-b)x(1-x)}$$

two equilibria $x = 0, 1$ but what about stability?



$a > b$

$a < b$

$a = b$ is "degenerate"

n types (instead of only 2).

$i = 1, \dots, n$

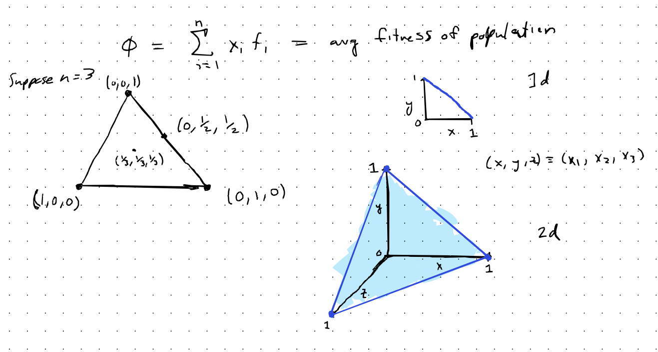
$x_i(t)$ is freq of type i

population is $\vec{x} = (x_1, \dots, x_n)$ where $\sum_{i=1}^{n} x_i = 1$

Let f_i be the fitness (rate of reproduction) of type i.

$$\dot{x}_i = f_i x_i - \phi x_i, \quad i = 1, \dots, n. \qquad (\heartsuit)$$

$$\phi = \sum_{i=1}^{n} x_i f_i = \text{avg fitness of population}$$



n types $\Rightarrow$ $(n-1)$-dim simplex

Eqn $(\heartsuit)$ is called the Replicator equation.

Equilibria where (non-degenerate) $\dot{\vec{x}} = \vec{0} \Rightarrow (f_i - \phi)x_i = 0 \quad \forall i$

$\Rightarrow \left(f_i - \sum_j x_j f_j\right) x_i = 0 \quad \forall i$

$\Rightarrow \left((1 - x_i) f_i - \sum_{j \neq i} x_j f_j\right) x_i = 0$

$x_i = 1, \; x_j = 0 \quad \forall j \neq i$

Only stable equilibrium is where
$f_i > f_j \quad \forall j \neq i$
"Survival of the fittest"

Now we add mutation. Consider two types first, w/ no selection advantages

u_1 is the rate type A mutates to type B
u_2 is the rate type B mutates to type A

So now we have

$$\dot{x} = (1 - u_1)x + u_2 y - \phi x$$
$$\dot{y} = (1 - u_2)y + u_1 x - \phi y$$

$\phi = 1$ (why?)

Thus $\dot{x} = u_2 - (u_1 + u_2)x$

stable equilibrium of $x^* = \frac{u_2}{u_1 + u_2}$ when $u_1 + u_2 > 0$

mutation leads to coexistence of A & B

n types, q_{ij} is mutation rate from i to j $\sum_j q_{ij} = 1$

$$\dot{x}_i = \left[\sum_{j=1}^{n} q_{ji} x_j\right] - \phi x_i, \quad i = 1, \dots, n$$

$$Q = [q_{ij}] \Rightarrow \dot{\vec{x}} = \vec{x} Q - \phi \vec{x}$$

Equilibria where $\vec{x}^* Q = \phi \vec{x}^*$

In the case of neutral evolution, $\phi = 1$

So we are looking for the left hand eigenvector w/ corresponding eigenvalue 1

Now put it all together!

n types $i = 1, \dots, n$
frequencies x_i
fitnesses f_i
mutation rates $Q = [q_{ij}]$

$$(\heartsuit\heartsuit) \qquad \dot{x}_i = \left[\sum_{j=1}^{n} x_j f_j q_{ji}\right] - \phi x_i, \quad i = 1, \dots, n$$

where $\phi = \sum_{i=1}^{n} x_i f_i$ = avg fitness

Eqn. $(\heartsuit\heartsuit)$ is called the quasispecies equation.

- If $f_1 = f_2 = \dots = f_n$, then there is no selection advantage. This is known as "neutral evolution"
- If f_i does not depend on $\vec{x}$, this is "constant selection"
- If f_i may depend on $\vec{x}$, this is "frequency-dependent selection". This is the realm of evolutionary game theory
- If $Q = I$, there are no mutations.

