Stochastic Process

Markov, Moran and Branching

Sergio Peignier sergio.peignier@insa-lyon.fr

Associate Professor
INSA Lyon
Biosciences department

Table of contents

Markov Chains

Integer-time stochastic process

Stochastic process $\{X_n\}_{n \in N}$:

- Defined at **integer times** $n \in N, \quad N \subseteq \mathbb{N}^*$
- The **rv** X_n is called **state at time** n.
- $X_n \in S$, the **state space.**
  - $S = \mathbb{N} \rightarrow$ **Countable infinite set**
  - $S = \{1, \ldots, N\} \rightarrow$ **Countable finite set**

Difference with counting process:

$\{N(t)\}_{t \in T}$ changes at discrete times but is defined in $\mathbb{R}_+^*$.

Discrete-Time Markov Chain (MC)

Integer-time rand. process satisfying the **Markov property**:

$\boxed{\text{Prob. of the } \textbf{next state} \text{ only depends on the } \textbf{current} \text{ one.}}$

Integer-time rand. process $\{X_1, X_2, \dots\}$ is a **MC** if $\forall n > 1$:

$$\boxed{P(X_{n+1} = x | X_1 = x_1, \dots, X_n = x_n) = P(X_{n+1} = x | X_n = x_n)}$$

i.e., the **future** state is **independent** from the **past** states **given** the **present** state.

$$\boxed{X_{n+1} | X_n \quad \perp\!\!\!\perp \quad X_1, X_2, \dots, X_{n-1}}$$

Markov Chain of Order n

- Also known as **Markov chain with memory**
- The **next** state **depends** only on its **previous** n states.

MC of order n, if for $n < m$:

$$P(X_m = x_m | X_1 = x_1, \ldots, X_{m-1} = x_{m-1}) =$$
$$P(X_m = x_m | X_{m-n} = x_{n-m}, \ldots, X_{m-1} = x_{m-1})$$

Chain $\{Y_t\}_{t \in T}$, s.t. $\forall n > m$, $Y_n = (X_n, X_{n-1}, ..., X_{n-m+1})$

has the **classical Markov property**

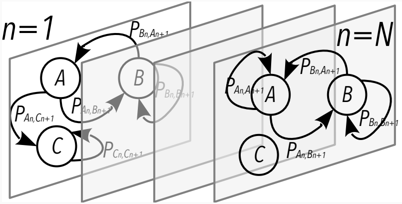
Time-Homogeneous Markov Chain (HMC)

Also called **Stationary/Homogeneous Markov Chain**.

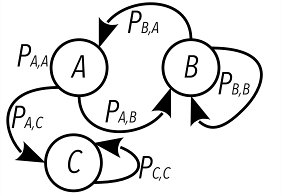
Prob. of state transition is **independent** of n, i.e., $\forall n$:

$$\boxed{P(X_{n+1} = x | X_n = y) = P(X_n = x | X_{n-1} = y)}$$

Markov Chain Representations



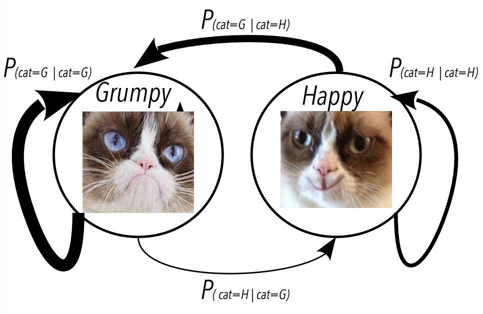
Non-Homogeneous MC:
Sequence of digraphs



Homogeneous MC:
Single digraph.

- **Nodes**: States
- **Edges**: Transition probabilities
- If $P(X_{n+1} = j | X_n = i) = 0$: arc $\langle i, j \rangle$ omitted.

