§ Adaptive Dynamics.

[O. Diekmann, A beginner's guide to AD (2005)]

Assuming a separation of ecological + evolutionary timescales.

- mutation is small and rare.

$\longrightarrow$ obtain evolutionary insights from standard ecological models.

Invasion Analysis and Pairwise-Invasibility Plot (PIP)

Consider a population with a one-dimensional phenotype $\alpha \in I \subseteq \mathbb{R}$.

Suppose the resident population has a dominant trait α and is at ecological equilibrium.

> Q If a mutant with trait $\beta \approx \alpha$ is introduced, can the mutant invade when rare?

The following question was considered in the spatial context by [A. Hastings, (1983)].

$$\begin{cases} u_t - \alpha \Delta u = u(m(x) - u - v) \\ v_t - \beta \Delta v = v(m(x) - u - v) \\ \text{Neumann b.c.} \\ (u_0, v_0) \approx E_1 = (\theta_\alpha, 0) \end{cases}$$

Thm

$\alpha < \beta \Rightarrow E_1$ is lin. stable

$\alpha > \beta \Rightarrow E_1$ is lin. unstable

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The invasibility of $E_1 = (\theta_\alpha, 0)$ is determined by the eigenvalue problem.

$$\begin{cases} \beta \Delta \phi + (m(x) - \theta_\alpha)\phi + \mu \phi = 0 & \text{in } \Omega \\ n \cdot \nabla \phi = 0 & \text{on } \partial\Omega. \end{cases}$$

which has a p.e.v. $\lambda(\beta, \alpha)$,

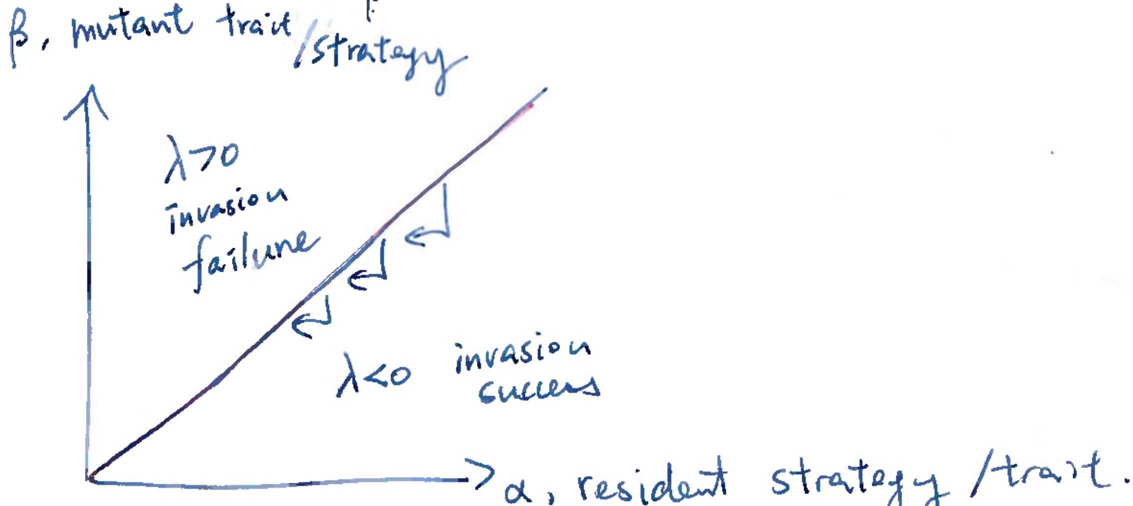
We call $\lambda(\beta,\alpha)$ the invasion exponent

$-ve \Rightarrow$ invation
$+ve \Rightarrow$ no invasion

and $\left.\frac{\partial \lambda}{\partial \beta}\right|_{\beta=\alpha=\alpha_0}$ the selection gradient.

In this case $\left.\frac{\partial \lambda}{\partial \beta}\right|_{\beta=\alpha=\alpha} > 0$ (by monotonicity in diffusion).

PIP

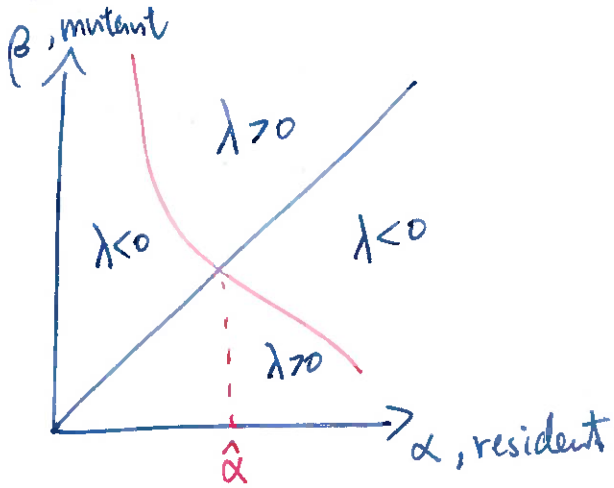


- Repeated invasion drives the overall diffusion rate smaller $\longrightarrow$ evolution of slow dispersal.

