

Le REPLICATOR - MUTATOR

'30 **Fisher**: "The genetical theory of natural selection"
 ↳ stats + bio! formalisme selecto naturelle, selecto sexuelle (proon) etc...

'32 **Haldane**: "The Causes of Evolution"
 ↳ pop. genetics, Chapter "What is Fitness?" ..

'65 **Kimura**: "A stochastic model concerning the maintenance of genetic variability in quantitative characters"
 ↳ eq diffus°, derive génétique ...

$t > 0$

$x \in \mathbb{R}^N$ espace phenotypique
 (Not souvent)

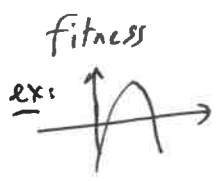
$u(t, \cdot)$ densité de proba du trait x
 fitness relative

Replicator:

$$u_t = u (W(x) - \bar{w}(t))$$

Rq: masse conservée (cf + tard)

signifie $\frac{\partial u}{\partial t}$



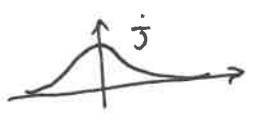
fitness moyenne

$$\bar{w}(t) = \int W(y) u(t, y) dy$$

(parfois notée $\bar{u}(t)$)

Mutator:

j densité probas sur \mathbb{R}^N



$x \rightsquigarrow x+y$ avec proba $j(y)$

Rq: je mets beaucoup de cotes = 1

$$u_t = \int j(x-y) u(t, y) dy - \int j(y-x) u(t, x) dy$$

arrivent en x partent de x

$$= \int j(x-y) u(t, y) dy - u(t, x)$$

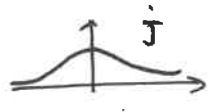
$$= j * u(t, \cdot) - u$$

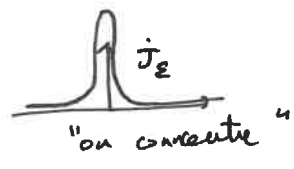
Rq: évidemment les "individus" sont conservés

RM:

$$u_t = (J * u - u) + u(w(x) - \bar{w}(t)) \quad \begin{matrix} t > 0 \\ x \in \mathbb{R}^N \end{matrix}$$

Approx diffusive:

$$j(y) \leftarrow \frac{1}{\varepsilon} j\left(\frac{y}{\varepsilon}\right)$$




$$j_\varepsilon * u - u = \int_{\mathbb{R}} \frac{1}{\varepsilon} j\left(\frac{y}{\varepsilon}\right) (u(t, x-y) - u(t, x)) dy$$

$$\frac{z}{\varepsilon} = z$$

$$= \int_{\mathbb{R}} j(z) (u(t, x - \varepsilon z) - u(t, x)) dz$$

Taylor $\approx \int_{\mathbb{R}} j(z) \left(-\varepsilon z u_x(t, x) + \frac{1}{2} \varepsilon^2 z^2 u_{xx}(t, x) \right) dz$

$$\approx \left(\frac{1}{2} \varepsilon^2 \int_{\mathbb{R}} z^2 j(z) dz \right) u_{xx} - \left(\varepsilon \int_{\mathbb{R}} z j(z) dz \right) u_x$$

" si j pair

$$\approx \text{cte}_\varepsilon u_{xx}$$

RM diffusif

$$u_t = \Delta u + u(w(x) - \bar{w}(t)) \quad \begin{matrix} t > 0 \\ x \in \mathbb{R}^N \end{matrix}$$

" u_{xx} si N=1

↑ puis Lande '75, Fleming '79, Bürger 80-90

+ Réaumont Alfaro, Bansaye, Cloez, Gebniel, Hamel, Kaviani, Martin, Nourahmi, Patout, Raouf, Vermeté...

