École EDP proba pour les sciences du vivant

Equilibria of quantitative genetics models, sexual, age-structured populations

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Plan

Mutation-selection model

Adaptation

- **Adaptation** to a local environment: result of a mutation/selection process acting on phenotypical traits x
- **Adapted** population: dominant trait equals optimal trait

Population dynamics

$$\partial_t f(t,x) + \mu(x)\, f(t,x) = \beta \, \mathrm{B}_\sigma(f(t,\cdot))(x)$$

- $f(t,x)$ density of population, continuous trait $x \in \mathbb{R}$
- **Selection:** $\mu(x)$ heterogeneous mortality rate, symmetric: best adapted trait $x = 0$
- β birth rate, B_σ reproduction operator

Asexual/Sexual reproduction operators

Asexual reproduction

$$\mathrm{B}_\sigma(f)(x) = \int_{\mathbb{R}} \frac{1}{\sigma} K\left(\frac{x - x'}{\sigma}\right) f(x')\,\mathrm{d}x', \qquad K \text{ a probability measure.}$$

Sexual reproduction: infinitesimal model

$$\begin{aligned}\mathrm{B}_\sigma(f)(x) &= \frac{1}{\int_{\mathbb{R}} f(x)\,\mathrm{d}x} \iint_{\mathbb{R}^2} f(x')\, f(x'')\; G_\sigma\left(x - \frac{x' + x''}{2}\right) \mathrm{d}x'\,\mathrm{d}x'', \\ &= \frac{4}{\int_{\mathbb{R}} f(x)\;\mathrm{d}x}\; G_\sigma * f(2\,\cdot) * f(2\,\cdot),\end{aligned}$$

G_σ a centered Gaussian function with variance σ^2.

$$x_{\text{offspring}} = \frac{1}{2}(x_{\text{parent1}} + x_{\text{parent2}}) + \text{normally distributed random variable}$$

Age structure

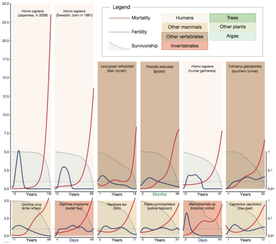


Figure : Jones *et al.*, Nature 2014

Ageing increases mortality.

$$\mu(a,x) = d + m(x)\,\mathbf{1}_{a>a^*};$$
$$\mu(a,x) = d + m(x)\,\delta_{a=a^*}.$$

- d intrinsic death rate
- a^* ageing impact threshold

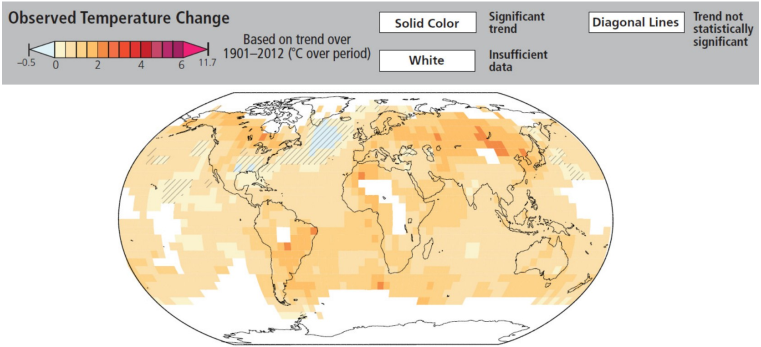
Model with ageing

$$\begin{cases} \partial_t f(t,a,x) + \partial_a f(t,a,x) + \mu(a,x)\,f(t,a,x) = 0, \\ f(t,0,x) = \mathrm{B}_\sigma \left(\int_0^\infty \beta(a) f(t,a,\cdot) \right)(x). \end{cases}$$

Time scales, changing environment

- evolutionary time scale $\gg$ ecological time scale
- changing environment: $\mu(x) \to \mu(y)$ with $y = x - ct$

lhs: $\partial_t f(t,x) + \mu(x)\, f(t,x) \to \ \partial_t f(t,y) - c\,\partial_y f(t,y) + \mu(y)\, f(t,y)$
rhs: unchanged



Goals

- What are the adaptive dynamics induced by a changing environment?
- How ageing (and sexual reproduction) affects adaptation to a changing environment?

