3 Cannings models

3.1 Definition of the model

3.1.1 Def. (Exchangeability)
Finitely many r.v. $X_1, \dots, X_N$ are called exchangeable, if $(X_{\pi 1}, \dots, X_{\pi N}) \stackrel{d}{=} (X_1, \dots, X_N)$ for all permutations π of $[N] := \{1, \dots, N\}$.

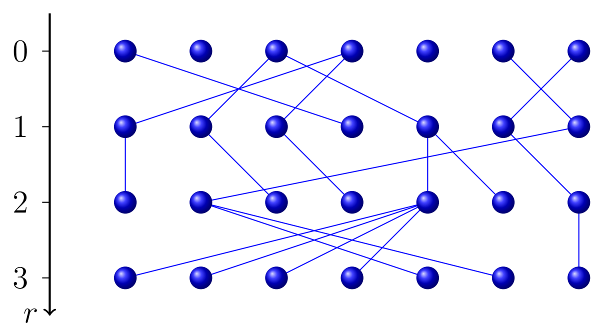
Rem.
X_n, $n \in [N]$, iid. $\Rightarrow$ X_n, $n \in [N]$, exchangeable. $\Rightarrow$ $X_n \stackrel{d}{=} X_m \ \forall\, n, m \in [N]$.

The following model was introduced by Cannings (1974, 1975).

3.1.2 Def. (Cannings Model)
A population model with non-overlapping generations $r \in \mathbb{N}_0$ and fixed population size $N \in \mathbb{N}$ in each generation is called a Cannings model, if the numbers $\nu_i^{(r)}$ of offspring of individual $i \in [N]$ alive in generation $r \in \mathbb{N}_0$ have the following properties.

(i) For each generation $r \in \mathbb{N}_0$ the r.v. $\nu_i^{(r)}$, $i \in [N]$, are exchangeable with $\nu_1^{(r)} + \cdots + \nu_N^{(r)} = N$.

(ii) The offspring vectors $\nu^{(r)} := (\nu_1^{(r)}, \dots, \nu_N^{(r)})$, $r \in \mathbb{N}_0$, are iid.



Representation of a Cannings model with population size $N = 7$

3.1.3 Examples

1. *Moran model (MM): $\nu^{(r)}$ is a random permutation of $(2, 1, \dots, 1, 0)$.*

2. *Wright–Fisher model (WFM): $\nu^{(r)}$ has a symmetric multinomial distribution, i.e., for all $n_1, \dots, n_N \in \mathbb{N}_0$ with $n_1 + \cdots + n_N = N$,*

$$P(\nu_1^{(r)} = n_1, \dots, \nu_N^{(r)} = n_N) \;=\; \frac{N! N^{-N}}{n_1! \cdots n_N!}.$$

3.2 Descendants and extinction probability

3.2.1 Def. (Descendants)
For $i \in \{0,\dots,N\}$ let $X_r^{(i)}$ denote the number of descendants of the individuals 1 to i of generation 0 in generation $r \in \mathbb{N}_0$. The process $X := (X_r^{(i)})_{r\in\mathbb{N}_0}$ is called descendant process or forward process.

Rem.
It is easily seen that X is a HMC with state space $\{0,\dots,N\}$, initial state $X_0^{(i)} = i$ and transition probabilities $\pi_{jk} := P(X_{r+1}^{(i)} = k \,|\, X_r^{(i)} = j)$ given by

$$\pi_{jk} \;=\; P(X_1^{(j)} = k) \;=\; P(\nu_1 + \cdots + \nu_j = k), \qquad j,k \in \{0,\dots,N\},$$

where $\nu_i := \nu_i^{(0)}$, $i \in [N]$.

3.2.2 Example
For the WFM, $\nu_1 + \cdots + \nu_j$ has a binomial distribution with parameters N and $p_j := j/N$, i.e.

$$\pi_{jk} \;=\; B(N,p_j,k) \;:=\; \binom{N}{k}\left(\frac{j}{N}\right)^k\left(1-\frac{j}{N}\right)^{N-k}.$$

3.2.3 Def. (Extinction Probability)
Let $N \in \mathbb{N}$. For $i \in \{0,\dots,N\}$ let

$$q_i \;:=\; P(X_r^{(i)} = 0 \text{ eventually}) \;=\; P\Bigg(\bigcup_{r\in\mathbb{N}_0}\{X_r^{(i)} = 0\}\Bigg) \;=\; \lim_{r\to\infty} P(X_r^{(i)} = 0)$$

denote the extinction probability of the descendants of i individuals.

