# IV The Fokker-Planck approximation of substitution sequences.

Monomorphic resident population with strategy $x \in \mathbb{R}$.

$p(x,t)$ : probability density of of strategy $x$ at time $t$.

$K(\Delta, x)$ : probability density flux of substitution step size $\Delta$ given res. strat. $x$.

The "master equation":

$$\boxed{\frac{\partial p(x,t)}{\partial t} = \int K(\Delta, x-\Delta)\, p(x-\Delta, t)\, d\Delta + - \int K(\Delta, x)\, p(x,t)\, d\Delta .}$$

If $K$ is very concentrated around $\Delta = 0$, then we make the $2^{nd}$-order Taylor approximation:

$$\boxed{\begin{aligned} K(\Delta, \underline{x-\Delta})\, p(\underline{x-\Delta}, t) \doteq\; & K(\Delta, x)\, p(x,t) - \Delta \frac{\partial}{\partial x}\big(K(\Delta,x)\, p(x,t)\big) \\ & + \tfrac{1}{2}\Delta^2 \frac{\partial^2}{\partial x^2}\big(K(\Delta,x)\, p(x,t)\big) \end{aligned}}$$

Substitution into the "master equation" gives

$$\frac{\partial p(x,t)}{\partial t} = -\frac{\partial}{\partial x}\int \Delta K(\Delta,x)\, p(x,t)\, d\Delta + \frac{1}{2}\frac{\partial^2}{\partial x^2}\int \Delta^2 K(\Delta,x)\, p(x,t)\, d\Delta$$

$$= -\frac{\partial}{\partial x}\Big(\mathcal{E}\{\Delta|x\}\, p(x,t)\Big) + \frac{1}{2}\frac{\partial^2}{\partial x^2}\Big(\mathcal{E}\{\Delta^2|x\}\, p(x,t)\Big)$$

In other words, when evolutionary steps are small, we can approximate the "master equation" (which is exact) by the Fokker-Planck equation

$$\boxed{\partial_t p = -\partial_x(v_E p) + \frac{1}{2}\partial_{xx}(D_E p)}$$

where

$v_E(x) := \mathcal{E}\{\Delta|x\}$ is the average evol. step size.

$D_E(x) := \mathcal{E}\{\Delta^2|x\}$ is the average of the squared step size.

$v_E(x)$ is also called the deterministic drift, and $D_E(x)$ the diffusion coefficient.
(Some people absorb the factor $\frac{1}{2}$ into $D_E(x)$ )

## How to calculate $v(x)$ and $D(x)$?

Decompose $K(\Delta, x)$ into the following (more elementary) factors:

$$\boxed{K(\Delta, x) = \mu(x)\, b_E(x)\, n_E(x)\, \pi_E(x+\Delta)\, \varphi(\Delta, x)}$$

where

$\mu(x)$ : mutation probability per birth event

$b_E(x)$ : per capita birth rate in resident environment E

$n_E(x)$ : resident equilibrium pop. size (we assume res. equil. indeed)

$\pi_E(x+\Delta)$ : invasion probability for mutant $y = x+\Delta$ in resident environment E.

$\varphi(\Delta, x)$ : mutation stepsize distribution.

- $\mu(x)$, $b_E(x)$ and $\varphi(\Delta, x)$ are basic model ingredients and therefore are given.
- $n_E(x)$ can be calculated from the resident dynamics.
- $\Pi_E(x+\Delta)$ we have to calculate here.

<u>This is how we do that</u>:

$b := b_E(x+\Delta)$ percapita birth rate for mutant $y = x+\Delta$ in res. env. E

$d := d_E(x+\Delta)$ percapita death rate for mutant $y = x+\Delta$ in res. env. E.

$$\Rightarrow \quad S_E(x+\Delta) = b_E(x+\Delta) - d_E(x+\Delta) \quad \underline{\text{inv. fitness}}$$

Even if $S_E(x+\Delta) > 0$, the mutant may go extinct just by bad luck. The reason is that initially the mutant is very rare: only one or a few copies around.

→ Demographic stochasticity important.