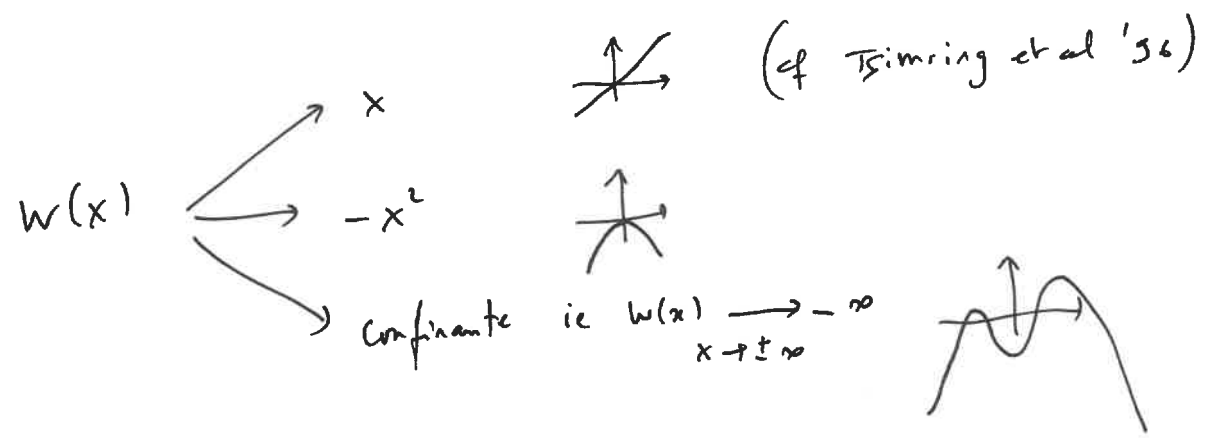
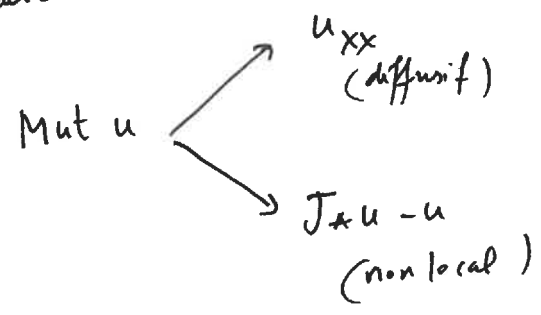
Derivato of RM from IBM:

- Fournier, Nélédard '04
- Champagnat, Fournier, Nélédard '08
- Wakano, Iwanski, Yokoyama '17

On regarde donc :

RM $u_t = Mut u + u (w(x) - \bar{w}(t))$ N=1

avec



Rq: $m(t) := \int_{\mathbb{R}} u(t, x) dx$

En "intégrant" RM :

$$\begin{cases} \frac{dm}{dt} = \bar{w}(t)(1 - m(t)) \\ m(0) = 1 \end{cases}$$

↑
car u_0 densité proba.

" \implies " $m(t) \equiv 1$ MASSE CONSERVÉE

Rq: c'est un "Gronwall" par un "Cauchy Lipschitz" of pbs + tend...

① Sol. gaussiennes (diffusif + $\begin{cases} x \\ -x^2 \end{cases}$)

$$u(t, x) = \sqrt{\frac{a(t)}{2\pi}} e^{-\frac{a(t)(x-m(t))^2}{2}}$$

$m(t) = \text{moyenne}$
 $\frac{1}{a(t)} = V(t) = \text{variance}$

(1) $u_t = \frac{\dot{a}}{2a} u + u \left(-\frac{\dot{a}(x-m)^2}{2} + a\dot{m}(x-m) \right)$