3.2.4 Theorem
The process $X := (X_r^{(i)})_{r\in\mathbb{N}_0}$ is a nonnegative bounded martingale, which converges a.s. and in L^p ($p > 0$) as $r \to \infty$ to a r.v. $X_\infty^{(i)}$ and $(X_r^{(i)})_{r\in\mathbb{N}_0\cup\{\infty\}}$ is a martingale. If $P(\nu_1 = 1) < 1$, then the states $1,\dots,N-1$ are transient and $X_\infty^{(i)}$ takes a.s. the values 0 and N with probability q_i and $1-q_i$ respectively.

Proof.
For all $j \in \{0,\dots,N\}$ with $P(X_r^{(i)} = j) > 0$,

$$\begin{aligned}
\mathrm{E}(X_{r+1}^{(i)} \,|\, X_r^{(i)} = j) \;&=\; \sum_{k=0}^N kP(X_{r+1}^{(i)} = k \,|\, X_r^{(i)} = j) \;=\; \sum_{k=0}^N k\pi_{jk} \\
&=\; \sum_{k=0}^N kP(\nu_1 + \cdots + \nu_j = k) \;=\; \mathrm{E}(\nu_1 + \cdots + \nu_j) \;=\; j.
\end{aligned}$$

$\Rightarrow X$ is a nonnegative martingale (Exercise 1.3.2).

Let $p > 0$. $\sup_{r\in\mathbb{N}_0} |X_r^{(i)}|^p \le N^p$. $\Rightarrow X$ is p-times uniformly integrable, and hence converges a.s. and in L^p (see Bauer, 'Probability Theory', Corollary 19.4) to a r.v. $X_\infty^{(i)}$ such that $(X_r^{(i)})_{r\in\mathbb{N}_0\cup\{\infty\}}$ is still a martingale. Assume now that $P(\nu_1 = 1) < 1$. Then[2] for $i \in \{1,\dots,N-1\}$

$$\sum_{j=i+1}^{N} \pi_{ij} \;=\; P(\nu_1 + \cdots + \nu_i > i) \;>\; 0.$$

From a state $i \in \{1,\dots,N-1\}$ one reaches in one step a state $j > i$ with positive probability. State space is finite. $\Rightarrow$ One reaches (iteratively) from a state i after a finite number $n_i \in \mathbb{N}$ of steps the absorbing state N with positive probability, i.e. $\pi_{iN}^{(n_i)} > 0$. Define $n := \max(n_1,\dots,n_{N-1})$. $\Rightarrow \pi_{iN}^{(n)} \ge \pi_{iN}^{(n_i)}\pi_{NN}^{(n-n_i)} = \pi_{iN}^{(n_i)} > 0$. From $\pi_{00}^{(n)} = \pi_{NN}^{(n)} = 1$ it follows that $\inf_{0\le i\le N}(\pi_{i0}^{(n)} + \pi_{iN}^{(n)}) > 0$. Thus, for $m \in \mathbb{N}$

$$\begin{aligned} &P(0 < X_{nm}^{(i)} < N) \\ &\quad= \sum_{j=1}^{N-1} P(0 < X_{nm}^{(i)} < N \,|\, X_{n(m-1)}^{(i)} = j)\, P(X_{n(m-1)}^{(i)} = j) \\ &\quad= \sum_{j=1}^{N-1} P(0 < X_{n}^{(j)} < N)\, P(X_{n(m-1)}^{(i)} = j) \\ &\quad= \sum_{j=1}^{N-1} (1 - \pi_{j0}^{(n)} - \pi_{jN}^{(n)})\, P(X_{n(m-1)}^{(i)} = j) \\ &\quad\le \alpha\, P(0 < X_{n(m-1)}^{(i)} < N) \quad \text{with } \alpha := 1 - \inf_{0\le i\le N}(\pi_{i0}^{(n)} + \pi_{iN}^{(n)}) < 1. \end{aligned}$$

Induction on m. $\Rightarrow P(0 < X_{nm}^{(i)} < N) \le \alpha^m \;\forall\, m \in \mathbb{N}$.

$X_{nm}^{(i)} \xrightarrow[m\to\infty]{d} X_\infty^{(i)}$. $\Rightarrow P(0 < X_\infty^{(i)} < N) \le \lim_{m\to\infty} \alpha^m = 0$.

