Lecture 5: Finite Populations

MATH 242
9/30/2025

(Source: Evolutionary dynamics, Nowak 2006

What we have seen so far:

Name	Selection	Mutation?	Population size	Stochastic?
Replicator Equation	Constant	No	∞	No
Quasi-species Equation	Constant	Yes	∞	No
Replicator-Mutator Equation	Frequency Dependent	Yes	∞	No
Moran Process	Constant	No	Finite, constant	Yes
Birth-Death Process	Frequency Dependent	Yes	Finite, constant	Yes

Today!

Evolutionary dynamics in finite populations

1. The abundance of individuals is given by an integer instead of a continuous variable
2. Description of dynamics is no longer deterministic differential equations, but rather requires stochastic formulation

Note:

- When studying a biological problem, try a deterministic description first, then move to stochastic analysis when deterministic approach misses relevant phenomena.
- [illegible] equations [illegible] typically easier to analyze

- Differential equations are typically easier to analyze than stochastic formulations, but biological effects often arise only in the stochastic context (e.g., neutral drift)

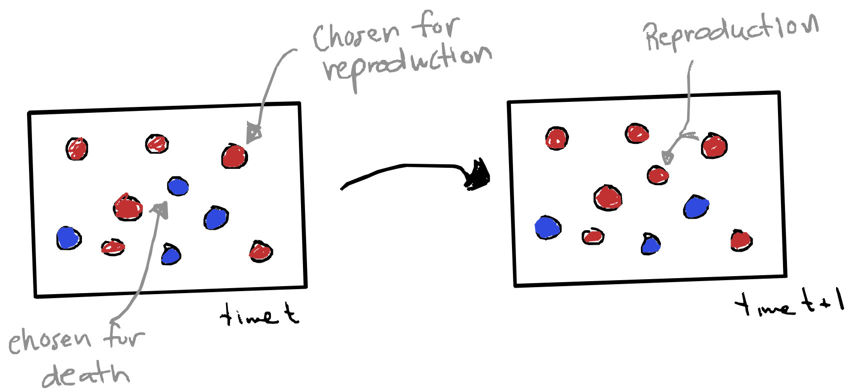
Neutral Drift

Model (Moran 1958):

- population size N ← integer
- two types of individuals, A & B
- both types of individuals have same $\underbrace{\text{reproduction rate}}_{\text{"fitness"}}$
- At each time step $t = 0, 1, 2, \ldots$

No mutations →
1. random individual is chosen for reproduction
2. random individual is chosen for death

with replacement



Features

- Always exactly 1 birth & 1 death in each step
  - ↳ Population size remains constant
- The only stochastic variable is the number of A individuals, denoted by i
  (B " " $N-i$)
  - ↳ State spaces is $i = 0, 1, \ldots, N$
- Probability of choosing A individual is i/N (reproduction or death)
- No state change possible when $i=0$ or $i=N$
  "extinction" "absorption" "fixation"

At each time step, only 4 possible events when state is currently $i \in \{1, \ldots, N-1\}$:

Type chosen for reproduction	Type chosen for death	Probability of event	New State

reproduction			
A	A	$\frac{i}{N} \cdot \frac{i}{N}$	i
A	B	$\frac{i}{N} \cdot \frac{N-i}{N}$	$i+1$
B	A	$\frac{N-i}{N} \cdot \frac{i}{N}$	$i-1$
B	B	$\frac{N-i}{N} \cdot \frac{N-i}{N}$	i

Analysis

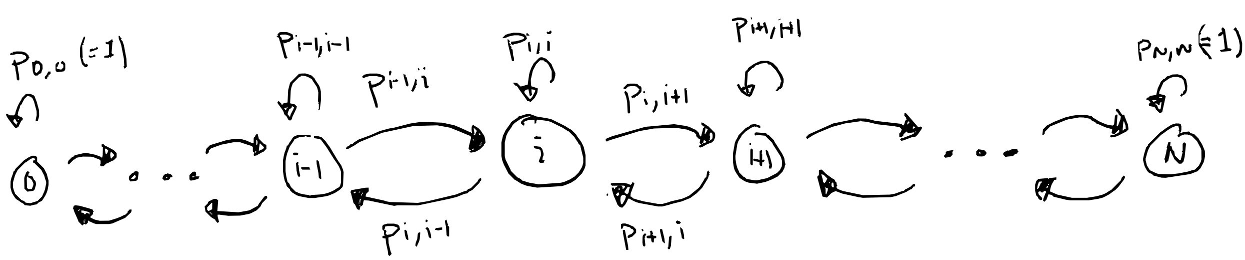
Let $P = [p_{ij}]$ be the $(N+1) \times (N+1)$ row stochastic matrix where

p_{ij} = prob. transition from state i to state j.