In particular, quantification of the impacts of the change of environment:

- *load* $\lambda_c - \lambda_0$, global adaptation of the population,
- *lag* $y_c = \operatorname{argmax} f \ (y_0 = 0)$, dominant trait

Background

Infinitesimal operator

- Blmer, 1980
- Turelli-Barton, 1994
- Tufto, 2000
- Mirrahimi, Raoul, 2013
- Cotto, Ronce, 2014

Concentration around the dominant trait

- Diekmann, Jabin, Mischler, Perthame, 2005

Ansatz for F^ε

Small mutations, long time dynamics

- concentrated mutation kernel B_ε
- $t \to t\varepsilon^{-\alpha}$, $\alpha > 0$,

$$\varepsilon^\alpha(\partial_t f^\varepsilon - c\,\partial_y f^\varepsilon) + \mu(y) f^\varepsilon = \beta\,\mathrm{B}_\varepsilon(f^\varepsilon(t,\cdot))(y)$$

Adaptive dynamics limit: spectral approach

$$f^\varepsilon(t,y) = \exp(\lambda_c\, t\varepsilon^{-\alpha}) F^\varepsilon(y)$$

$$\lambda_c\, F^\varepsilon - \varepsilon^\alpha c\,\partial_y F^\varepsilon + \mu(y) F^\varepsilon = \beta\,\mathrm{B}_\varepsilon(F^\varepsilon)(y)$$

Maximal speed c^* for which population persists: $\lambda_{c^*} = 0$

Concentration around dominant trait

$$\mathbf{U}^\varepsilon = -\varepsilon^\alpha \ln \mathbf{F}^\varepsilon$$

$$\lambda^\varepsilon + c\partial_x U^\varepsilon(x) + \mu(x) = \frac{\beta}{F^\varepsilon(x)}\,\mathrm{B}_\varepsilon(F^\varepsilon)(x)$$

Asexual reproduction

$$(\lambda^\varepsilon, U^\varepsilon) \approx (\lambda_0, U_0) + \varepsilon^\alpha (\lambda_1, U_1) + \varepsilon^{2\alpha} (\lambda_2, U_2)$$

time scaling $t \to t/\varepsilon$

$$\frac{1}{F^\varepsilon(x)} \mathrm{B}_\varepsilon(F^\varepsilon)(x) = \int_{\mathbb{R}} \frac{1}{\varepsilon} K\left(\frac{x-x'}{\varepsilon}\right) \exp\left(-\frac{U^\varepsilon(x')}{\varepsilon}\right) \mathrm{d}x' \exp\left(\frac{U^\varepsilon(x)}{\varepsilon}\right)$$
$$= \int_{\mathbb{R}} K(y) \exp\left(\frac{U^\varepsilon(x) - U^\varepsilon(x-\varepsilon y)}{\varepsilon}\right) \mathrm{d}y \approx \int_{\mathbb{R}} K(y) \exp\left(y \partial_x U^\varepsilon(x)\right) \mathrm{d}y$$

$$\lambda_0 + c U_0'(x) + \mu(x) = \beta H(U_0'(x))$$

Hamiltonian H: two-sided Laplace transform

Adaptive dynamics for sexual reproduction without ageing

- **Time scaling:** $t \to t/\varepsilon^2$
- **0^{th} order, equilibrium of $\mathcal{G}_\sigma$.**

$$U_0(x) = \frac{1}{4\sigma^2}(x - x_c)^2, \quad x_c \textit{ unknown}$$

- **1^{st} order.**

$$\lambda_0 + cU_0'(x) + \mu(x) = \beta \exp\left(-(LU_1)(x)\right)$$

Non local derivation: $(LU)(x) = 2U\left(\frac{x + x_c}{2}\right) - U(x) - U(x_c)$

$$\lambda_0 + \mu(x_c) = \beta, \quad \mu'(x_c) + \frac{c}{2\sigma^2} = 0 \quad \to \quad x_c, \lambda_0, LU_1$$

Particular solution to $LU = f$:

$$U_1(x_c + h) = U_1(x_c) + hU_1'(x_c) + \sum_{n=0}^{\infty} 2^n f(2^{-n}h),$$

with $f(h) = 1 + \frac{1}{\beta}\left(\mu(h + x_c) - \mu(x_c) - h\mu'(x_c)\right)$.

