ETH zürich D BSSE Computational Biology Group

Evolutionary Dynamics

Exercises 3

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

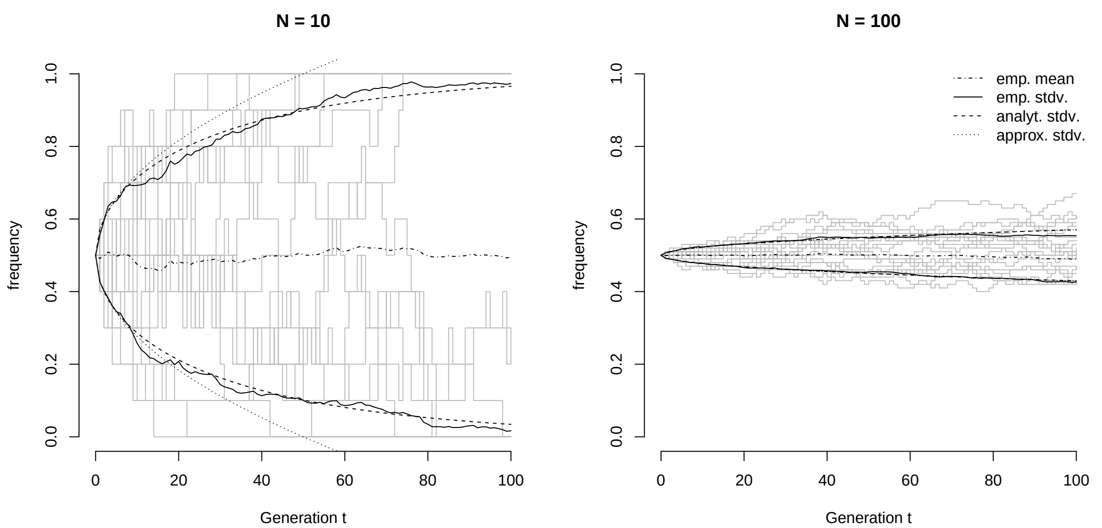
(ii) Then use that $\forall t > 0$ $\mathrm{Var}[X(t) \mid X(t-1) = i] = \mathrm{Var}[X(1) \mid X(0) = i]$ (why?) and the *law of total variance*, $\mathrm{Var}[Y] = E_Z[\mathrm{Var}_Y[Y \mid Z]] + \mathrm{Var}_Z[E_Y[Y \mid Z]]$, to derive

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

(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) In your favourite programming language, 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 $t = 1, \dots, 100$, and compute empirical mean and variance. Your results could look like this: **(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 2: Absorption in a birth-death process

Consider a birth-death process with state space $\{0, 1, \dots, N\}$, 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 $x = (x_0, \dots x_N)^T$ 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 $r \to 1$.