Canonical equation Let $\hat{\alpha}(t)$ be the dominant trait

$$\frac{d}{dt}\hat{\alpha} = -C(\hat{\alpha}(t))\frac{\partial \lambda}{\partial \beta}(\hat{\alpha}(t), \hat{\alpha}(t)) < 0.$$

Other forms of PIP.



$\lambda > 0 \Rightarrow$ invasion failure
$\lambda < 0 \Rightarrow$ invasion success

Evolutionarily Stable Strategy $\boxed{\text{ESS}}$ [Maynard Smith + Price 1973]

Def ① $\hat{\alpha} \in I$ is said to be an ESS

if $\lambda(\beta, \hat{\alpha}) > 0$ for all $\beta \neq \hat{\alpha}$.

i.e. the resident phenotype with trait/strategy $\hat{\alpha}$ can resist invasion by any other phenotype.

② $\hat{\alpha} \in I$ is said to be a local ESS

if $\lambda(\beta, \hat{\alpha}) > 0$ for all $\beta \neq \hat{\alpha}$, $\beta \approx \hat{\alpha}$.

Related Question. Suppose $\hat{\alpha}$ is ESS

Can the phenotype $\hat{\alpha}$ invade nearby phenotype when rare?

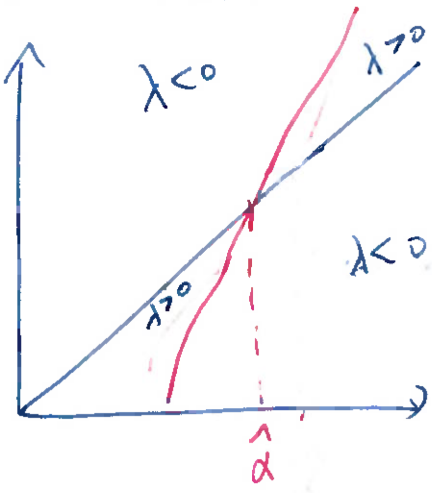
" ESS $\Rightarrow$ Neighborhood Invader Strategy "

[S. Geritz et. al., J. Math. Biol. (2002)] Finite-dim. ODE.

[Cantrell - Cosner - L., J.D.E. (2017)] Inf.-dim. syst.

(Special thanks to Prof Diekmann, who raised the question in a summer school in 2014.)

Evolutionary Branching Point.



<u>Def</u> $\hat{\alpha} \in I$ is said to be a branching point (BP)

if $\quad \frac{\partial\lambda}{\partial\beta}(\hat{\alpha},\hat{\alpha})=0 \quad$ and $\quad \frac{d}{ds}\left[\frac{\partial\lambda}{\partial\beta}(s,s)\right]_{s=\hat{\alpha}} > 0$

($\hat{\alpha}$ attracts monomorphic population)

and $\quad \lambda(\beta,\hat{\alpha})<0 \quad$ for $\beta\neq\hat{\alpha}$, $\beta\approx\hat{\alpha}$.

(resident adopting trait $\hat{\alpha}$ is invadable by nearby strategy.)

In this case, a trait substitution brings the population to a neighborhood of $\hat{\alpha}$, but then the population tends to split into two subpopulations adopting two distinct traits.

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Case study

Population in advective environmt.

$$
(1)\quad \begin{cases}
u_t - \alpha u_{xx} + q u_x = u\,(r(x) - u - v) & 0<x<L,\ t>0 \\
v_t - \beta v_{xx} + q v_x = v\,(r(x) - u - v) & 0<x<L,\ t>0 \\
\alpha u_x - q u = 0 = \beta v_x - q v & x=0,\ t>0 \\
\alpha u_x - q u = -bqu, \quad \beta v_x - q v = -bqv & x=L,\ t>0 \\
u(x,0) = u_0(x), \quad v(x,0) = v_0(x) & 0<x<L.
\end{cases}
$$

[Lutscher-Pachepsky-Lewis SIAM Rev (2005)]

$\boxed{b=0}$ Phytoplankton in a watercolumn. q: sinking velocity

$\boxed{b=1}$ Stream-to-lake population

$\boxed{b=+\infty}$ Stream-to-sea population where $u(L,t)=0=v(L,t)$.

Thm (Evolution of fast dispersal).

Let $r(x)$ be a positive constant and $0 \le b \le 1$.

If $\alpha < \beta$, then $(u,v) \longrightarrow (0, \theta_\beta)$ provided $u_0 \not\equiv 0$, $v_0 \not\equiv 0$.