- **2^{nd} order.** Determination of $U_1'(x_c)$, λ_1, LU_2 ; $U_2'(x_c)$ missing

Proof: 0^{th} order

$$\lambda^\varepsilon + c\,(U^\varepsilon)'\,(x) + \mu(x) = \frac{\beta}{F^\varepsilon(x)}\,\mathcal{G}_\varepsilon(F^\varepsilon)(x)$$

- lhs: $\lambda_0 + cU_0'(x) + \mu(x) + \varepsilon^2\left(\lambda_1 + cU_1'(x)\right)$
- rhs:

$$\frac{\beta \displaystyle\iint_{\mathbb{R}^2} \exp\left[-\varepsilon^{-2}\left(U^\varepsilon(x') + U^\varepsilon(x'') + \frac{1}{2\sigma^2}\left(x - \frac{x'+x''}{2}\right)^2 - U^\varepsilon(x)\right)\right]\mathrm{d}x'\,\mathrm{d}x''}{\varepsilon\sigma\sqrt{2\,\pi}\displaystyle\int_{\mathbb{R}} \exp(-\varepsilon^{-2}U^\varepsilon(x))\,\mathrm{d}x}$$

$$\forall x \in \mathbb{R} \qquad \inf_{x',x''\in\mathbb{R}} f(x') + f(x'') + \frac{1}{2\sigma^2}\left(x - \frac{x'+x''}{2}\right)^2 - f(x) = 0$$

Legendre transformation: $f^*(s) = \sup_{x\in\mathbb{R}}\Big(sx - f(x)\Big)$

$$f^*(s) - 2f^*\left(\frac{s}{2}\right) = \frac{\sigma^2 s^2}{2} \qquad f^*(s) = \sigma^2 s^2 + x_c s \qquad f^{**}(x) = \frac{1}{4\sigma^2}(x - x_c)^2$$

Proof: 1^{st} order

$$U^\varepsilon = U_0 + \varepsilon^2 U_1$$

- **Denominator concentrates at $x = x_c$** $\quad x = x_c + \varepsilon z$

$$\varepsilon 2\sqrt{\pi}\sigma \exp(-U_1(x_c))$$

- **Numerator concentrates at $x' = x'' = \frac{x+x_c}{2}$**
The form q has a minimum value (0) at $x' = x'' = \frac{x+x_c}{2}$:

$$q(x', x'') = (x' - x_c)^2 + (x'' - x_c)^2 + 2\left(x - \frac{x' + x''}{2}\right)^2 - (x - x_c)^2$$

$$\varepsilon^2 2^{3/2}\pi\sigma^2 \exp\left(-\left(2U_1\left(\frac{x+x_c}{2}\right) - U_1(x)\right)\right)$$

- **2^{nd} order.** Determinations of $U_1'(x_c)$, then λ_1:

$$\begin{cases} \beta\sigma^2 U_1''(x_c) + 2cU_1'(x_c) + 2\lambda_1 = 0, \\ -U_1'(x_c)U_1''(x_c) + \frac{3}{4}U_1'''(x_c) + \frac{c}{\beta\sigma^2}U_1''(x_c) = 0 \end{cases}$$

Numerics

Scheme on proportions: $p(t,x) = \frac{f^\varepsilon(t,x)}{\int_{\mathbb{R}} f^\varepsilon \, \mathrm{d}x}$: add viscosity term ωp

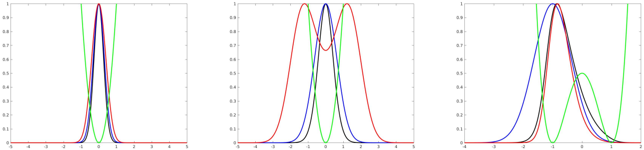


Figure : Profiles f^ε, $\varepsilon = 0,05; 0,2$.

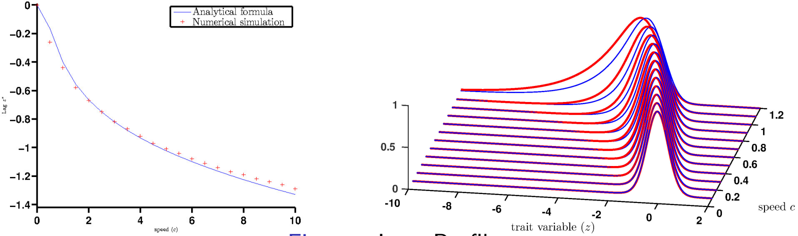


Figure : Lag. Profiles.

