

## Selection-Mutation Models

Consider a population with overlapping generations. Individuals are characterized by a quantitative trait  $z$  (such as body size, reproduction timing, size of offspring, migration rate...) or by alleles at a certain gene locus.

$$u_\varepsilon = u_\varepsilon(z, t), \quad z \in \Omega \subseteq \mathbb{R}^n, \quad t > 0.$$

Employing techniques from population genetics, one can derive the following model

$$(1) \left\{ \begin{array}{l} \partial_t u_\varepsilon - \varepsilon^2 \Delta_z u_\varepsilon = \left( m(z) - \int_\Omega m(y) u_\varepsilon(y, t) dy \right) u_\varepsilon \quad \Omega \times (0, \infty) \\ n \cdot \nabla u_\varepsilon = 0 \quad \partial \Omega \times (0, \infty) \\ u_\varepsilon(z, 0) = u_0(z) \quad \Omega \end{array} \right.$$

where  $\rho_\varepsilon(t) = \int_\Omega m(y) u_\varepsilon(y, t) dy$  is the mean fitness, and  $m(z) > 0$  is the fitness of type  $z$ .

Thm For each  $\varepsilon > 0$ , (1) has a unique equilibrium  $O_\varepsilon$ , which attracts all nonneg., nontrivial solutions. If  $m$  attains a unique global maximum at  $\hat{z} \in \bar{\Omega}$ , then  $O_\varepsilon(z) \rightarrow \delta(z - \hat{z})$  in dist.

For fixed  $\varepsilon > 0$ , the equilibrium maintains selection-mutation balance. As  $\varepsilon \rightarrow 0$ , the type with maximal fitness is selected.

Pf. Fix  $\varepsilon > 0$ . Let  $\mu_\varepsilon$  and  $\phi_\varepsilon$  be p.e.v. / p.e.f of

$$(2) \begin{cases} -\varepsilon^2 \Delta \phi = m(z) \phi + \mu \phi & \text{in } \Omega \\ n \cdot \nabla \phi = 0 & \text{on } \partial \Omega \\ \int_{\Omega} m \phi = 1 \end{cases}$$

• Max. prin  $\Rightarrow -\max_{\Omega} m \leq \mu_\varepsilon \leq -\min_{\Omega} m < 0$ .

•  $\theta_\varepsilon = -\mu_\varepsilon \phi_\varepsilon$  is the unique positive equilibrium.

• By previous results, as  $\varepsilon \rightarrow 0$ ,

$$\phi_\varepsilon \rightarrow \frac{1}{m(\hat{z})} \int_{\Omega} (z - \hat{z}) \quad , \quad \mu_\varepsilon \rightarrow -\max_{\Omega} m = -m(\hat{z})$$

$$\Rightarrow \theta_\varepsilon \rightarrow \int_{\Omega} (z - \hat{z})$$

Define  $\mathcal{L} = -\varepsilon^2 \Delta - m - \mu_\varepsilon$  and define  $v(t) = e^{-t\mathcal{L}} [v_0]$

by 
$$(2) \left\{ \begin{array}{l} \partial_t v + \mathcal{L}v = 0 \quad \text{in } \Omega \times (0, \infty) \\ n \cdot \nabla v = 0 \quad \text{on } \partial\Omega \times (0, \infty) \\ v(z, 0) = v_0(z) \quad \text{in } \Omega \end{array} \right.$$

By exponential separation,  $\exists C, \gamma > 0$  s.t.

$$\|e^{-t\mathcal{L}} v_0\|_{C(\bar{\Omega})} \leq C e^{-\gamma t} \|v_0\|_{C(\bar{\Omega})} \quad \text{for } t > 0$$

provided  $\int_{\Omega} v_0 \phi_\varepsilon dy = 0$ .

Given  $u_0 \not\equiv 0$ , write

$$u_0(z) = k_0 \phi_\varepsilon(z) + v_0(z) \quad \text{with } k_0 = \frac{\int \phi_\varepsilon u_0}{\int \phi_\varepsilon^2}, \quad \int v_0 \phi_\varepsilon = 0$$

$$\Rightarrow e^{-t\mathcal{L}} u_0 = k_0 \phi_\varepsilon + e^{-t\mathcal{L}} v_0 \rightarrow k_0 \phi_\varepsilon \quad \text{as } t \rightarrow \infty.$$

Now, let  $u(z, t)$  be sol. to (1) with initial data  $u_0$ , set

$$\rho(t) = \int m(z) u(z, t) dy > 0. \quad \sigma(t) = \int_{\Omega} \phi_\varepsilon(z) u(z, t) dy > 0.$$

