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Evolutionary Dynamics

Exercises 3

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Problem 1: Neutral Moran process

Consider the neutral Moran process $\{X(t) \mid t = 0, 1, 2, \ldots\}$ 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:

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

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:

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

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.

Problem 2: 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

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

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*

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

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

Problem 3: Accumulation of deleterious mutations

Suppose that we extend the Moran process such that each new individual (the result of a birth event) has a small chance μ of acquiring a mutation. Further suppose that the overwhelming majority of mutations are slightly deleterious, such that each mutation independently reduces fitness by 1%.

(a) If $N = 1000$ and the population is initially homogeneous, what is the probability that a mutation will fixate (assuming that no other mutations occur before fixation)?

(b) If each individual's genome contains 10^6 sites that can undergo deleterious mutation, and $\mu = 10^{-5}$ for each site, what is the probability that a new individual acquires at least one new mutation?

(c) What can you predict about the longterm future of this population?

(d) What factors might prevent this outcome in natural populations?