Transition Matrix | HMC



$$M = \begin{array}{c} \\ G \\ H \end{array} \begin{bmatrix} G & H \\ 0.9 & 0.1 \\ 0.7 & 0.3 \end{bmatrix}$$

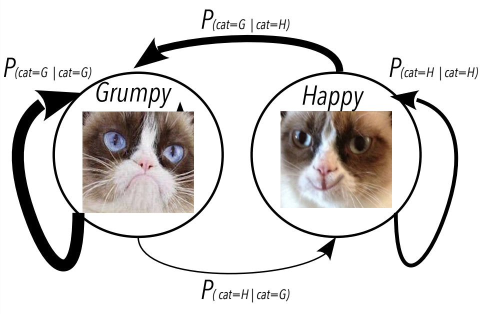
- $\forall i, j, \quad M_{i,j} \geq 0$
- $\sum_j M_{i,j} = 1$

$M_{i,j} \rightarrow$ **Prob.** to go **from state** i **to state** j

Example:

$P(cat_{n+1} = G|cat_n = H) =?; \quad P(cat_{n+1} = G|cat_n = G) =?$

$P(cat_{n+1} = H|cat_n = G) =?; \quad P(cat_{n+1} = H|cat_n = H) =?$



$$M = \begin{array}{c} \\ G \\ H \end{array}\begin{array}{cc} G & H \\ \hline \end{array}$$

$$M = \begin{bmatrix} & G & H \\ G & 0.9 & 0.1 \\ H & 0.7 & 0.3 \end{bmatrix}$$

- $\forall i, j, \quad M_{i,j} \geq 0$
- $\sum_j M_{i,j} = 1$

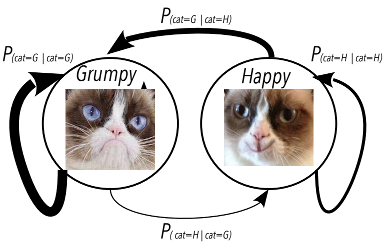
$M_{i,j} \rightarrow$ **Prob.** to go **from state** i **to state** j

Example:

$P(cat_{n+1} = G | cat_n = H) = .7; \quad P(cat_{n+1} = G | cat_n = G) = .9$

$P(cat_{n+1} = H | cat_n = G) = .1; \quad P(cat_{n+1} = H | cat_n = H) = .3$

Transitions | HMC



$$M = \begin{array}{c|cc} & G & H \\ G & 0.9 & 0.1 \\ H & 0.7 & 0.3 \end{array}$$

$\Pi_n \rightarrow$ Distribution at step n

$\Pi_{n+1} = \Pi_n \cdot M$

Example:

$$P(cat_{n+1} = H) = P(cat_n = H)M_{H,H} + P(cat_n = G)M_{G,H}$$
$$P(cat_{n+1} = G) = P(cat_n = G)M_{G,G} + P(cat_n = H)M_{H,G}$$

n-Step Transitions, Chapman-Kolmogorov Equation

Probability to go **from state i** to **state j** in **n steps**:
$p^{(n)}_{i\to j} = P(X_n = j | X_0 = i)$

If $p^{(k)}_{i\to r} > 0$ and $p^{(n-k)}_{r\to j} > 0 \quad$ then $\quad p^{(n)}_{i\to j} > 0$

Chapman–Kolmogorov equation: $\forall k$ s.t., $0 \geq k \geq n$:

$$\boxed{p^{(n)}_{i\to j} = \sum_{r\in S} p^{(k)}_{i\to r} \cdot p^{(n-k)}_{r\to j}}$$

For **HMC** (time independent):

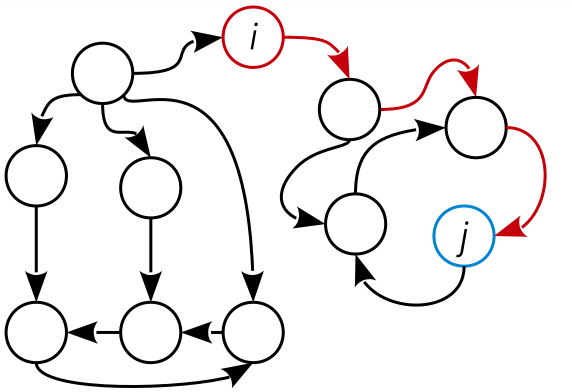
$p^{(n)}_{i\to j} = P(X_{k+n} = j \mid X_k = i), \quad \forall k$ s.t., $0 \geq k \geq n$:

$$\boxed{\Pi_n = \Pi_k \cdot M^{n-k}}$$

Accessibility

State j is **accessible** from state i (**Notation:** $i \to j$) if:

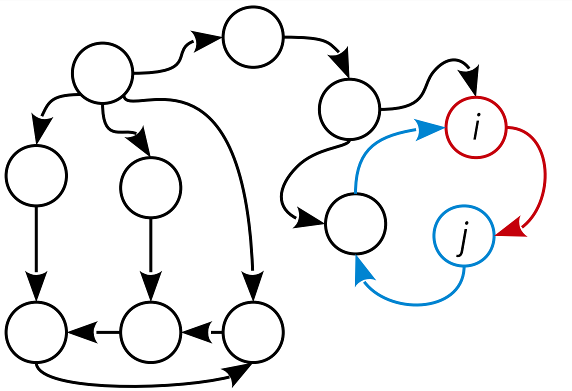
$$\exists n \geq 0, \quad \boxed{p_{i \to j}^{(n)} > 0}$$



Communication

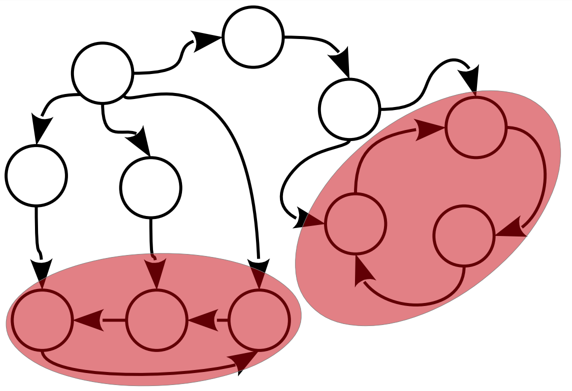
State j **communicates** with state i (**Notation:** $i \leftrightarrow j$) if:

$$\boxed{i \rightarrow j \text{ and } j \rightarrow i}$$



Communication Class

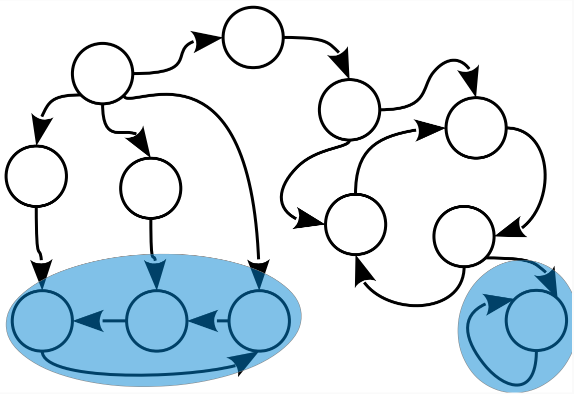
Maximal set of communicating states.



Closed Communication Class

Communicating states s.t. Prob.(leaving the class) = 0

i.e., no outgoing arrows

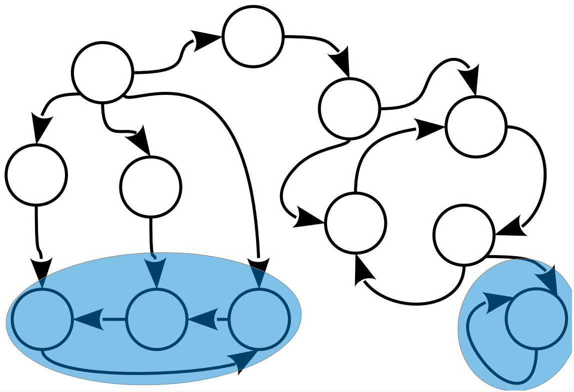


Essential/Final State

State i is **essential/final** if:

$$\forall j \quad \text{s.t.} \quad i \to j \quad \text{then} \quad j \to i$$

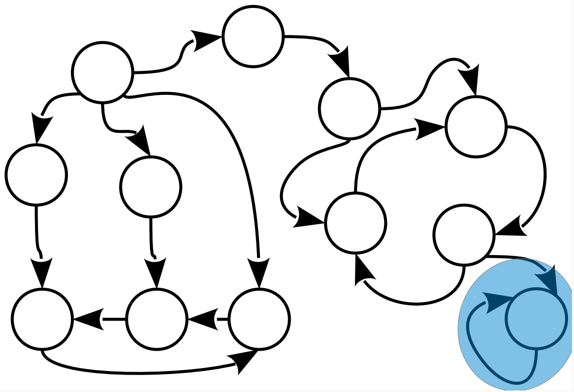
State $i \in$ **closed communicating class**.