(2) $u_x = -a(x-m)u$

(3) $u_{xx} = -au + a^2(x-m)^2 u$

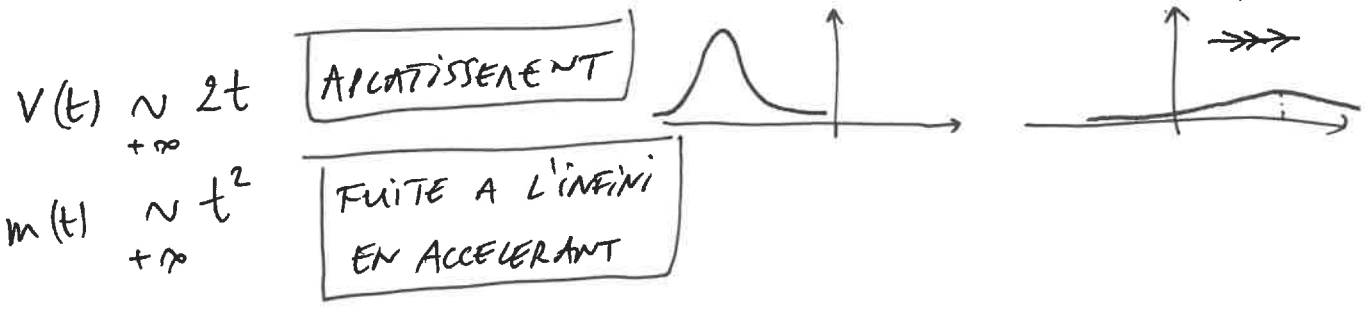
①.1 $W(x) = x$ ie $u_t = u_{xx} + u(x - \bar{x})$

On met (1) ici, (3) ici, m ici puis on égalise les termes en x^2 , en x et en x^0 . On arrive à :

x^2 : $-\frac{\dot{a}}{2} = a^2$
 x : $\cancel{m\dot{a}} + a\dot{m} = -\cancel{2a^2m} + 1$
 x^0 : $\cancel{\frac{\dot{a}}{2a}} - \frac{\dot{a}m^2}{2} - a\dot{m} = -\cancel{a} + \cancel{a}m^2 - m$ } c'est les mêmes!

$\frac{1}{a(t)} = \frac{1}{a_0} + 2t$ ie $V(t) = V_0 + 2t$

$\dot{m}(t) = \frac{1}{a_0} + 2t$ ie $m(t) = t^2 + V_0 t + m_0$



1.2

$$w(x) = -x^2 \text{ i.e. } u_t = u_{xx} + u(-x^2 + \overline{x^2})$$

$$V + m^2 = \frac{1}{a} + m^2$$

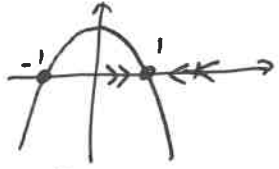
Idem ci-dessus, on arrive à:

$\dot{a} = 2(1-a^2)$ qu'on peut résoudre explicitement mais

Après les sol. positives vérifient

$$a(t) \xrightarrow{t \rightarrow +\infty} 1$$

car



$$\frac{\dot{m}}{m} = -\frac{2}{a}$$

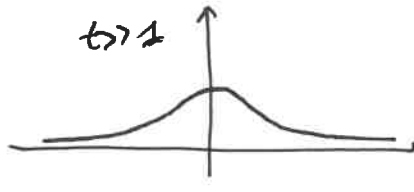
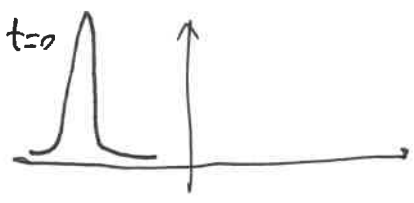
ie

$$m(t) = m_0 e^{-2 \int_0^t \frac{ds}{a(s)}} \xrightarrow{t \rightarrow +\infty} 0$$

(car $a(t) \rightarrow 1$)

Bilan

$$\begin{matrix} v(t) \rightarrow 1 \\ m(t) \rightarrow 0 \end{matrix} \quad \boxed{\text{STABILISATION et CENTRAGE}}$$



2) Sol. explicites (nm gaussiennes) (diffusif + $\begin{cases} x \\ m \\ -x^2 \end{cases}$)

Lemme 1 $u_t = u_{xx} + u(w(x) - \bar{u}(t)) \iff v_t = v_{xx} + w(x)v$

"Proof": $\Rightarrow v(t, x) = u(t, x) e^{\int_0^t \bar{u}(s) ds}$

et c'est "inversible" car, en multipliant par $w(x)$ puis intégrant:

$\bar{v}(t) = \bar{u}(t) e^{\int_0^t \bar{u}(s) ds}$
 $= \frac{d}{dt} \left(e^{\int_0^t \bar{u}(s) ds} \right) \Rightarrow \int_0^t \bar{v}(s) ds = e^{\int_0^t \bar{u}(s) ds} - 1$

et donc

$u(t, x) = \frac{v(t, x)}{1 + \int_0^t \bar{v}(s) ds} = \frac{v(t, x)}{m_v(t)}$

avec $m_v(t) = \int_{\mathbb{R}} v(t, y) dy$

En effet $\frac{d}{dt} m_v(t) = \bar{v}(t)$ par l'éq sur v
donc $m_v(t) = 1 + \int_0^t \bar{v}(s) ds$