Multiply (1) by  $\phi_\varepsilon$ , integrate by part in  $z$

$$(3) \quad \frac{d}{dt} \sigma(t) = (-\mu_\varepsilon - \rho(t)) \sigma(t)$$

which implies

$$\sigma(t) = \sigma(0) e^{-\mu_\varepsilon t - \int_0^t \rho(\tau) d\tau}$$

Next, observe that  $\tilde{u}(z, t) = e^{\mu_\varepsilon t + \int_0^t p} u(z, t)$

satisfies (2), with initial condition  $u_0$ ,

$$\Rightarrow \tilde{u}(\cdot, t) = e^{-tz} [u_0] = k_0 \phi_\varepsilon + o(1).$$

$$\begin{aligned} \Rightarrow u(\cdot, t) &= e^{-\mu_\varepsilon t - \int_0^t p} \tilde{u}(\cdot, t) \\ &= \frac{\sigma(t)}{\sigma(0)} (k_0 \phi_\varepsilon + o(1)). \end{aligned}$$

Mult by  $m(z)$  and integrate,

$$p(t) = \frac{\sigma'(t)}{\sigma(t)} (k_0 + o(1)) \quad \text{as } \int \phi_\varepsilon m = 1.$$

Substitute back into (3),

$$\frac{d}{dt} \sigma(t) = \left( -\mu_\varepsilon - \frac{k_0 \sigma'(t)}{\sigma(t)} + o(1) \right) \sigma(t)$$

$$\Rightarrow \frac{\sigma'(t)}{\sigma(t)} \longrightarrow -\frac{\mu_\varepsilon}{k_0} \quad \text{as } t \rightarrow \infty$$

$$\Rightarrow u(z, t) = \left( -\frac{\mu_\varepsilon}{k_0} + o(1) \right) (k_0 \phi_\varepsilon + o(1)) = -\mu_\varepsilon \phi_\varepsilon + o(1)$$

#

Rmk1. When  $\Omega = \mathbb{R}$  and  $m(z)$  is confining,

i.e.  $m(z) \rightarrow -\infty$  as  $|z| \rightarrow \infty$ .

Then the conclusion of the theorem also holds

[Alfaro-Vervete 2019]

Rmk2. The assumption "m has a unique global max" leads to a uni-modal distribution.

Suppose  $m(z) = \sup_{\Omega} m$  in  $M = \{x_i\}_{i=1}^N$

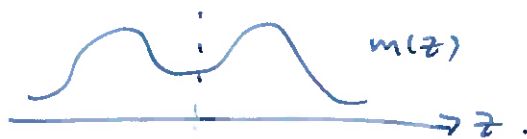
then in general, the p.e.f.  $\phi_\varepsilon$ , for small  $\varepsilon$ , is supported in a subset of  $M$  (but not necessarily at every point of  $M$ ). In general, it depends on how much mutation decreases fitness near each point. [Alfaro-Vervete 2019]

[Lorenzi-Pouchol 2020]

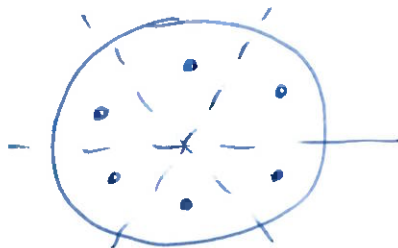
In the latter paper, the authors also studied the pure selection model  $\partial_t u = u(m(z) - \int m(y)u(y,t)dy)$  and compared the long-time limit of the problem with mutation.

Nonetheless, a sufficient condition for multimodal distribution can be obtained in symmetric domains.

$$\Omega = (-1, 1)$$



$$\Omega = B_1(0)$$





Rmk In fact, in the classical selection-mutation model for a haploid population, a unique globally stable equilibrium exists for arbitrary fitness function and arbitrary irreducible mutation operators. [Bürger, Math Z. (1988)]

Rmk If we replace  $\int m(y) u_\varepsilon(y, t) dy$  by  $\int \psi(y) u_\varepsilon(y, t) dy$ , the result is similar.

Rmk If we replace  $\int m(y) u_\varepsilon(y, t) dy$  by  $\int K(z, y) u_\varepsilon(y, t) dy$ , then (1) can have multiple stable equilibria [L. (2018)] or equilibrium that is supported at more than one type as  $\varepsilon \rightarrow 0$ .