Absorbing State

State i is **absorbing** if:

$$\forall n \geq 0 \quad \boxed{P(X_{n+1} = i | X_n = i) = 1}$$

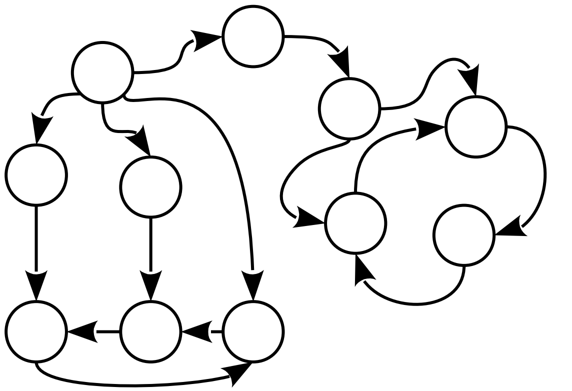


Reducibility

Irreducible Markov Chain:

State space is a single communicating class

Example: Add edges to make an Irreducible Markov Chain



Transience

Let T_i be a **rv** denoting the **first return time to state** i.

$$T_i = min\{n \geq 1 \quad \text{s.t.} \quad X_n = i | X_0 = i\}$$

- State i is **transient** if:

  $$P(T_i = \infty) > 0 \quad \text{and} \quad P(T_i < \infty) < 1$$

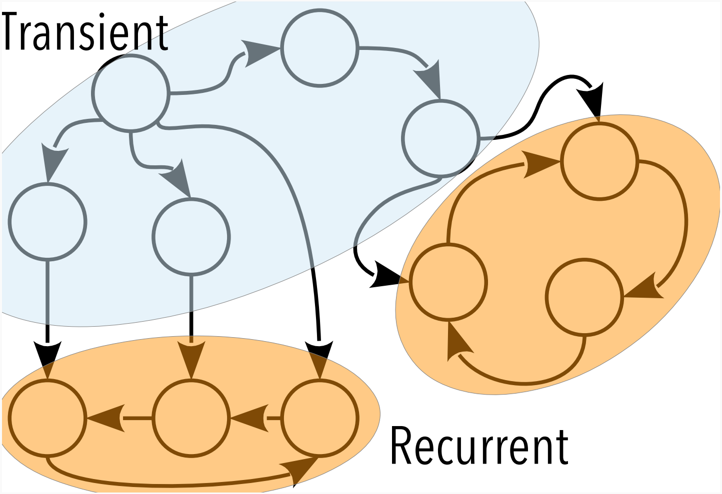
  i.e., we are **not sure to come back**

- State i is **recurrent** or **persistent** if:

  $$p(T_i = \infty) = 0 \quad \text{and} \quad P(T_i < \infty) = 1$$

  i.e., we are **sure to come back**

Transience



Transience (exercise)

Prove the following **theorem**:

For **any finite MC**, the states in a **communication class** are **all transient** or **all recurrent**.

Transience (proof)

- Let $i \in S$ be **transient**
  and $i \in C$ **communication class**.
- Thus: $\exists j \in S \quad \text{s.t.} \quad i \to j \quad \text{but} \quad j \not\to i$
- Let $m \in C \implies m \leftrightarrow i$
- Since $m \to i$ and $i \to j$ then: $m \to j$
- If m is recurrent then: $j \to m$
- Since $j \to m$ and $m \to i$ then: $j \to i$
- **Contradiction:** so m is transient.

Mean recurrence time

$$\boxed{E[T_i] = \sum_{n=1}^{\infty} n \cdot P(T_i = n)}$$

- State i is **positive recurrent** if: $E[T_i]$ is **finite**.
- State i is **null recurrent** if: $E[T_i]$ is **infinite**.