2.1) $w(x) = x$

Lemme 2 $v_t = v_{xx} + xv \iff w_t = w_{xx}$

"Proof": $v(t, x) = w(t, x + \frac{t^2}{3}) e^{tx + \frac{t^3}{3}}$

cf Avron-Herbst formula en méca. quantique

En combinant Lemme 1 et Lemme 2 on a:

Th

$$u_t = u_{xx} + u(x - \bar{x}(t))$$

$$\hookrightarrow u(t, x) = \frac{e^{tx} \int_{\mathbb{R}} \frac{1}{\sqrt{4\pi t}} e^{-\frac{(x+t^2-y)^2}{4t}} u_0(y) dy}{\int_{\mathbb{R}} e^{ty} u_0(y) dy}$$

$$\bar{u}(t) = t^2 + \frac{\int_{\mathbb{R}} e^{ty} u_0(y) dy}{\int_{\mathbb{R}} e^{ty} u_0(y) dy}$$

as long as denominator $< +\infty$

Cor: Extinction for heavy tails

$$\left[\begin{array}{l} u_0(y) \sim e^{-\alpha y} \Rightarrow u \equiv 0 \text{ at } T = \alpha \\ u_0(y) \sim \frac{1}{y^\alpha} \Rightarrow u \equiv 0 \text{ immediately} \end{array} \right.$$

Cor

$$\left[u_0 \right. \begin{array}{c} \text{graph of } u_0 \end{array} \Rightarrow \sup_x \left| u(t, x) - \frac{1}{\sqrt{4\pi t}} e^{-\frac{(x-t)^2}{4t}} \right| \leq \frac{c}{t}$$

↓

c'est la gaussienne qui fait et s'ajuste trouvée en ①.

elle est aussi obtenue en mettant $u_0(y) = \delta_0(y)$ dans la formule $u(t, x)$ du Th.

Ref: Alfaro, Carlos 2014

2.2 $w(x) = -x^2$

Lemma 2' $v_t = v_{xx} - x^2 v \iff w_t = w_{xx}$

"Proof" $v(t,x) = \frac{1}{\sqrt{4h2t}} e^{-\frac{h2t}{2} x^2} w\left(\frac{h2t}{2}, \frac{x}{\sqrt{4h2t}}\right)$ of Lens transform

Th. \llbracket sol. explicite globale (in contrast with 2.1)

Cor $\left[\sup_x \left| u(t,x) - \frac{1}{\sqrt{2\pi h2t}} e^{-\frac{1}{2h2t} x^2} \right| \leq \frac{C}{sh2t} \right]$

$\downarrow \approx$
 $\varphi(x) := \frac{1}{\sqrt{2\pi}} e^{-x^2/2}$

c'est la gaussienne centrée et "stabilisée" autour de ①

Ref Alfaro, Cordes 2017

Bilan: Diffusif et $w(x) = \begin{cases} x \\ \text{ou} \\ -x^2 \end{cases}$ OK!

Tout est EXPLICITE !!!

Explicit η letism $\frac{t}{t}$ vs. cv to steady state $(-x^2)$
 ⑧

③ Approche CGF

$$m_n^{(t)} = \int x^n u(t, x) dx \quad 9$$

Fct. gen. des moments

$u(t, x)$ densité proba \rightarrow MGF $M(t, z) := \mathbb{E}[e^{zX}] = \int_{\mathbb{R}} e^{zx} u(t, x) dx$ *Transfo Laplace*

$$= \int_{\mathbb{R}} \sum_n \frac{z^n x^n}{n!} u(t, x) dx$$

$$= \sum_n \frac{m_n(t)}{n!} z^n$$

$$\Rightarrow m_n(t) = \frac{d^n}{dz^n} M(t, z) \Big|_{z=0}$$

Fct. gen. des cumulants

CGF $C(t, z) := \ln M(t, z) = \ln \int_{\mathbb{R}} e^{zx} u(t, x) dx$ $t > 0$
 $z \in \mathbb{R}$