Donation game

$$\begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array} \qquad b > c > 0$$

$\leftarrow$ form of Prisoner's dilemma

$$\begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array}$$

reward, sucker, temptation, punishment

$T > R > P > S$

Consider x is relative freq of cooperators, $y = 1 - x$ defectors

If a cooperator plays against everyone once in the population, its total payoff is $P_C = [(b-c)x] + [-c(1-x)]$
$= bx - cx - c + cx$
$= bx - c$

For a defector, $P_D = bx + 0(1-x)$
$= bx$

To get the fitness (from its payoff) of each strategy, we use (for example) the map $P \xmapsto{f} 1 - w + wP$ where $w \in [0,1]$ strength of selection

We consider weak selection (ie when $w \ll 1$)

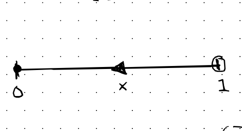
$1 - w + wP > 0$

$P > \frac{w-1}{w} = 1 - \underbrace{\frac{1}{w}}_{}$ Blows up when w is small

$f_C = 1 - w + wP_C$
$f_D = 1 - w + wP_D$

Replicator equation gives

$$\dot{x} = (f_C - f_D)x(1-x)$$
$$= \underbrace{[-wc]}_{<0} \underbrace{x(1-x)}_{>0}$$



Cooperators loose ☹.

Direct reciprocity through repeated games

From last lecture, $\delta \in [0,1]$ is prob. of a next round in a repeated game.

We calculated for the donation game

$$\begin{array}{c c} & \begin{array}{cc} TFT & ALLD \end{array} \\ \begin{array}{c} TFT \\ ALLD \end{array} & \begin{pmatrix} b-c & -c(1-\delta) \\ b(1-\delta) & 0 \end{pmatrix} \end{array}$$

Let x be relative freq. of TFT strategies in the population.

Then $P_{TFT} = x(b-c) + (1-x)(-c(1-\delta))$ $= -c(1-\delta) + cx(1-\delta)$
$= bx - cx + cx(1-\delta) - c(1-\delta)$
$= bx - \delta cx - c(1-\delta)$
$= (b - \delta c)x - c(1-\delta)$

$P_{ALLD} = x(b(1-\delta)) + (1-x) \cdot 0$
$= (1-\delta)bx$

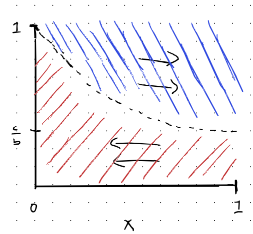
So $f_{TFT} = 1 - w + wP_{TFT}$
$f_{ALLD} = 1 - w + wP_{ALLD}$ $\phi = x f_{TFT} + (1-x) f_{ALLD}$

$$\begin{aligned}
\dot{x} &= (f_{TFT} - f_{ALLD})x(1-x) \\
&= [(b - \delta c)x - c(1-\delta) - (1-\delta)bx]\, x(1-x) \\
&= [\cancel{bx} - \delta cx - c(1-\delta) - \cancel{bx} + \delta bx]\, x(1-x) \\
&= [\underbrace{\delta(b-c)x - c(1-\delta)}_{:=\gamma}]\, \underbrace{x(1-x)}_{>0}
\end{aligned}$$

$\gamma = 0 \Leftarrow \delta(b-c)x = c(1-\delta)$
$\Leftrightarrow \delta(b-c)x + \delta c = c$
$\Leftrightarrow \delta[(b-c)x + c] = c$
$\Leftrightarrow \boxed{\delta = \frac{c}{(b-c)x + c} =: \delta^*}$ $\Rightarrow x^* = \frac{\left(\frac{c}{\delta} - c\right)}{b-c} = \frac{c\left(\frac{1}{\delta} - 1\right)}{b-c}$

$$\boxed{x^* = \frac{c(1-\delta)}{\delta(b-c)}}$$

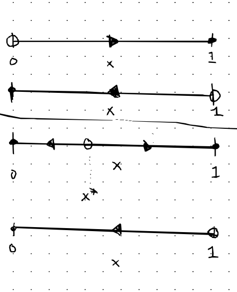
$x > x^* \Rightarrow \gamma > 0 \Rightarrow$ selection favors TFT
$x < x^* \Rightarrow \gamma < 0 \Rightarrow$ selection favors ALLD



$\delta \le \frac{c}{b} \Rightarrow x^* \ge 1$

$\equiv \delta > \frac{c}{b} \Rightarrow x^* < 1$

$\frac{1}{1-\delta}$ expected rounds



$\delta = 1 \Rightarrow$ ∞ rounds

$\delta = 0 \Rightarrow$ 1 round

$\delta = \frac{1}{2} \Rightarrow$ if $b/c > 2$ Geom$(\frac{1}{2})$ rounds

$x^* = \frac{c}{b-c}$ $\delta = \frac{1}{2}$

$\Rightarrow$ if $b/c \le 2$ $x^* < 1 \Leftrightarrow b - c > c$
$\Leftrightarrow b/c > 2$

We are missing a crucial component of the dynamics

We have not accounted for drift

Our deterministic analysis gives us the relative growth rates, but in actuality there is lot of stochasticity involved.

We will introduce a stochastic process for evolution next class!