Number of visits

$$\boxed{N_i = \#\{n \geq 1 \quad \text{s.t.} \quad X_n = i | N_0 = i\}}$$

- $P(N_i = k) = P(T_i < \infty)^k$
- If state i is **recurrent**: $\quad P(N_i \geq 1) = 1$
- If state i is **transient**: $\lim\limits_{k \to +\infty} P(N_i = k) = 0$

Periodicity

State i has **period** k_i if return times are multiples of k:

$$\boxed{k_i = \text{gcd}\{n > 0 \quad \text{s.t.} \quad P(X_n = i | X_0 = i) > 0\}}$$

gcd: greatest common divisor

- State i is **aperiodic** if: $k_i = 1$
- MC **aperiodic** if: **every state is aperiodic**
- **Irreducible** MC with **1 aperiodic state** $\implies$ **aperiodic**

e.g., Bipartite graph $\rightarrow$ even period

Ergodicity

- State i is **ergodic** if:
  - i is **aperiodic**:
    period = 1
  - i is **positive recurrent**:
    $P(T_i < \infty) = 1$ and $E[T_i] < \infty$
- MC is **ergodic** if:
  Every state $i \in S$ is ergodic.

Stationary distribution: Vector Π s.t.:

- $0 \leq \Pi_i \leq 1, \quad \forall i \in S$
- $\sum_i \Pi_i = 1$
- $\Pi_j = \sum_{i \in S} \Pi_i p_{i \to j}$

Theorem:

An **irreducible** MC has a **stationary distribution Π if** the MC is **ergodic**. In this case Π is unique:

$$\Pi_i = \frac{C}{E[T_i]} \quad \text{with } C > 0 \text{ a constant}$$

The MC converges to Π regardless of Π_0:

$$\lim_{n \to +\infty} p_{i \to j}^{(n)} = \Pi_j$$

Stationary distribution Π and Transition Matrix M:

$$\boxed{\Pi = \Pi \cdot M}$$

Π is also a normalized multiple of the left eigenvector of M, with eigenvalue 1.

Perron-Frobenius Theorem

Let A be a $n \times n$ **positive matrix** or a **non-negative irreducible matrix**[1], then:

$$\exists \quad r \in \mathbb{R}_+^* \quad \text{and} \quad \exists \quad v = (v_1, ..., v_n) \quad \text{s.t. } M \cdot v = r \cdot v$$

r: **eigenvalue**[2] and v: **eigenvector**[3] of M s.t.:

- **Other eigenvalues** λ are s.t., $|\lambda| < r$.
- $\forall i \quad v_i > 0$, and $\nexists$ **other positive eigenvectors**.

[1] Adjacency matrix of a strongly connected graph
[2] Perron–Frobenius/leading/dominant eigenvalue
[3] Perron–Frobenius/leading/dominant eigenvector

Perron-Frobenius Theorem

Consequence:

Finite irreducible HMC with transition matrix M.

$$\boxed{\exists ! \Pi \quad \text{s.t.} \quad \Pi \cdot M = \Pi}$$

Only one Steady-State distribution vector.

$$\boxed{\Pi_n = \Pi_0 \cdot M^n \quad \text{and} \quad \lim_{n\to\infty} \Pi_n = \Pi \quad \text{Then} \quad \lim_{n\to\infty} M^n = \mathbf{1} \cdot \Pi}$$

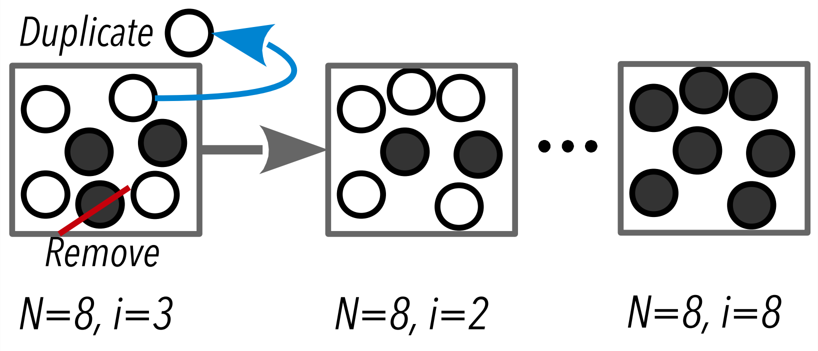
Moran Process

Moran process

- Simple stochastic process used in biology
  - Model **finite populations** (N individuals)
  - **Variety-increasing effects** (e.g., mutations)
  - **variety-reducing effects** (e.g., drift, selection)
- Main characteristics
  - **Constant population size** N
  - **Two populations**: Vector $(i, N - i)$ with $i \geq 0$.
- At each **iteration**:
  - **Reproduce** 1 individual at **random**
  - **Kill** 1 individual at **random**