Disons $u_t = \text{pdf}(u) + u(x - \bar{x})$

$$(1) \frac{\partial C}{\partial t} = \frac{\int e^{zx} u_t}{\int e^{zx} u} = \frac{\int e^{zx} \text{pdf}(u)}{\int e^{zx} u} + \frac{\int e^{zx} x u}{\int e^{zx} u} - \bar{x}$$

$$(2) \frac{\partial C}{\partial z} = \frac{\int e^{zx} x u}{\int e^{zx} u} \quad \text{et en particulier} \quad \frac{\partial C}{\partial z}(t, z=0) = \frac{\int x u}{\int u} = \bar{x} = \text{moyenne}$$

$$(3) \frac{\partial^2 C}{\partial z^2} = \frac{\int e^{zx} x^2 u}{\int e^{zx} u} - \left(\frac{\int e^{zx} x u}{\int e^{zx} u} \right)^2 \quad \text{et en part} \quad \frac{\partial^2 C}{\partial z^2}(t, z=0) = \int x^2 u - (\int x u)^2 = \text{Variance}$$

(1) et (2) donnent :

$$\frac{\partial C}{\partial t} = \frac{\partial C}{\partial z} - \frac{\partial C}{\partial z}(z=0) + \frac{\int e^{zx} \text{Mitt} u}{\int e^{zx} u.}$$

3.1 $\text{Mitt} u = u_{xx}$ Diffusion

$$\frac{\int e^{zx} u_{xx} \downarrow \text{2 IPP}}{\int e^{zx} u} = \frac{\int z^2 e^{zx} u}{\int e^{zx} u} = z^2$$

$$C_t = C_z - C_z(z=0) + z^2$$

EDP d'ordre 1
Loi de conservation
non locale avec source

(★)

+ CI $C(0, z) = \ln \int e^{zx} u_0(x) dx =: C_0(z)$

+ CB en $z=0$ $C(t, 0) = \ln 1 = 0$

$$\begin{cases} C_t = C_z - C_z(z=0) + z^2 & t > 0 \\ C(t, 0) = 0 & z > 0 \\ C(0, z) = C_0(z) & z = 0 \\ & t = 0 \end{cases}$$

Méthode des caractéristiques: Pour $t > 0$ donné (pt cible)
 $z > 0$

$$\psi(s) = C(t+s, z-s) \quad -t \leq s \leq z$$

$$\begin{aligned} \psi'(s) &= C_t(t+s, z-s) - C_z(t+s, z-s) \\ &= \beta(z-s) - C_z(t+s, 0) \end{aligned}$$

disme $\beta(z) = z^2$

qu'on intègre de $s=-t$ à $s=0$:

$$\begin{aligned} C(t, z) - C_0(z+t) &= \int_{-t}^0 \beta(z-s) ds - \int_{-t}^0 C_z(t+s, 0) ds \\ &= \int_0^t \beta(z+s) ds - \int_0^t C_z(s, 0) ds \end{aligned}$$

$$C(t, z) = C_0(z+t) + \int_0^t \beta(z+s) ds - \int_0^t C_z(s, 0) ds \quad (*) \quad 12$$

IMPLICITTE mais

$$\partial_z C = C_0'(z+t) + \beta(z+t) - \beta(z)$$

qu'on évalue en $z=0$:

$$C_z(z=0) = C_0'(t) + \beta(t) - \beta(0) \quad \text{qu'on remplace dans } (*):$$

$$C(t, z) = C_0(z+t) + \int_0^t \beta(z+s) ds - \int_0^t (C_0'(s) + \beta(s)) ds$$

$$\text{ie } C(t, z) = C_0(z+t) - C_0(t) + \int_0^t (\beta(z+s) - \beta(s)) ds$$

$C(t, z)$ nous intéresse par... ce qu'on veut c'est $\frac{\partial C}{\partial z} |_{z=0}$, $\frac{\partial^2 C}{\partial z^2} |_{z=0}$...