0^{th} and 1^{st} orders with ageing

$$\begin{cases} \lambda^\varepsilon + c\partial_x U^\varepsilon - \varepsilon^{-2}\partial_a U^\varepsilon + \mu(a,x) = 0 \\ 1 = \dfrac{1}{F^\varepsilon(0,x)}\,\mathcal{G}_\varepsilon\left(\displaystyle\int_0^\infty \beta(a)F^\varepsilon(a,\cdot)\right)(x) \end{cases}$$

$$U_1(a,x) = U_1(0,x) + V(a,x), \quad V(a,x) = \lambda_0\, a + \int_0^a \mu(a',x)\,\mathrm{d}a'$$

$$U_0(x) = \tfrac{1}{4\sigma^2}(x - x_c)^2$$

$$\frac{B(x_c)}{B\left(\frac{x+x_c}{2}\right)^2} = \exp\left(-(LU_1(0,\cdot))(x)\right)$$

with $B(x) = \int_0^\infty \beta(a)\exp(-V(a,x))\,\mathrm{d}a$

Implicit determinations of x_c, then λ_0: $B(x_c) = 1, B'(x_c) = 0$.

Nonlinear effects of Age-structure: Bistability

$$\mu(a,x) = m(x)\,\delta_{a=a^*} = \frac{1}{2}x^2\,\delta_{a=a^*}$$

$$B(x) = \frac{1}{\lambda_0 + c(x - x_c)}\left(1 - [1 - \exp(-m(x))]\exp\left(-(\lambda_0 + c(x - x_c))\,a^*\right)\right)$$

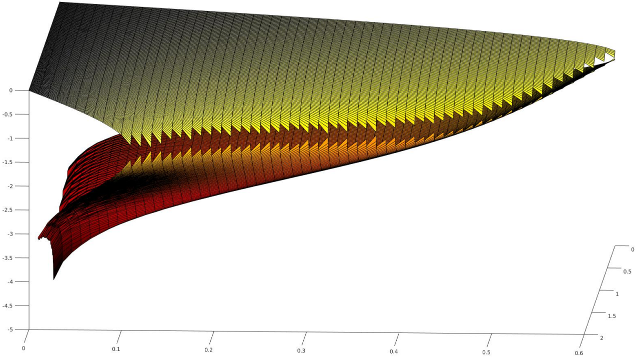


Figure : Maximum speed $f(a^*)$: $c > f(a^*)$ no principal eigenelements.

More Numerics for aging

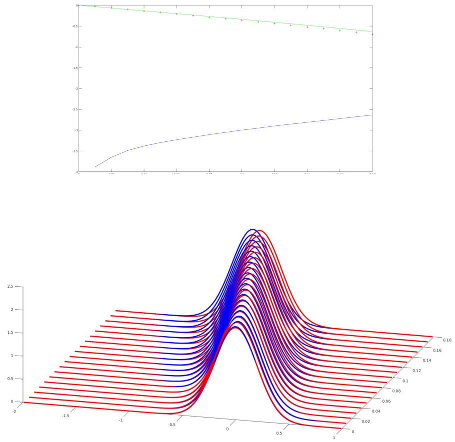


Figure : Lag. Profiles.

Uniqueness: discretized problem, traits $0, \pm 1$

- **Discretized operator**

$$\begin{cases} \mathcal{G}(f)(1) = (x+y+z)^{-1}\left(ax^2+2bxy+cy^2+2cxz+2dyz+ez^2\right) \\ \mathcal{G}(f)(0) = (x+y+z)^{-1}\left(cx^2+2bxy+ay^2+2axz+2byz+cz^2\right) \\ \mathcal{G}(f)(-1) = (x+y+z)^{-1}\left(ex^2+2dxy+cy^2+2cxz+2byz+az^2\right) \end{cases},$$

with: $x = f(1), y = f(0), z = f(-1), a = G(0), b = G\left(\pm\frac{1}{2}\right), c = G(\pm 1), d = G\left(\pm\frac{3}{2}\right), e = G(\pm 2)$.

- **Mass conservation:** $a = 1-2e, 2b = 1-d, c = e$
- K nonnegative orthant, $K^+ = int(K)$, $K_0 = K - \{0\}$, standard simplex $S = \{x \in K \mid \langle x, 1\rangle = 1\}$ ($\langle\ ,\ \rangle$ cip in $\mathbb{R}^3$)
- **Positivity:** $\mathcal{G} : K^+ \to K^+$ iff $0 \leqslant d \leqslant 1$ and $0 \leqslant e \leqslant \frac{1}{2}$
- mass conservation: if λ ev associated to ev $x \in K_0$ then $\lambda = 1$