We have

$$\begin{cases} p_{0,0} = p_{N,N} = 1 \\ \left.\begin{aligned} p_{i,i-1} = p_{i,i+1} &= i(N-i)/N^2 \\ p_{i,i} &= 1-(p_{i,i-1} + p_{i,i+1}) \end{aligned}\right) \text{for remaing } i \\ \text{All other entries are zero} \end{cases}$$

Question: Starting in state i, what is the probability of reaching state N? (i.e., "fixation probability")



Let x_i = probability the process ends in state N given it started in state i.

(Note that $1-x_i$ is the probability of ending in state 0 when starting in state i.)

We have

$$x_0 = 0$$
$$x_N = 1$$
$$x_i = p_{i,i-1} x_{i-1} + p_{i,i} x_i + p_{i,i+1} x_{i+1}$$
for $i=1,\dots,N-1$

Note that $p_{i,i-1} = p_{i,i+1}$ and thus $p_{i,i} = 1 - 2p_{i,i+1}$, so for $i=1,\dots,N-1$:

$$x_i = p_{i,i+1} x_{i-1} + (1-2p_{i,i+1}) x_i + p_{i,i+1} x_{i+1}$$
$$= x_i + p_{i,i+1} [x_{i-1} - 2x_i + x_{i+1}]$$

$$\Leftrightarrow \quad x_i - x_{i-1} = x_{i+1} - x_i \qquad (*)$$

$$\Rightarrow \quad x_i = i/N \quad \text{for} \quad i = 0, 1, \dots, N$$

(Note, $(*) \Rightarrow \exists \Delta$ s.t. $x_i - x_{i-1} = \Delta \quad \forall i \in \{1, \dots, N\}$

$$\Rightarrow \underbrace{\sum_{i=1}^{N} (x_i - x_{i-1})}_{= \Delta N} = x_N - x_0 = 1$$

$$\Rightarrow \Delta = 1/N$$
$$\Rightarrow x_i = i/N \quad \forall i$$
)

Birth-Death Process

Model: State space still $i = 0, \dots, N$

From state i, in the next time step

- Move to state $i+1$ w/ prob $\alpha_i > 0$
  $i-1$ $\quad \beta_i > 0$
  i $\quad 1 - (\alpha_i + \beta_i)$

Let $i = 0, N$ be absorbing states,
so $\alpha_0 = \beta_0 = \alpha_N = \beta_N = 0$

Then we get

$$p_{0,0} = p_{N,N} = 1$$
$$p_{i,i+1} = \alpha_i$$
$$p_{i,i-1} = \beta_i$$
$$p_{i,i} = 1 - (\alpha_i + \beta_i)$$

Zero everywhere else

We get
$$x_0 = 0$$
$$x_N = 1$$
$$x_i = \beta_i x_{i-1} + (1-\alpha_i-\beta_i)x_i + \alpha_i x_{i+1} \quad (**)$$
$$i=1,\dots,N-1$$

In vector notation: $\vec{x} = P\vec{x}$

$\Rightarrow$ $\vec{x}$ is right eigenvector of P for eigenvalue 1.

Let $y_i = x_i - x_{i-1}$

$\gamma_i = \beta_i / \alpha_i$

$\forall i = 1,\dots,N-1$

Then $(**) \Rightarrow$
$$\underbrace{\beta_i x_i - \beta_i x_{i-1}}_{=\,\beta_i \underbrace{(x_i - x_{i-1})}_{y_i}} = \underbrace{\alpha_i x_{i+1} - \alpha_i x_i}_{=\,\alpha_i \underbrace{(x_{i+1} - x_i)}_{y_{i+1}}}$$

$$\Rightarrow \beta_i y_i = \alpha_i y_{i+1}$$

$$\Rightarrow y_{i+1} = \frac{\beta_i}{\alpha_i} y_i = \gamma_i y_i$$

$$\Rightarrow y_{i+1} = \gamma_i y_i = \gamma_i(\gamma_{i-1} y_{i-1})$$
$$\vdots$$
$$= \gamma_i \gamma_{i-1} \cdots \gamma_1 y_1$$
$$= \gamma_i \gamma_{i-1} \cdots \gamma_1 x_1$$