$\boxed{b=1}$ [Lou-Lutscher JMB (2014)]

$\boxed{0<b<1}$ [Lou-Zhou JDE (2015)]

Intuition: Faster dispersal allows the population to utilize resources upstream.

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The same result cannot hold for $b \gg 1$.

e.g. $b = +\infty$, then faster disperser does not persist.

Open Question: Can we characterize

$$b_* := \sup\{ b > 0 : \text{Faster disperser wins in (1)} \}.$$

[Hao - L. - Lou DCDS-B (2021)]

We exploit the asymptotic expansion of θ_α, $\alpha \gg 1$ to explicitly calculate $\lambda(\beta, \alpha)$, and obtained 9 qualitatively different PIP's.

In particular, $b_* \in (0, 3/2)$.

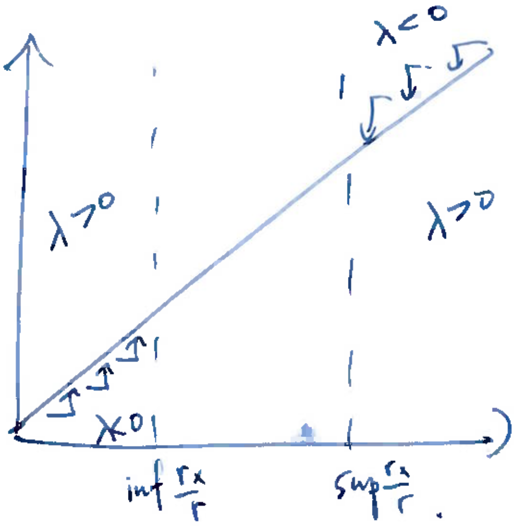
The case $r(x) \neq$ const.

[L.-Lou-Lutscher J. Biol. Dyn. (2014)].

Thm Suppose $r > 0$ and $r_x \geq 0$ in $[0,L]$

(i) $q/\alpha < \inf \frac{r_x}{r} \implies \frac{\partial \lambda}{\partial \beta}(\alpha,\alpha) < 0$

(ii) $q/\alpha > \sup \frac{r_x}{r} \implies \frac{\partial \lambda}{\partial \beta}(\alpha,\alpha) > 0$.



Special cases: $r_x \equiv 0$.

$\frac{r_x}{r} \equiv$ const. $\to$ later.

Thm Suppose $r > 0$ and $r_x > 0$ in $[0,L]$ and $2 \inf \frac{r_x}{r} > \sup \frac{r_x}{r}$

① If $\log r$ is strictly concave, then there is a unique local ESS $\hat{\alpha} = \hat{\alpha}(q)$ for all $0 < q \ll 1$.

② If $\log r$ is strictly convex, then there is a unique evolutionary branching point $\hat{\alpha} = \hat{\alpha}(q)$ $\forall\ 0 < q \ll 1$.

Intuition: $\log r$ concave $\to$ "one patch"

$\log r$ convex $\to$ "two patches" that generates a trade-off between fast & slower types.

Ideal Free Distribution

In previous results:

[Hastings (1983)]

Diffusion creates a mismatch of resource → diffusion is selected against.

If $q=0$ $\theta_\alpha \to m_+$ as $\alpha \to 0$

Diffusion reduces mismatch → diffusion is selected for.

If $q>0$, $r \equiv$ const, $\theta_\alpha \to r$ as $\alpha \to \infty$. [Lou-Lutcher, Lou-Zhou].

[McPeek-Holt Am. Nat. (1992)]

→ Selection could favor dispersal that does not create such a mismatch. $\theta_\alpha \equiv m(x)$.

[Fretwell-Lucas Acta Biotheor. (1969)]

Ideal free distribution (in bird population) where fitness is equilibrated across space.

Consider single population model.

$$(1) \begin{cases} u_t - \underbrace{\mu \nabla\cdot[\nabla u - u\nabla P(x)]}_{(\mu, Q):\text{ dispersal strategy}} = u\,\underbrace{[m(x)-u]}_{\text{Fitness / effective growth rate.}} & \text{in } \Omega\times(0,\infty) \\ n\cdot[\nabla u - u\nabla P] = 0 & \text{on } \partial\Omega\times(0,\infty) \\ u(x,0) = u_0(x) & \text{in } \Omega. \end{cases}$$

Intuition: To choose (μ, P) such that the corresponding equilibrium $\theta \equiv m$.