$\Rightarrow\; P(X_\infty^{(i)} \in \{0,N\}) = 1$. From $X_r^{(i)} \xrightarrow[r\to\infty]{d} X_\infty^{(i)}$ it follows that

$$P(X_\infty^{(i)} = 0) \;=\; \lim_{r\to\infty} P(X_r^{(i)} = 0) \;=\; P(X_r^{(i)} = 0 \text{ eventually}) \;=\; q_i$$

[2] The assumption $\nu_1+\cdots+\nu_i \le i$ together with $\mathrm{E}(\nu_1+\cdots+\nu_i) = i$ yields $\nu_1+\cdots+\nu_i \equiv i$ and from the exchangeability it follows that $\nu_{k_1} + \cdots + \nu_{k_i} \equiv i$ for arbitrary distinct $k_1,\dots,k_i$. Substraction of two of such equations with $k_1 := k$, $l_1 := l$ and $l_j = k_j$ for $j \in \{2,\dots,i\}$ shows that $\nu_k \equiv \nu_l$ for all $k,l \in \{1,\dots,N\}$. Since $\sum_{k=1}^N \nu_k = N$ it follows that $P(\nu_1 = 1) = 1$.

and hence $P(X_\infty^{(i)} = N) = 1 - q_i$. Moreover,

$$\begin{aligned} P(X_r^{(i)} \in \{0,N\} \text{ eventually}) &= P\Big(\bigcup_{r\in\mathbb{N}_0} \{X_r^{(i)} \in \{0,N\}\}\Big) \\ &= \lim_{r\to\infty} P(X_r^{(i)} \in \{0,N\}) = P(X_\infty^{(i)} \in \{0,N\}) = 1. \end{aligned}$$

Thus, $P(0 < X_r^{(i)} < N\ \infty\text{-often}) = 0$.

$\Rightarrow$ The states $1,\ldots,N-1$ are transient. □

3.2.5 Lemma
Let $N \in \mathbb{N}$. $q = (q_0,\ldots,q_N)^\top$ is an eigenvector of the transition matrix Π to the eigenvalue 1, i.e. $\Pi q = q$. Moreover, q is uniquely determined by this fixed point equation and the boundary conditions $q_0 = 1$ and $q_N = 0$.

Proof.
Obviously, $q_0 = 1$, $q_N = 0$. By the MP and the time homogeneity, for $i \in \{0,\ldots,N\}$ and $r \in \mathbb{N}_0$

$$P(X_{r+1}^{(i)} = 0) = \sum_{j=0}^N P(X_{r+1}^{(i)} = 0 \,|\, X_1^{(i)} = j)\,\pi_{ij} = \sum_{j=0}^N P(X_r^{(j)} = 0)\,\pi_{ij}.$$

Letting $r \to \infty$ yields $q_i = \sum_{j=0}^N q_j\,\pi_{ij}$. Thus, $\Pi q = q$.

Uniqueness: Let $x = (x_0,\ldots,x_N)^\top$, $\Pi x = x$, $x_0 = 1$ and $x_N = 0$. $\Rightarrow \Pi^r x = x\ \forall\, r \in \mathbb{N}$. $\Rightarrow$

$$x_i = \sum_{j=0}^N \pi_{ij}^{(r)}\,x_j = \sum_{j=0}^N P(X_r^{(i)} = j)\,x_j \quad \forall\, i \in \{0,\ldots,N\}.$$

$X_r^{(i)} \xrightarrow[r\to\infty]{d} X_\infty^{(i)}$, $P(X_\infty^{(i)} = 0) = q_i = 1 - P(X_\infty^{(i)} = N)$.

Letting $r \to \infty$ yields

$$x_i = \sum_{j=0}^N P(X_\infty^{(i)} = j)\,x_j = q_i\,x_0 + (1-q_i)\,x_N = q_i. \qquad \square$$

Rem.
The map $\varphi : [0,1]^{N+1} \to [0,1]^{N+1}$, defined via $\varphi(x) := \Pi x$ for all $x \in [0,1]^{N+1}$, is not contractive, since $\|\Pi\| := \sup_i \sum_j \pi_{ij} = 1$. The Banach fixed point theorem is hence not applicable to φ.