Lorz - Mirrahimi - Perthame. (2011)

$$\left\{ \begin{aligned} \varepsilon \partial_t u_\varepsilon - \varepsilon^2 \Delta u_\varepsilon &= u_\varepsilon (m(z) - p_\varepsilon(t)) && \text{for } z \in \mathbb{R}^n, t > 0 \\ p_\varepsilon(t) &= \int u_\varepsilon(z, t) dz. \\ u_\varepsilon(z, 0) &= \exp\left(-\frac{|z-z_0|^2 + o(1)}{\varepsilon}\right) \approx \delta(z-z_0) \end{aligned} \right.$$

Take  $W_\varepsilon(x, z, t) = -\varepsilon \log u_\varepsilon(x, z, t)$

then

$$\left\{ \begin{aligned} \partial_t W_\varepsilon - \varepsilon \Delta W_\varepsilon + |\partial_z W_\varepsilon|^2 + m(z) - p_\varepsilon(t) &= 0 && z \in \mathbb{R}^n, t > 0 \\ W_\varepsilon(z, 0) = W_\varepsilon^0(z) &\approx (z-z_0)^2 \end{aligned} \right.$$

By establishing appropriate estimates, it can be

shown that  $W_\varepsilon(z, t) \rightarrow w(z, t)$  in  $C_{loc}(\mathbb{R}^n \times \mathbb{R}_+)$  and

$\exists p \in BV(\mathbb{R}_+)$  s.t.  $p_\varepsilon(t) \rightarrow p(t)$  in  $L^1_{loc}(\mathbb{R}_+)$ .

$$\text{s.t. } \left\{ \begin{aligned} \partial_t w + |\partial_z w|^2 + m(z) - p(t) &= 0 && \text{in } \mathbb{R}^n \times \mathbb{R}_+ \text{ in viscosity sense} \\ \inf_{\mathbb{R}^n} w(\cdot, t) &= 0 && \forall t > 0. \end{aligned} \right.$$

$$W_\varepsilon(z, t) \xrightarrow{\varepsilon \rightarrow 0} p(t) \delta(z - \bar{z}(t)) \quad \text{s.t. } m(\bar{z}(t)) = p(t).$$

Canonical equation of Adaptive Dynamics

$$\frac{d}{dt} \bar{z}(t) = \left( -D^2 u(\bar{z}(t), t) \right)^{-1} \cdot \nabla m(\bar{z}(t)), \quad \bar{z}(0) = z_0.$$

# Direct Competition Model

$$\begin{cases} \varepsilon \partial_t u = \varepsilon^2 \Delta_{zz} u + u \left( m(z) - \int_{\Omega} K(z, z') u(z', t) dz' \right) \\ n \cdot \nabla u = 0 \quad \text{for } z \in \partial\Omega, t > 0 & \text{for } z \in \Omega, t > 0 \\ u(z, 0) = u_0(z) \quad \text{for } z \in \Omega \end{cases}$$

- Competition of infinitely many species.

Formally, set  $\varepsilon = 0$ , and consider solutions of

the form  $\sum_{i=1}^N U_i(t) \delta(z - z_i)$ , then

$$\varepsilon \partial_t U_i(t) = U_i(t) \left[ m(z_i) - \sum_{j=1}^N K(z_i, z_j) U_j(t) \right] \quad 1 \leq i \leq N, \quad t > 0.$$

→ Lotka-Volterra model of  $N$  competing species.

- [Lorz et al. CPDE (2011)]  $\Omega = \mathbb{R}^n$ , convexity assumptions on coefficients,

$$u(z, t) \approx p(t) \delta(z - \bar{z}(t)) \quad \text{as } \varepsilon \rightarrow 0.$$

- [Sasaki, J.T.B. (1997)] nonlocal in space competition

$$\text{with } K(x, y) = C \exp\left(-\frac{|x-y|^2}{2\sigma^2}\right)$$

- Derivation from individual based models.