$$\frac{\partial C}{\partial z} = C_0'(z+t) + \beta(z+t) - \beta(z) \xrightarrow{z=0} \boxed{\text{moyenne} = C_0'(t) + \beta(t)} = C_0'(t) + t^2$$

$$\frac{\partial^2 C}{\partial z^2} = C_0''(z+t) + \beta'(z+t) - \beta'(z) \xrightarrow{z=0} \boxed{\text{variance} = C_0''(t) + \beta'(t)} - \beta'(0) = C_0''(t) + 2t$$

Effet distribution initiale

Effet mutation

cf 1.1 et 2.1

mais tout ça on le savait déjà

3.2 ~~1/2~~ $u = J * u - u$ NL

$$\int_x e^{zx} (J * u) dx = \int_x e^{zx} \int_y J(x-y) u(t,y) dy dx$$

$$= \int_y u(t,y) e^{zy} \left(\int_x J(x-y) e^{z(x-y)} dx \right) dy$$

" $\int_{\theta} J(\theta) e^{z\theta} d\theta =: M(z)$ c'est la MGF du noyau J

$$= M(z) \int_x u(t,x) e^{zx} dx$$

et (★) devient:

$$C_t = C_z - C_z(z=0) + \underbrace{M(z) - 1}_{= \beta(z)} \quad \text{et } \underline{\underline{OK!}}$$

$$m(t) = C_0'(t) + \beta(t)$$

$$V(t) = C_0''(t) + \beta'(t) - \beta'(0)$$

Recall that ds le cas de diffu $m(t) \rightarrow +\infty$
 $V(t) \rightarrow +\infty$

Preons $u_0 = \delta_{m_0}$

$$C_0'(z) = \frac{\int x e^{zx} u_0}{\int e^{zx} u_0} = \frac{m_0 e^{zm_0}}{e^{zm_0}} = m_0$$

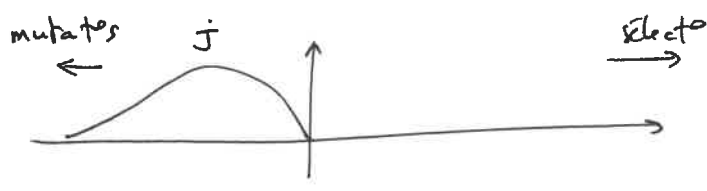
$$C_0''(z) = \frac{\int x^2 e^{zx} u_0}{\int e^{zx} u_0} - \left(\frac{\int x e^{zx} u_0}{\int e^{zx} u_0} \right)^2 = m_0^2 - m_0^2 = 0$$

$$\beta(t) = -1 + \int J(\theta) e^{t\theta} d\theta$$

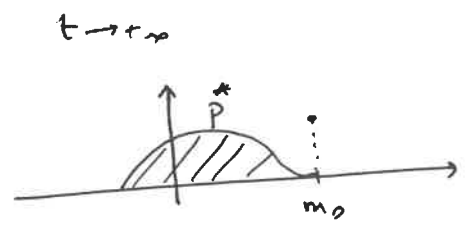
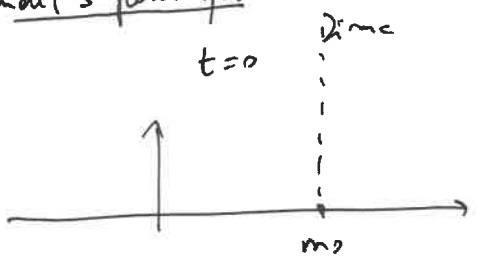
$t \rightarrow +\infty \rightarrow -1$
 $t \rightarrow +\infty \rightarrow +\infty$

si $\text{supp } J \subset (-\infty, 0]$
 ie Ho les mutations sont délétères
 et ds ce cas $V(t) \rightarrow \text{cte} > 0$

si $\text{supp } J \cap (0, +\infty) \neq \emptyset$
 ie \exists mutations bénéfiques
 et ds ce cas $V(t) \rightarrow +\infty$



Conditions pour que:



$$p_{\infty} = e^{\delta m_0} + (1-e)^{\delta} p_j^*$$

même synthèse dans (-∞, m_0]