$q(k)$ : probability that a mutant individual produces $k \geq 0$ offspring during its life.

$$q(k) = \int_0^\infty \underbrace{\frac{(bt)^k}{k!} e^{-bt}}_{\substack{\uparrow \\ \text{poisson-distr.} \\ \text{offspring nr.}}} \underbrace{d e^{-dt}}_{\substack{\uparrow \\ \text{exp. distr.} \\ \text{lifetime}}} dt =$$

$$= \underbrace{\left(\frac{b}{b+d}\right)^k \frac{d}{b+d}}_{\substack{\uparrow \\ k \text{ birth events and one} \\ \text{(final) death event}}} \quad \left(\begin{array}{c}\text{Geometric} \\ \text{distribution}\end{array}\right)$$

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$z_n$ : probability that the mutant family (= founder + descendants) has died out before the $n^{th}$ generation (founder in zeroth generation)

$z_0 = 0$

$$\boxed{z_{n+1} = \sum_{k=0}^\infty \underbrace{q(k)}_{\substack{\uparrow \\ \text{prob. that} \\ \text{founder has} \\ k \text{ children.}}} \cdot \underbrace{z_n^k}_{\substack{\uparrow \\ \text{prob. that each of} \\ \text{the lineages founded} \\ \text{by the } k \text{ children} \\ \text{has died out before} \\ n^{th} \text{ generation.}}} =: g(z_n)}$$

moment generating function of $q$.

$g(z) := \sum_{k=0}^{\infty} z^k q(k)$ is the moment generating function of the prob. distr. $q$.

Since $q$ is Geometric (page 5) we have

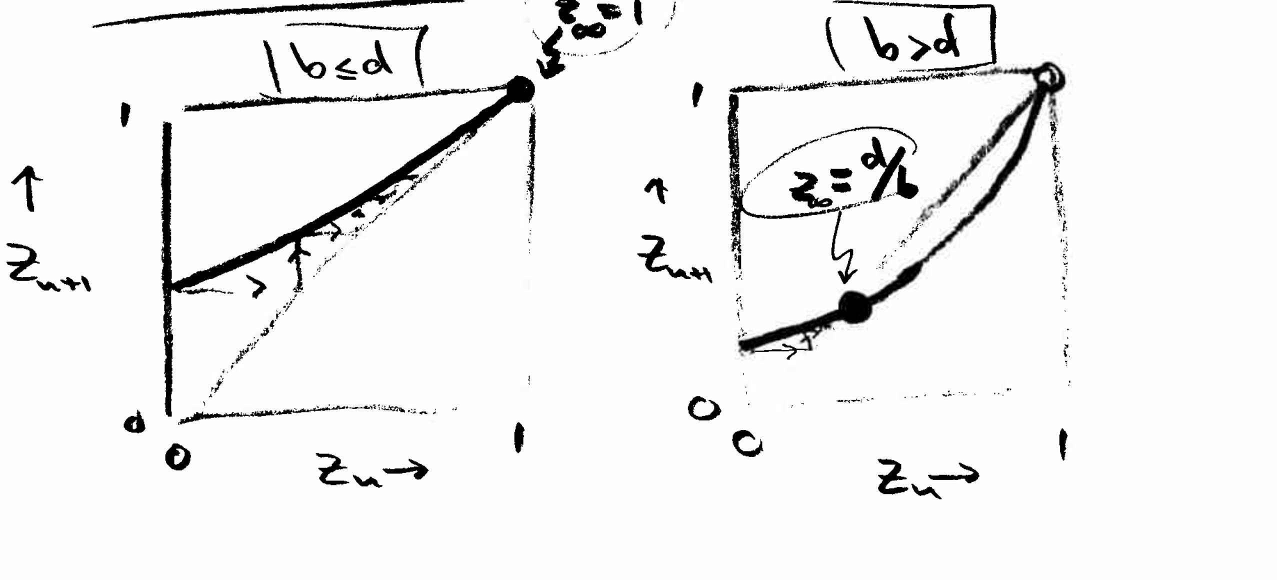
$$\boxed{g(z) = \frac{d}{(1-z)b+d}}$$

From the last equation on the previous page we have

$$z_{n+1} = g(z_n) \quad , \quad z_0 = 0$$

We want to know $z_\infty$, i.e., the probability of eventual extinction:

**Two cases.**



Conclusion:

$$Z_\infty = \begin{cases} 1 & \text{if } b \le d \\ d/b & \text{if } b > d. \end{cases}$$

The probability of invasion thus is

positive part

$$\pi_E(x+\Delta) = 1 - Z_\infty = \left[1 - \frac{d_E(x+\Delta)}{b_E(x+\Delta)}\right]^+$$

$$= \left[\frac{b_E(x+\Delta) - d_E(x+\Delta)}{b_E(x+\Delta)}\right]^+$$

$$= \frac{s_E(x+\Delta)^+}{b_E(x+\Delta)} =$$

$$\doteq \frac{[s'_E(x)\cdot\Delta]^+}{b_E(x)} + O(\Delta^2)$$

small $\Delta$

Substitution into $\vartheta(x)$ (page 2 & 3) gives:

$$\boxed{v_E(x)} = \mathcal{E}\{\Delta \mid x\} = \int \Delta K(\Delta, x)\, d\Delta =$$

$$= \mu(x)\, b_E(x)\, n_E(x) \int \Delta\, \pi_E(x+\Delta)\, \varphi(\Delta, x)\, d\Delta =$$

$$= \mu(x)\, \cancel{b_E(x)}\, n_E(x) \int \Delta\, \frac{[s_E'(x)\Delta]^+}{\cancel{b_E(x)}}\, \varphi(\Delta, x)\, d\Delta =$$

$$= \mu(x)\, n_E(x)\, \frac{1}{2} \int \Delta^2\, s_E'(x)\, \varphi(\Delta, x)\, d\Delta =$$

assume $\varphi(\Delta) = \varphi(-\Delta)$

$$= \boxed{\frac{1}{2}\, \mu(x)\, n_E(x)\, \sigma^2(x)\, s_E'(x)}$$

variance of the mutation step distribution.

selection gradient.

<u>Note</u> that the deterministic drift $v_E(x)$ is proportional to the <u>variance</u> $\sigma^2(x)$ and <u>not</u> to the standard deviation $\sigma(x)$.

Likewise we find (see page 283).

$$D_E(x) = \mathcal{E}\{\Delta^2 | x\} = \int \Delta^2 K(\Delta | x)\, d\Delta =$$

$$= \mu(x)\, b_E(x)\, n_E(x) \int \Delta^2 \pi_E(x+\Delta)\, \varphi(\Delta, x)\, d\Delta =$$

$$= \mu(x)\, \cancel{b_E(x)}\, n_E(x) \int \Delta^2 \frac{[S_E'(x)\Delta]^+}{\cancel{b_E(x)}}\, \varphi(\Delta, x)\, d\Delta =$$

$\varphi(\Delta) = \varphi(-\Delta)$

$$= \mu(x)\, n_E(x)\, \frac{1}{2} \int |\Delta|^3 \cdot |S_E'(x)|\, \varphi(\Delta, x)\, dx =$$

$$= \frac{1}{2}\, \mu(x)\, n_E(x)\, \Theta^3(x)\, |S_E'(x)|$$

third abs. moment $\mathcal{E}_\varphi\{|\Delta|^3 | x\}$.

## Summary.

$$\boxed{\frac{\partial p}{\partial t} = -\frac{\partial v_E p}{\partial x} + \frac{1}{2} \frac{\partial^2 D_E p}{\partial x^2}}$$

with

$$v_E(x) = \frac{1}{2}\, \mu(x)\, \sigma^2(x)\, n_E(x)\, S_E'(x)$$

$$D_E(x) = \frac{1}{2}\, \mu(x)\, \Theta^3(x)\, n_E(x)\, |S_E'(x)|.$$

# The canonical equation of adaptive dynamics.

Take the Fokker-Planck equation on the previous page and ignore the diffusion part:

$$\Rightarrow \quad \frac{\partial p}{\partial t} = -\frac{\partial v_E p}{\partial x} \qquad \text{(transport equation)}$$

explain

$$\Longleftrightarrow \quad \frac{dx}{dt} = v_E(x) = \frac{1}{2}\mu(x)\,\sigma^2(x)\,n_E(x)\,S_E'(x)$$