Thus we have
$$\sum_{j=1}^{N} y_j = \sum_{j=1}^{N} (x_j - x_{j-1}) = x_N - x_0 = 1$$
$$\| $$
$$\sum_{j=1}^{N} \left(\prod_{k=1}^{j-1} \gamma_k \right) x_1$$
$$\| $$
$$x_1 \left[1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \gamma_k \right]$$

$$\Rightarrow \quad x_1 = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \gamma_k}$$

In general (why? hint: what is x_i in terms of $\vec{y}$?)

$$x_i = \frac{1 + \sum_{j=1}^{i-1} \prod_{k=1}^{j} \gamma_k}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \gamma_k}$$

Motivation

Suppose we have a population of N reproducing individuals of type B. Then a rare event occurs: a type B individual gives birth to a type A individual (mutation). What is the probability that type A eventually fixates (denoted ρ_A)?

By above,

fixation of B in all A population

$$\rho_A = x_1 = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \gamma_k}, \quad \rho_B = 1 - x_{N-1} = \rho_A \prod_{k=1}^{N-1} \gamma_k$$

$$\Rightarrow \quad \frac{\rho_B}{\rho_A} = \prod_{k=1}^{N-1} \gamma_k$$

If $\rho_B / \rho_A > 1$, then selection favors B

$\boxed{\text{Random drift w/ constant selection}}$

We study the same process but now assume type A has fitness r and type B has fitness 1

$$P_{i,i+1} = \frac{ri}{} \quad \frac{N-i}{}$$

$$\overline{ri + (N-1)} \cdot \overline{N}$$

$$p_{i,i-1} = \frac{N-i}{ri + (N-i)} \cdot \frac{i}{N}$$

So $\gamma_i = \dfrac{p_{i,i-1}}{p_{i,i+1}} = \dfrac{1}{r}$

$$\Rightarrow \quad x_i = \frac{1 - 1/r^i}{1 - 1/r^N} \qquad \text{(when } r \neq 1\text{)}$$

Thus

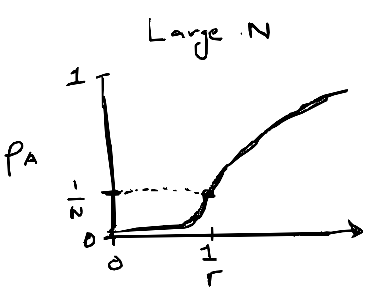
$$\rho_A = \frac{1 - 1/r}{1 - 1/r^N}, \quad \rho_B = \frac{1-r}{1-r^N}$$

So

$$\rho_B/\rho_A = \frac{1-r}{1-r^N} \cdot \frac{1 - \frac{1}{r^N}}{1 - \frac{1}{r}}$$

$$= \frac{1-r}{1-r^N} \cdot \frac{-r^N \cdot [1 - \frac{1}{r^N}]}{-r^N \cdot [1 - \frac{1}{r}]}$$

$$= \frac{1-r}{1-r^N} \cdot \frac{1 - r^N}{r^{N-1}[1-r]} = r^{1-N}$$



Selection favors A when $r > 1$
B < 1

For large N, $\rho_A \approx 1 - 1/r$ when $r > 1$

$\boxed{\text{Rate of evolution}}$ (To think about at home)

With mutation probability u,
$B \to A$

how long do we need to wait until type A fixates? Suppose type A has fitness r and type B has fitness 1.

Assume u is tiny (ie, $Nu \ll 1$).

Note that

① Most mutants are deleterious ($r<1$)
(so likely don't fix)

② Of the remaining mutants,
very few are advantageous ($r>1$)

③ Thus most of the non-deleterious mutants we see at the molecular level are close to neutral ($r \approx 1$)

Tensions between adaptationists and neutralists

- Per generation ($\approx N$ steps) rate of A arising is Nu $\left(\sim Exp\left(\frac{1}{Nu}\right)\right)$
- probability A fixates is p_A

(Assuming separation of timescales)

$$\text{rate of evolution} = (Nu) \cdot p_A$$

\# newly fixated mutants per generation $=$ rate of evolution $= K$

A is neutral ($\Rightarrow p_A = 1/N$) $\Rightarrow$ $K = u$