Existence: Brouwer theorem

- fixed point in the convex compact set K of $\mathbb{R}^3$

Uniqueness: Hilbert's projective metric, Birkhoff's theorem

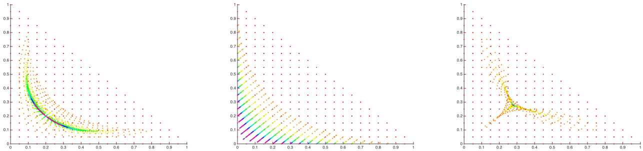
- $$\forall x, y \in K^+ \quad d(x,y) = \log \max_{1 \leqslant i,j \leqslant n} \frac{x_i}{y_i}\frac{y_j}{x_j}$$

  metric on half-lines included in $int(K)$
- A *linear* positive:

  $$k(A) := \inf\{\lambda \mid \forall x, y \in K^+ \ d(Ax, Ay) \leqslant \lambda d(x,y)\} = \text{th}\left(\frac{1}{4} diam(A(K^+))\right)$$

  If $A(K^+)$ is bounded, A is a contraction for d.

Here $k(\mathcal{G}) > 1$ but uniqueness.



Principal eigenelements, age structure, speed $c = 0$

$$f(t,a,x) = e^{\lambda t} F(a,x)$$

$$\begin{cases} \lambda F(a,x) + \partial_a F(a,x) + \mu(a,x) F(a,x) = 0, \\ F(0,x) = \mathcal{G}_\sigma\Big(\int_0^\infty \beta(a) F(a,\cdot)\, da \Big)(x), \\ \int_{\mathbb{R}} F(0,x)\, \mathrm{d}x = 1 \qquad\qquad \text{(homogeneity).} \end{cases}$$

Hypothesis. There exists $\lambda_0 \in \mathbb{R}$:

$$\forall x \in \mathbb{R} \quad 1 \leqslant \int_0^\infty \beta(a) e^{-\lambda_0 a} e^{-\int_0^a \mu(a',x)\,\mathrm{d}a'}\, \mathrm{d}a \leqslant \int_0^\infty \beta(a) e^{-\lambda_0 a}\, \mathrm{d}a < \infty$$

Theorem. There exists a solution (λ, F).

Proof 1/2: Properties and difficulties

Properties of $\mathcal{G}_\sigma$

- 1-homogeneous operator (non linear), not increasing ~~(Krein-Rutman/Mahadevan)~~
- double convolution: regularizing effect
- $\mathcal{G}_\sigma$ conserves moments of orders 0 and 1 ($M_k(f) = \int_{\mathbb{R}} x^k f(x)\,\mathrm{d}x$)
- If $M_0(f) = 1, M_1(f) = 0$: $M_2(\mathcal{G}_\sigma(f)) = M_2(G_\sigma) + \frac{1}{2}M_2(f)$.

  $\{f \in \mathrm{L}^1 \mid M_0(f) = 1, M_1(f) = 0, M_2(f) \leqslant 2M_2(G_\sigma)\}$
  is mapped into itself by $\mathcal{G}_\sigma$

Age structure

- breaks conservation of moments
- no dispersion relation

Proof 2/2: Sketch

- (transport in age) $F(a,x)$ is determined by $\varphi(x) = F(0,x)$:
  $\varphi(x) = \mathcal{G}_\sigma\Big(\nu(\lambda,\cdot)\,\varphi\Big)(x)$, with

$$\nu(\lambda,x) = \int_0^\infty \beta(a) e^{-\lambda a} e^{-\int_0^a \mu(a',x)\,\mathrm{d}a'}\,\mathrm{d}a$$

- (dispersion relation) If φ is positive, $\int_{\mathbb{R}} \varphi\,\mathrm{d}x = 1$, there exists a unique $\lambda = \lambda(\varphi) \in \mathbb{R}$ such that:

$$\int_{\mathbb{R}} \nu(\lambda,x)\varphi(x)\,\mathrm{d}x = 1.$$

- (Schauder theorem) Closed convex set of $\mathrm{L}^1(\mathbb{R})$, mapped into itself by $\mathcal{M} : \varphi \mapsto \mathcal{G}_\sigma\Big(\nu(\lambda(\varphi),\cdot)\,\varphi\Big)$:

$$\mathcal{C} = \left\{ f \in \mathrm{L}^1 \mid f \geqslant 0, M_0(f) = 1, f(-x) = f(x), M_2(f) \leqslant 2\,M_2(G_\sigma) \right\}.$$

  Regularizing effect of $\mathcal{G}_\sigma$: $\mathcal{M}(\mathcal{C})$ relatively compact