Ref: Gil, Hamel, Martin, Roques 2017 *SIAM J. Appl. Math.*
 _____ 2019 *Nonlinearity*

Ry: CGF + Avram. Herbst in
 A., Veruete 2020 *DCDS B.*

4. CAS CONTINUANT "général"

4.1
Cas linéaire
local:

$$\frac{\partial u}{\partial t} = \frac{\mu^2}{2} \Delta u + w(x)u$$

Hyp: $w(x) \xrightarrow{x \rightarrow \pm \infty} -\infty$ Fitness
amplificatrice $+ w < 0$

$u(t, x) \leftarrow \varphi(x)e^{-\lambda t}$ donne $-\frac{\mu^2}{2} \Delta \varphi - w(x)\varphi = \lambda \varphi$ pb
valeur propre
fct° propre

on * φ puis \int et:

$$\frac{\mu^2}{2} \int |\nabla \varphi|^2 - \int w(x)\varphi^2 = \lambda \int \varphi^2$$

Prop:

$$\lambda := \text{Min } \mathcal{Q}(\varphi) := \frac{\mu^2}{2} \int |\nabla \varphi|^2 - \int w(x)\varphi^2$$

$$\varphi \in H^1$$

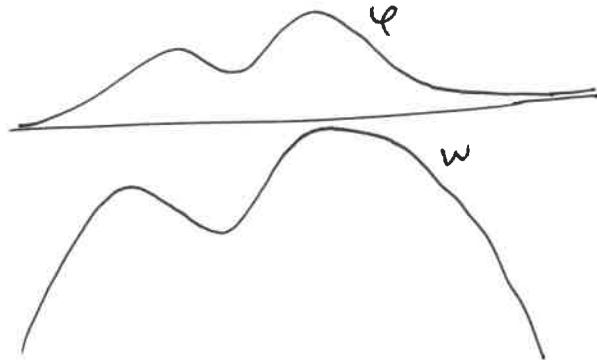
$$\varphi \in L_w^2 := \{ \varphi, x \mapsto \sqrt{-w(x)}\varphi(x) \in L^2 \}$$

$$\int \varphi^2 = 1$$

Minimum atteint en $\varphi > 0 \leftarrow$ unique positive fct° propre
(et $-\varphi < 0$)

$$-\frac{\mu^2}{2} \Delta \varphi - w(x)\varphi = \lambda \varphi$$

De +, $\varphi > 0$
 $\varphi \in H^1 \cap L_w^2$ + $\varphi \in C_0^\infty(\mathbb{R})$ (et même décroissance exponentielle en $\pm \infty$)
 $\int \varphi^2 = 1$



De + $\left[\text{Survie} \Leftrightarrow \lambda \leq 0 \right]$

Rq: $-\frac{\mu^2}{2} \Delta - W(x) : \exists$ BON (ds L^2) de \vec{v}_p :

$$\lambda_0 = \lambda < \lambda_1 \leq \lambda_2 \leq \dots$$

$$\begin{matrix} \downarrow & \downarrow & \downarrow & \dots \\ \varphi_0 = \varphi & \varphi_1 & \varphi_2 & \dots \end{matrix}$$

$$\hookrightarrow u(t, x) = \sum_{k=0}^{+\infty} a_k e^{-\lambda_k t} \varphi_k(x) \quad \text{avec } a_k = \langle \varphi_k, u_0 \rangle$$

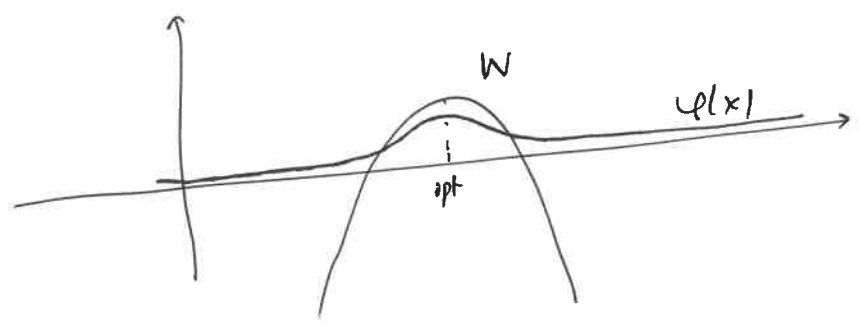
$$\Rightarrow u(t, \cdot) \xrightarrow{t \rightarrow +\infty} a_0 \varphi_0 \quad \text{dans } L^p \quad 1 \leq p \leq +\infty$$

cf A. Vennet 2019 J. Dynamics Diff. Eq.