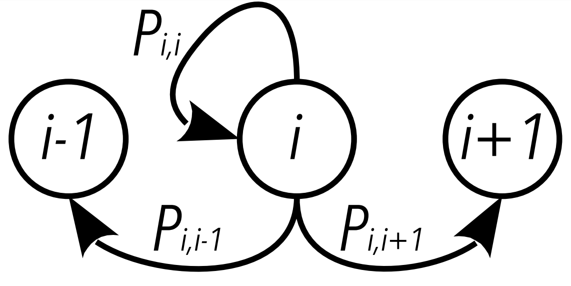
    (The **same** individual **can** be **chosen twice**)
  - If **only 1 type** of individuals $\rightarrow$ **End**

Moran process



Moran process

Markov Process with state i, (i.e, nb. of individuals of type 1)



$$\boxed{p_{i,i} + p_{i,i-1} + p_{i,i+1} = 1}$$

Absorbing states: 0 and N.

Fixation probability | Birth death process

x_i : **Probability of reaching** state N **from** state i.

$$x_i = \begin{cases} 0 & \text{if } i = 0 \\ p_{i,i-1}x_{i-1} + p_{i,i+1}x_{i+1} + p_{i,i}x_i & \text{if } 0 < i < N \\ 1 & \text{if } i = N \end{cases}$$

Theorem: Fixation probabilities

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

With $\gamma_j = \frac{p_{k,k-1}}{p_{k,k+1}}$

Proof:? **Hint:** Compute $x_{i+1} - x_i$

Proof

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

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

$$x_{i+1} - x_i = \frac{p_{i,i-1}}{p_{i,i+1}}(x_i - x_{i-1}) = \gamma_i(x_i - x_{i-1})$$

$$x_{i+1} - x_i = \prod_{k=1}^{i} \gamma_K x_1$$

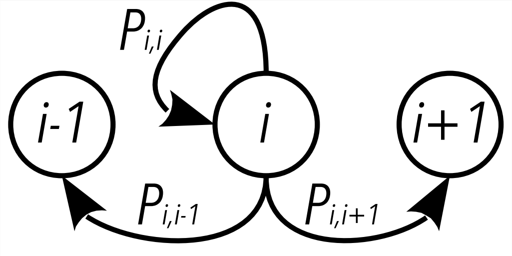
$$x_i = \sum_{j=0}^{i-1} x_{j+1} - x_j = x_1(1 + \sum_{j=1}^{i-1} \prod_{k=1}^{j} \gamma_k)$$

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

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

Neutral drift

Markov Process with state i,i.e, nb. of individuals of type 1):



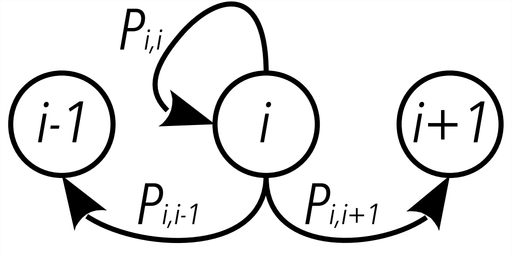
- $p_{i,i-1} = \frac{i(N-i)}{N^2}$
- $p_{i,i+1} = \frac{i(N-i)}{N^2}$
- $p_{i,i} = 1 - p_{i,i-1} - p_{i,i+1}$

Absorbing states: 0 and N.

$$p_{i,i+1} = p_{i,i-1} \implies \gamma_i = 1$$

Selection

Markov Process with state i, i.e, nb. of individuals of type 1
Fitness: f_i (type 1) and g_i (type 2).



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

Absorbing states: 0 and N.

