

# Evolutionary Dynamics Homework 6

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## Problem 1: One-dimensional Fokker-Planck equation

Consider the one-dimensional Fokker-Planck equation with constant coefficients,

$$\partial_t \psi(p, t) = -m \partial_p \psi(p, t) + \frac{v}{2} \partial_p^2 \psi(p, t), \quad (1)$$

with  $p \in \mathbb{R}, v > 0$ .

(a) See below.

Show that for vanishing selection,  $m = 0$ ,

$$\psi(p, t) = \frac{1}{\sqrt{2\pi vt}} \exp\left(-\frac{p^2}{2vt}\right) \quad (2)$$

solves the Fokker-Planck equation. To which initial condition does this solution correspond?

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For vanishing selection  $m = 0$ , the Fokker-Planck equation can be written as simply

$$\partial_t \psi(p, t) = \frac{v}{2} \partial_p^2 \psi(p, t) \quad (3)$$

Let's compute the left-hand side and the right-hand side to show that the solution is correct.

LHS of (3)

$$\begin{aligned} \partial_t \psi(p, t) &= \partial_t \left( \frac{1}{\sqrt{2\pi vt}} \exp\left(-\frac{p^2}{2vt}\right) \right) \\ &= -\frac{1}{\sqrt{2\pi vt}} \cdot \frac{1}{2t} \cdot \exp\left(-\frac{p^2}{2vt}\right) + \frac{1}{\sqrt{2\pi vt}} \cdot \frac{p^2}{2vt^2} \cdot \exp\left(-\frac{p^2}{2vt}\right) \\ &= \frac{p^2 - vt}{2vt^2} \cdot \frac{1}{\sqrt{2\pi vt}} \cdot \exp\left(-\frac{p^2}{2vt}\right) \end{aligned} \quad (4)$$

RHS of (3)

$$\begin{aligned}
\frac{v}{2} \partial_p^2 \psi(p, t) &= \frac{v}{2} \partial_p \left( \partial_p \left( \frac{1}{\sqrt{2\pi vt}} \exp \left( -\frac{p^2}{2vt} \right) \right) \right) \\
&= \frac{v}{2\sqrt{2\pi vt}} \partial_p \left( \partial_p \left( \exp \left( -\frac{p^2}{2vt} \right) \right) \right) \\
&= \frac{v}{2\sqrt{2\pi vt}} \partial_p \left( \left( -\frac{p}{vt} \right) \cdot \exp \left( -\frac{p^2}{2vt} \right) \right) \\
&= \frac{v}{2\sqrt{2\pi vt}} \cdot \left( -\frac{1}{vt} \exp \left( -\frac{p^2}{2vt} \right) + \frac{p^2}{v^2 t^2} \cdot \exp \left( -\frac{p^2}{2vt} \right) \right) \\
&= -\frac{1}{\sqrt{2\pi vt} \cdot 2t} \cdot \exp \left( -\frac{p^2}{2vt} \right) + \frac{1}{\sqrt{2\pi vt}} \cdot \frac{p^2}{2vt^2} \cdot \exp \left( -\frac{p^2}{2vt} \right) \\
&= \frac{p^2 - vt}{2vt^2} \cdot \frac{1}{\sqrt{2\pi vt}} \cdot \exp \left( -\frac{p^2}{2vt} \right)
\end{aligned} \tag{5}$$

It's clear that (4) equals (5), so (2) is indeed the solution.

To investigate the initial condition, we need to examine the behavior of  $\psi(p, t)$  as  $t \rightarrow 0^+$ . As  $t \rightarrow 0^+$ , we have:

- The exponential term  $\exp(-p^2/(2vt))$  approaches:
  - 0,  $\forall p \neq 0$  because  $-p^2/(2vt) \rightarrow -\infty$
  - 1 for  $p = 0$ .
- The prefactor  $\frac{1}{\sqrt{2\pi vt}}$  approaches  $\infty$  for  $t \rightarrow 0^+$ .

This behavior is consistent with the Dirac delta function  $\delta(p)$ . Hence, the initial condition is

$$\psi(p, 0) = \delta(p),$$

where  $\delta(p)$  is the Dirac delta function defined as

$$\delta(p) = \begin{cases} 0, & \text{if } p \neq 0, \\ \infty, & \text{if } p = 0. \end{cases}$$

This means the initial distribution is concentrated at  $p = 0$ , which represents the fact that the starting population is initially at a single allele frequency.