3.2.6 Corollary (Extinction probability)
For all Cannings models, $q_i = 1 - i/N$*,* $i \in \{0, \dots, N\}$*.*

Proof.
First proof. By Lemma 3.2.5 it suffices to verify that $q = (q_0, \dots, q_N)^\top$ with $q_i := 1 - i/N$ is a solution to the equation $\Pi q = q$. This is obvious, since for $i \in \{0, \dots, N\}$,

$$(\Pi q)_i \;=\; \sum_{j=0}^{N} \pi_{ij} q_j \;=\; \sum_{j=0}^{N} \pi_{ij}\Big(1 - \frac{j}{N}\Big) \;=\; 1 - \frac{\mathrm{E}(X_1^{(i)})}{N} \;=\; 1 - \frac{i}{N} \;=\; q_i. \qquad \square$$

Second proof. $(X_r)_{r \in \mathbb{N}_0 \cup \{\infty\}}$ is a martingale. $\Rightarrow$ $N(1 - q_i) = \mathrm{E}(X_\infty^{(i)}) = \mathrm{E}(X_0^{(i)}) = i$. $\Rightarrow$ $q_i = 1 - i/N$. $\square$

3.3 Ancestors

3.3.1 Def. (Ancestors)
Let $N \in \mathbb{N}$*. For* $n, r \in \mathbb{N}_0$ *with* $n \le r$ *let* $R_n^{(r)}$ *denote the number of ancestors of all the* N *individuals of generation* r *in generation* $r - n$*.*

Rem.
It is readily seen that $(R_n^{(r)})_{n \in \{0,\dots,r\}}$ is a HMC, called the ancestral process or backward process. The following lemma shows in particular that the transition probabilities

$$p_{ij} \;:=\; P(R_{n+1}^{(r)} = j \,|\, R_n^{(r)} = i)$$

neither depend on n nor on r.

3.3.2 Lemma (Transition Probabilities)
Let $n, r \in \mathbb{N}_0$ *with* $n < r$*. Then, for all* $i, j \in \{0, \dots, N\}$*,*

$$p_{ij} \;=\; \frac{\binom{N}{j}}{\binom{N}{i}} \sum_{\substack{m_1,\dots,m_j \in \mathbb{N} \\ m_1 + \cdots + m_j = i}} \mathrm{E}\left(\binom{\nu_1}{m_1} \cdots \binom{\nu_j}{m_j}\right).$$

In particular, $p_{ii} = \mathrm{E}(\nu_1 \cdots \nu_i)$*.*

Proof.
We have

$$p_{ij} \;=\; \sum_k \underbrace{P(R_{n+1}^{(r)} = j \,|\, \nu^{(r-n-1)} = k, R_n^{(r)} = i)}_{=:A} \underbrace{P(\nu^{(r-n-1)} = k \,|\, R_n^{(r)} = i)}_{=:B},$$

where the sum extends over all $k = (k_1, \dots, k_N)$ with $P(\nu^{(r-n-1)} = k, R_n^{(r)} = i) > 0$.

$R_n^{(r)}$ is independent of $\nu^{(r-n-1)} \stackrel{d}{=} \nu$. $\Rightarrow B = P(\nu = k)$.

In order to compute A consider the following equivalent problem.

Given: N colors and one box. The box contains N balls (children), more precisely, k_s balls of color s ($1 \le s \le N$).

Now sample i balls (without replacement) from the box. Question: What is the probability, that among the i drawn balls one sees exactly j colors? Multivariate hypergeometric distribution. $\Rightarrow$

$$A = \sum_m \frac{\binom{k_1}{m_1} \cdots \binom{k_N}{m_N}}{\binom{N}{i}},$$

where the sum extends over all $m = (m_1, \dots, m_N) \in \mathbb{N}_0^N$ with $m_1 + \cdots + m_N = i$ and $|\{s \mid 1 \le s \le N, m_s > 0\}| = j$. Plugging in A and B and interchanging the two occurring sums yields

$$p_{ij} = \sum_m \frac{1}{\binom{N}{i}} \mathrm{E}\left(\binom{\nu_1}{m_1} \cdots \binom{\nu_N}{m_N} \right).$$

The result follows from the exchangeability and since $m_s > 0$ for exactly j indices. □

3.3.3 Example
For the WFM,

$$p_{ij} = \frac{(N)_j}{N^i} S(i,j),$$

where the numbers $S(i,j)$ are the Stirling numbers of the second kind and $(N)_j := N(N-1)\cdots(N-j+1)$.

Proof. *This follows from Lemma 3.3.2, but the calculations are somewhat tedious. We provide a different proof. In the WFM each child chooses at random and independently of all other individuals its parent. Thus, p_{ij} is the probability to obtain exactly j nonempty boxes, when i balls (the children) are allocated at random and independently to N boxes (the parents). Altogether there are N^i such allocations. For the j boxes which should be nonempty, one has $N(N-1)\cdots(N-j+1) = (N)_j$ choices, and $S(i,j)$ is (by def.) the number of ways to partition the i balls into j groups, where then the balls of the k-th group, $k \in \{1, \dots, j\}$, are allocated in box k.*