Selection | Fixation Probability

- **Fixation**: Prob. to take over the **entire population**
- $\gamma_i = \frac{P_{i,i-1}}{P_{i,i+1}} = \frac{g_i}{f_i} = \frac{1}{r}$

$$x_i = \frac{1 - r^{-i}}{1 - r^{-N}}$$

Selection | Evolution Rate

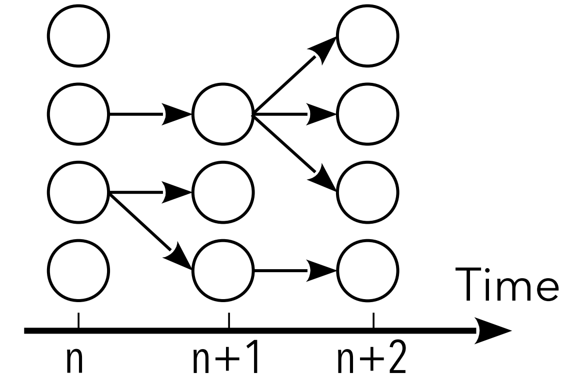
- Population 1 $\rightarrow$ **mutants**
- Only one mutant $i = 1$
- **Fixation**: Prob. mutants take over the **entire population**

$$\rho = x_1 = \frac{1 - r^{-1}}{1 - r^{-N}}$$

Branching Process

Branching Process

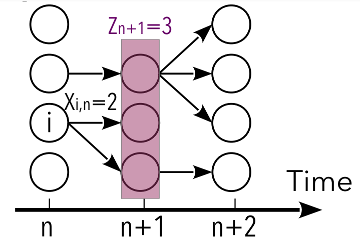
Population of individuals producing, each generation n, a random number of children.



Formal Definition | Galton–Watson process

- Individual lifespan = 1.
- **nb. children** of i at n. $X_{n,i} \in \{1, 2, ...\}$
- $P(X_{n,i} = k) = p_k$
- $X_{n,i}$ are **iid rv.**
- **State/size** of **generation**: $Z_{n+1} = \sum_{i=1}^{Z_n} X_{n,i}; \quad Z_0 = 1$

- **Branching Process:** $\{Z_n\}_{n\in\mathbb{N}}$



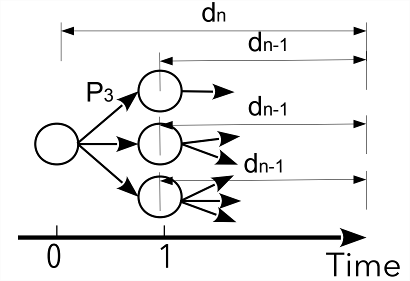
Extinction problem

Extinction probability after n **generation** n:

$$d_n = p_0 + p_1 d_{n-1} + p_2 d_{n-1}^2 + p_2 d_{n-1}^3 + \cdots = h(d_{n-1})$$

Ultimate Extinction probability:

$$d = \lim_{n \to \infty} d_n = \lim_{n \to \infty} P(Z_n = 0) \quad \text{and thus:} \quad \boxed{d = h(d)}$$

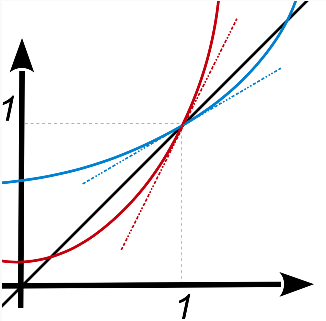


Extinction problem

$$\begin{cases} h'(d) = p_1 + 2p_2 d + 3p_3 d^2 + \ldots \geq 0 & \Longrightarrow \ h(d) \text{ is increasing} \\ h''(d) = 2p_2 + 6p_3 d + 12p_4 d^2 \ldots \geq 0 & \Longrightarrow \ h(d) \text{ is convex} \end{cases}$$

$\boxed{d = h(d)}$ and $d = 1$ is a solution $\to \exists$ 3 cases:

- $\exists$ Another intersect < 1
  $\to d < 1$ or $d = 1$.
- $d = 1$ is the only intersect
  $\to d = 1$.
- $\exists$ Another intersect > 1
  $\to d = 1$ (since $0 \geq d \geq 1$).



Extinction problem

$$h'(1) = p_1 + 2p_2 + 3p_3 + \cdots = \mathbb{E}(X_{n,i})$$

$$\begin{cases} \mathbb{E}(X_{n,i}) \leq 1 & \implies d = 1 \\ \mathbb{E}(X_{n,i}) > 1 & \implies d < 1 \text{ or } d = 1 \end{cases}$$