ex quadratique: $W(x) = r_{\max} - \alpha \frac{(x - \text{opt})^2}{2}$ permis de select.

$$\varphi(x) = C e^{-\frac{\sqrt{\alpha}}{2\mu} (x - \text{opt})^2}$$

$\lambda = \frac{\mu}{2} \sqrt{\alpha} - r_{\max}$ qu'on veut < 0 si μ pt (Fardeau de mutato)
 α pt (pu de pression)
 r_{\max} gd



4.2 Asymptotique non local

$$\frac{\partial u}{\partial t} = \frac{\mu^2}{2} (j_{*u} - u) + W(x)u$$

Le ground state peut être une mesure singulière (avec atomes) phénomènes de concentration

- cf Bürger 88
- Bürger - Bonze 96
- Coville et al 10, 13, 17
- Briette 19

A., Gabriel, Kavian soon in DCDS B \blacktriangle

5) RM PATCH-MODEL

1 pathogène s'adaptant sur H hôtes
 ou 1 pop. \longleftrightarrow H environnements

épidémiologie
 agroécologie

$H=1$ $\partial_t u = \frac{\mu^2}{2} \Delta u + u(r(x) - \alpha \frac{\|x - 0\|^2}{2})$ $r(x) = r_{max} - \alpha \frac{\|x - 0\|^2}{2}$

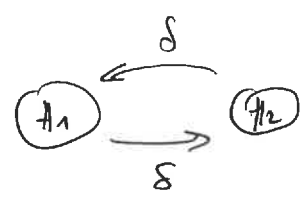
$0 \in \mathbb{R}^N$
 le trait optimal pour vivre de cet hôte

$\lambda_1 = \frac{\mu^2}{2} \sqrt{\alpha} - r_{max}$
 $\varphi(x) = C \exp\left(-\frac{\sqrt{\alpha}}{2\mu} \|x - 0\|^2\right)$

$H=2$

$$\begin{cases} \partial_t u_1 = \frac{\mu^2}{2} \Delta u_1 + r_1(x) u_1 + \delta (u_2 - u_1) \\ \partial_t u_2 = \frac{\mu^2}{2} \Delta u_2 + r_2(x) u_2 + \delta (u_1 - u_2) \end{cases}$$

$r_i(x) = r_{max} - \alpha \frac{\|x - O_i\|^2}{2}$



Éléments propres:

$$\begin{cases} -\frac{\mu^2}{2} \Delta \varphi_1 - r_1(x) \varphi_1 - \delta (\varphi_2 - \varphi_1) = \lambda_2 \varphi_1 \\ -\frac{\mu^2}{2} \Delta \varphi_2 - r_2(x) \varphi_2 - \delta (\varphi_1 - \varphi_2) = \lambda_2 \varphi_2 \end{cases}$$

$\lambda_2 = \inf_{\int \varphi_1^2 + \varphi_2^2 = 1} \left(\frac{\mu^2}{2} \int (|\nabla \varphi_1|^2 + |\nabla \varphi_2|^2) - \int r_1(x) \varphi_1^2 - \int r_2(x) \varphi_2^2 + \delta \int (\varphi_1 - \varphi_2)^2 \right)$

ici est $\geq d_1 \int \varphi_1^2 + d_2 \int \varphi_2^2 + \delta \int (\varphi_1 - \varphi_2)^2$
 par le Q. de Rayleigh de d_1

$\lambda_1'' + \delta \int (\varphi_1 - \varphi_2)^2$

Donc $\lambda_1 \leq d_2$ et $d_1 < d_2$ dès que $O_1 \neq O_2$

Diversification \Rightarrow prolifération du pathogène

of Hamel, Laurique, Roques 2021 J. Natl. Biology

17

$H=3$ slides...

6 MODELES ECO-EVO

slides...