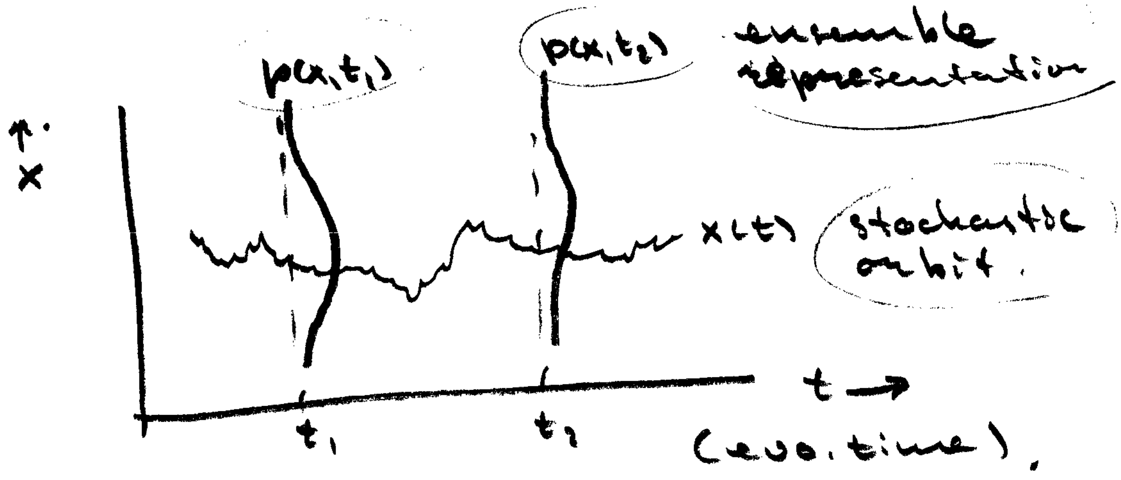
In a polymorphic resident population of strategies $x_1,\dots,x_k$ this becomes

$$\boxed{\begin{array}{l} \dfrac{dx_i}{dt} = \dfrac{1}{2}\mu(x_i)\,\sigma^2(x_i)\,n_{\underline{x}}(x_i)\,S_{\underline{x}}'(x_i) \quad (i=1,\dots,k) \\[2ex] \underline{x} = (x_1,\dots,x_k) \end{array}}$$

This is known as the canonical equation of adaptive dynamics.

(→ Dieckmann et. al. 1996).

# The SDE approximation




Fokker-Planck: (FPE) — evolution of ensemble distribution of many realizations of the same process.

Stoch. Diff. Eqn.: (SDE). — evolution of one particular realization.

$$\boxed{\partial_t p = -\partial_x (v_E p) + \tfrac{1}{2}\,\partial_{xx}(D_E p)} \qquad \text{(FPE)}$$

$$\Longleftrightarrow \quad \boxed{\frac{dx}{dt} = v_E + \sqrt{D_E}\,\frac{dw}{dt}} \qquad \text{(SDE / Ito)}$$

white noise

**multi-strategy version:**

$$\boxed{\frac{dx_i}{dt} = v_E(x_i) + \sqrt{D_E(x_i)}\,\frac{dw_i}{dt} \qquad i=1,\dots,k}$$

i.i.d. whitenoise.

The FPE typically is difficult to integrate (numerically)

So, we use solutions of the SDE to sample the solution of the FPE.

The SDE is very easy to integrate:

$$\frac{dx_i}{dt} = v_E(x_i) + \sqrt{D_E(x_i)} \cdot \frac{dw_i}{dt} \qquad (\text{Ito})$$

$$\Leftrightarrow \quad dx_i = v_E(x_i)\,dt + \sqrt{D_E(x_i)}\; dw_i$$

Wiener increment $\sim \mathcal{N}(0, dt)$, iid $\forall t, i$ (Gaussian distribution)

$$\Leftrightarrow \quad dx_i = v_E(x_i)\,dt + \sqrt{D_E(x_i)\,dt}\; z_i(t)$$

$\sim \mathcal{N}(0,1)$ (iid $\forall t, i$).

This suggests the following numerical integration method.

$$\boxed{x_i(t+\Delta t) = x_i(t) + v_E(x_i(t))\,\Delta t + \sqrt{D_E(x_i(t))\,\Delta t}\; z_i(t)}$$

(Euler method)