[Champagnat et al, T.P.B. (2006)]



# Adaptive Dynamics

Let  $y$  be the type of resident, at equilibrium,  
and let  $x$  be the type of invader,

Invasion succeeds/fails dependy on the linear  
stability of equilibrium  ~~$(\frac{m(x)}{K(x,x)})$~~  of

$$\begin{cases} U'(t) = U(t) (m(x) - K(x,x)U(t) - K(x,y)V(t)) \\ V'(t) = V(t) (m(y) - K(y,x)U(t) - K(y,y)V(t)) \end{cases}$$

Define the invasion exponent

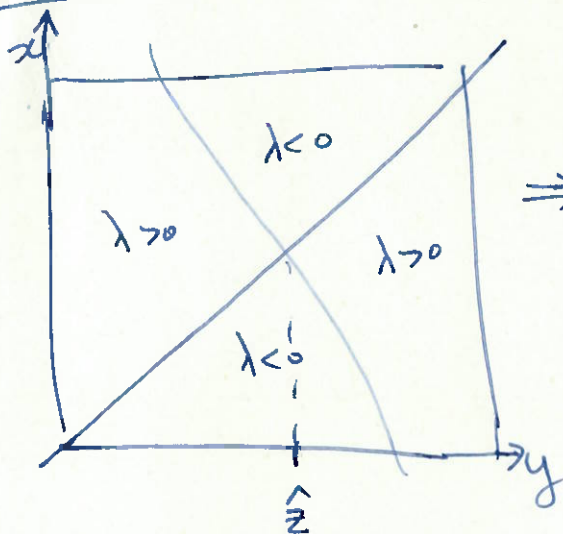
$$\lambda(x,y) = r(x) - K(x,y) \frac{r(y)}{K(y,y)} = \frac{r(x)r(y)}{K(y,y)} \left[ \frac{K(y,y)}{r(y)} - \frac{K(x,y)}{r(x)} \right]$$

then  $\lambda > 0 \Rightarrow$  type  $x$  invades type  $y$

$\lambda < 0 \Rightarrow$  type  $x$  cannot invade type  $y$ .

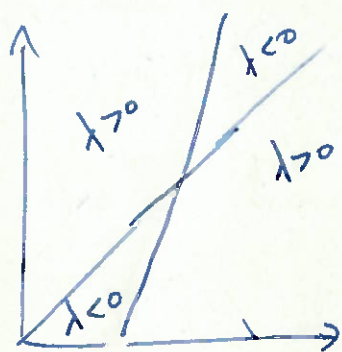
In the following, let  $\Omega = (-1, 1)$ .

Thm 1 (ESS)  $\partial_x^2 \left[ \frac{K(x,y)}{r(x)} \right] > 0 \quad \forall x, y$ , and



$$\Rightarrow \hat{u}_z(z) \rightarrow \frac{r(\hat{z})}{K(\hat{z}, \hat{z})} \delta(z - \hat{z}) \text{ in dist.}$$

Thm 2 (Branching Point)  $\frac{\partial^2}{\partial x^2} \left[ \frac{K(x,y)}{r(x)} \right] < 0 \quad \forall x,y$ , and



$$\rightarrow \begin{cases} u_\varepsilon(z) \rightarrow A f_0(z+1) + B f_0(z-1) \text{ in dist.} \\ \text{where} \\ \begin{pmatrix} K(1,-1) & K(1,1) \\ K(-1,1) & K(-1,-1) \end{pmatrix} \begin{pmatrix} A \\ B \end{pmatrix} = \begin{pmatrix} m(1) \\ m(-1) \end{pmatrix} \end{cases}$$

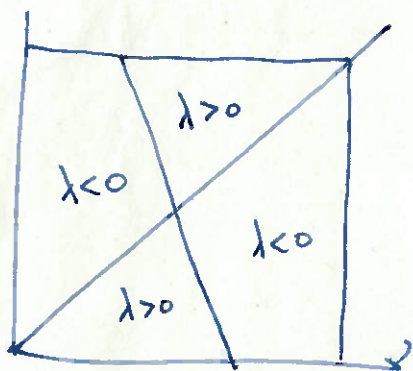
Pf of Thms 1 and 2

Classification of viscosity solutions of

$$|W(z)|^2 = H(z) \text{ in } (-1,1), \quad \inf W = 0.$$

In case  $H$  is convex (Thm 1) or concave (Thm 2).

Thm 3 (Bistability).



For  $0 < \varepsilon < 1$ , there exists at least two equilibria  $u_\varepsilon^+$ ,  $u_\varepsilon^-$ , such that

$$u_\varepsilon^+(z) \rightarrow \frac{r(1)}{K(1,1)} f_0(z-1)$$

$$u_\varepsilon^-(z) \rightarrow \frac{r(-1)}{K(-1,-1)} f_0(z+1)$$

Note that  $z=1$ ,  $z=-1$  are both ESS.

Pf of Thm 3. Construction of forward-invariant sets in which type  $+1$  or  $-1$  is dominant.

See [L. DCDS-B (2018)] for details.