Evolutionary Dynamics

Exercises 3

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Exercises marked with a "💻" are programming exercises. These can be solved in a programming language of your choice. Please make sure to hand in your code along with your answers to these exercises.

Problem 1: Random walk (tutorial exercise)
Consider a symmetric, time-discrete random walk in one dimension, $\{X(t) \mid X(t) \in \mathbb{Z}, t \in \mathbb{N}_0\}$. Let $a/2$ denote the probability of jumping forward or backward, respectively. Hence we have transition probabilities $P_{i,i+1} = P_{i,i-1} = a/2$, $P_{i,i} = 1 - a$ and otherwise $P_{i,j} = 0$.

Hint: Express $X(t)$ as the sum of increments $\Delta(t) \in \{-1, 0, +1\}$, i.e. $X(t) = X(0) + \Delta(1) + \cdots + \Delta(t)$ and use that the $\Delta(t)$ are iid (identically independently distributed).

(a) Argue why $\mathrm{E}[\Delta(t)] = 0$.

(b) Argue why $\mathrm{E}[X(t)] = x_0$, where $x_0 = X(0)$.

(c) Calculate the variance $\mathrm{Var}[\Delta(t)]$.
Hint: $\mathrm{Var}[X] = \sum_{i=1} p_i \cdot (x_i - \hat{x})^2$.

(d) Show that the variance of $X(t)$ equals $\mathrm{Var}[X(t)] = at$.

Problem 2: Neutral Moran process
Consider the neutral Moran process $\{X(t) \mid t = 0, 1, 2, \dots\}$ with two alleles A and B, where $X(t)$ is the number of A alleles in generation t.

(a) Show that the process has a stationary mean: **(1 point)**

$$E[X(t) \mid X(0) = i] = i.$$

Hint: First calculate $E[X(t) \mid X(t-1)]$ and use the *law of total expectation*, $E_Y[Y] = E_Z[E_Y[Y \mid Z]]$ with $Y = X(t)$ and $Z = X(t-1)$.

(b) Show that the variance of $X(t)$ is given by: **(2 points)**

$$\mathrm{Var}[X(t) \mid X(0) = i] = V_1 \frac{1 - (1 - 2/N^2)^t}{2/N^2}. \tag{1}$$

Consider the following steps:

(i) Show that $V_1 := \mathrm{Var}[X(1) \mid X(0) = i] = 2i/N(1 - i/N)$.

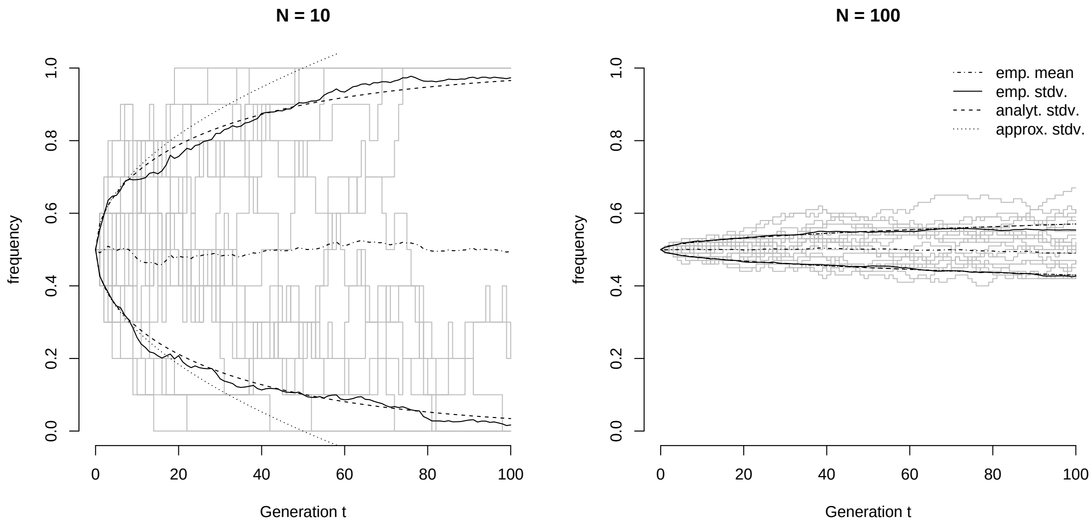
(ii) Then use that $\forall t > 0$ $\mathrm{Var}[X(t) \mid X(t-1) = i] = \mathrm{Var}[X(1) \mid X(0) = i]$ (why?) and the *law of total variance*, $\mathrm{Var}[Y] = E_Z[\mathrm{Var}_Y[Y \mid Z]] + \mathrm{Var}_Z[E_Y[Y \mid Z]]$, to derive

$$\mathrm{Var}[X(t) \mid X(0) = i] = V_1 + (1 - 2/N^2)\,\mathrm{Var}[X(t-1) \mid X(0) = i] \tag{2}$$

(iii) The inhomogeneous recurrence equation above can be solved by bringing it into the form $x_t - a = b(x_{t-1} - a)$, from which it follows that $x_t - a = b^{t-1}(x_1 - a)$.

(c) Derive an approximation of (1) for large N. **(1 point)**

(d) Write a small simulation to check the results from (a), (b) and (c). Use $N \in \{10, 100\}$ and $i = N/2$. Simulate 1000 trajectories for $t = 1, \ldots, 100$, and compute empirical mean and variance. Your results could look like on the figures below. 💻 **(2 points)**



Grey lines denote single realisations of the process. Shown are also empirical mean and empirical standard deviation, as well as the standard deviation according to (1) and its approximation for large N.

Problem 3: Absorption in a birth-death process
Consider a birth-death process with state space $\{0, 1, \ldots, N\}$, transition probabilities $P_{i,i+1} = \alpha_i$, $P_{i,i-1} = \beta_i > 0$, and absorbing states 0 and N.

(a) Show that the probability of ending up in state N when starting in state i is **(3 points)**

$$x_i = \frac{1 + \sum_{j=1}^{i-1} \prod_{k=1}^{j} \gamma_k}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \gamma_k} \tag{3}$$

Consider the following steps:

(i) The vector $x = (x_0, \ldots x_N)^T$ solves $x = Px$ where P is the transition matrix. (Why?) Set $y_i = x_i - x_{i-1}$ and $\gamma_i = \beta_i / \alpha_i$. Show that $y_{i+1} = \gamma_i y_i$.

(ii) Show that $\sum_{i=1}^{\ell} y_i = x_\ell$.

(iii) Show that $x_\ell = \left(1 + \sum_{j=1}^{\ell-1} \prod_{k=1}^{j} \gamma_k\right) x_1$.

(b) Using (3), show that for the Moran process *with selection* **(1 point)**

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

where r is the relative fitness advantage. Use *l'Hôpital's rule* to calculate the limit $r \to 1$.