**(b) Construct a solution for constant selection,  $m \neq 0$ , by substituting  $z = p - mt$  for  $p$  in (1). What is the mean and variance?**

Let  $z(p, t) = p - mt$ , then we have  $\partial_p z(p, t) = 1$ , and  $\partial_t z(p, t) = -m$ . Substitute  $z(p, t)$  into  $\psi(p, t)$  to obtain  $\psi(z, t)$ , using the chain rule, we have

$$\begin{aligned}
\frac{\partial \psi(p, t)}{\partial t} &= \frac{\partial \psi(z, t)}{\partial z} \frac{\partial z}{\partial t} + \frac{\partial \psi(z, t)}{\partial t} \frac{\partial \mathcal{H}}{\partial t} \\
&= -m \frac{\partial \psi(z, t)}{\partial z} + \frac{\partial \psi(z, t)}{\partial t}
\end{aligned} \tag{6}$$

$$\begin{aligned}
\frac{\partial \psi(p, t)}{\partial p} &= \frac{\partial \psi(z, t)}{\partial z} \frac{\partial z}{\partial p} \\
&= \frac{\partial \psi(z, t)}{\partial z}
\end{aligned} \tag{7}$$

Using (6) and (7), we can rewrite the Fokker-Planck equation:

$$\begin{aligned} \frac{\partial \psi(p, t)}{\partial t} &= -m \frac{\partial \psi(p, t)}{\partial p} + \frac{v}{2} \frac{\partial^2 \psi(p, t)}{\partial p^2} \\ \cancel{-m \frac{\partial \psi(z, t)}{\partial z}} + \frac{\partial \psi(z, t)}{\partial t} &= \cancel{-m \frac{\partial \psi(z, t)}{\partial z}} + \frac{v}{2} \frac{\partial^2 \psi(z, t)}{\partial z^2} \\ \frac{\partial \psi(z, t)}{\partial t} &= \frac{v}{2} \frac{\partial^2 \psi(z, t)}{\partial z^2} \end{aligned} \quad (8)$$

Voila! This equation (8) has exactly the same form as

## Problem 2: Diffusion approximation of the Moran process

Derive a diffusion approximation for the Moran process of two species. Assume the first species has a small selective advantage. (a) The general definition for the drift coefficient is  $M(p) = E[X(t) - X(t-1) | X(t-1) = i] / N$ , where  $p = i/N$  and  $X(t)$  denotes the abundance of the first allele. Evaluate this expression for the Moran process with selection. Show that the Fisher process from the lecture, divided by  $N$ . (1 point) (b) By a similar argument calculate the diffusion coefficient  $V(p)$ . (1 point) (c) Use your results from (a) and (b) in the forward Kolmogorov equation to present a diffusion equation for the Moran model. (1 point) (d) Now assume that  $s \ll 1$ . Approximate your results from (a) and (b) and use the general expression for the fixation probability  $\rho(p_0)$  to show that the fixation probability is given by: (1 point)  $\rho(p_0 = 1/N) = 1 - e^{-s}$   $1 - e^{-Ns}$ . (3) (e) Take the limit to derive a result for the fixation probability of a neutral allele,  $s = 0$ . Evaluate (3) for  $N = 10$  and  $N = 1000$  for both positive,  $s = 2\%$ , and negative selection,  $s = -2\%$ , respectively. Compare your results with  $p_1$  of the exact Moran process. (1 point) 1 Problem 3: Absorption time in the diffusion approximation In the diffusion approximation of a process with absorbing states 0 and 1 the expected fixation time, conditioned on absorption in state 1, reads:  $\tau_1(p_0) = 2(S(1) - S(0)) \int_{p_0}^1 \frac{\rho(p)(1 - \rho(p))}{e^{-A(p)} V(p)} dp + 1 - \rho(p_0)$   $\int_{p_0}^1 \frac{\rho(p)}{p^2} e^{-A(p)} V(p) dp$ , where  $\rho(p)$  denotes the fixation probability,  $A(p) = \int_{p_0}^p \frac{2M(p')}{V(p')} dp$ , and  $S(p) = \int_{p_0}^p \frac{1}{p'^2} \exp(-A(p')) dp'$ . (a) Calculate the conditional expected waiting time for fixation,  $\tau_1(p_0)$ , of an allele of frequency  $p_0$  in the neutral Wright-Fisher process. Approximate the result for small  $p_0$ . (1 point) (b) Compute  $\tau_0$ , the conditional expected waiting time until extinction (absorption in state 0) in the neutral Wright-Fisher process. Also derive the unconditional  $\tau$  until either fixation or extinction