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$\theta = m$ is possible if and only if

$$\mu \nabla\cdot(\nabla m - m\nabla P) = 0 \qquad n\cdot[\nabla\theta - \theta\nabla P]_{\partial\Omega} = 0$$

$$\Leftrightarrow \mu\nabla\cdot(e^{P}\nabla(e^{-P}m)) = 0 \quad \text{and} \quad n\cdot\nabla(e^{-P}\theta) = 0$$

$$\Leftrightarrow \quad e^{-P}m \equiv C$$

$$\Leftrightarrow \quad -P + \ln m = C'.$$

Consider

$$(2)\begin{cases} u_t - \mu\nabla\cdot(\nabla u - u\nabla \ln m) = u(m-u-v) & \Omega\times(0,\infty) \\ v_t - \nu\nabla\cdot(\nabla v - v\nabla Q) = v(m-u-v) & \Omega\times(0,\infty) \\ n\cdot(\nabla u - u\nabla\ln m) = n\cdot(\nabla v - v\nabla Q) = 0 & \partial\Omega\times(0,\infty). \\ u(x,0) = u_0(x), \quad v(x,0) = v_0(x) & \Omega. \end{cases}$$

[Cantrell-Cosner-Lou MBE (2010)] $(\mu, P) = (\mu, \ln m)$ is ESS.

Thm $Q \neq \ln m + C \Rightarrow (m,0)$ is locally asymp. stable.

[Averill-Munther-Lou JBD (2012)]

Thm $Q \neq \ln m + C \Rightarrow (m,0)$ is globally asymp. stable.

Proof ① (2) has no positive equilibria.

② $(0, \tilde{v})$ is linearly unstable.

Step ① suppose that (U, V) is a positive equilibrium

$$(3a)\quad \mu \nabla\cdot(\nabla U - U\nabla \ln m) + U(m-U-V) = 0 \qquad \Omega$$

$$(3b)\quad \nu \nabla\cdot(\nabla V - V\nabla Q) + V(m-U-V) = 0 \qquad \Omega$$

$$(3c)\quad n\cdot[\nabla U - U\nabla \ln m] = n\cdot[\nabla V - V\nabla Q] = 0 \qquad \partial\Omega.$$

Set $w = U/m$, then

$$\mu \nabla\cdot\left[\nabla(wm) - wm\frac{\nabla m}{m}\right] + wm(m-U-V)$$

$$(4)\quad \begin{cases} \mu\nabla\cdot(m\nabla w) + mw(m-U-V) = 0 & \text{in } \Omega \\ n\cdot\nabla w = n\cdot\left(\dfrac{m\nabla U - U\nabla m}{m^2}\right) = 0 & \text{on } \partial\Omega. \end{cases}$$

Divide by w and integrate,

$$\mu\int\frac{m|\nabla w|^2}{w^2} + \int m(m-U-V) = 0. \qquad (5)$$

Integrate (3a), (3b). $\displaystyle\int U(m-U-V) = 0 = \int V(m-U-V)$ (6)

Combining (5) & (6)

$$\mu\int\frac{m|\nabla w|^2}{w^2} + \int(m-U-V)^2 = 0$$

$\Rightarrow$ $m-U-V \equiv 0$ and $w \equiv s$ for some constant s. $\Rightarrow U = sm$

$\Rightarrow$ $V = m - U = (1-s)m$ for some constant $0<s<1$.

$$\Rightarrow \begin{cases} \nu\nabla\cdot(\nabla m - m\nabla Q) = 0 & \Omega \\ n\cdot[\nabla m - m\nabla Q] = 0 & \partial\Omega \end{cases} \Rightarrow \underline{\underline{Q = \ln m + C}}.$$

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Step ② We show $(0, \tilde{v})$ is unstable.

Let λ_1, ϕ be the p.e.v. and p.e.f of

$$(7)\quad \begin{cases} \mu \nabla\cdot[\nabla\phi - \phi\nabla \ln m] + (m-\tilde{v})\phi + \lambda_1\phi = 0 & \Omega \\ n\cdot[\nabla\phi - \phi\nabla\ln m] = 0 & \partial\Omega \end{cases}$$

Claim $\lambda_1 < 0$.

Set $\psi = \frac{\phi}{m}$, then rewrite

$$\mu\nabla\cdot(m\nabla\psi) + m(m-\tilde{v})\psi + \lambda m\psi \text{ in } \Omega, \quad n\cdot\nabla\psi\big|_{\partial\Omega} = 0$$

Divide by ψ and integrate by parts,

$$\mu\int m\frac{|\nabla\psi|^2}{\psi^2} + \int m(m-\tilde{v}) + \lambda_1\int m = 0$$

Integrate the eq. of $\tilde{v}$ $\begin{cases} \nu\cdot\nabla\cdot(\nabla\tilde{v} - \tilde{v}\nabla\ln m) + \tilde{v}(m-\tilde{v}) = 0 \\ \text{no-flux} \end{cases}$

$$\Rightarrow \int \tilde{v}(m-\tilde{v}) = 0$$

Combing $\mu\int m\frac{|\nabla\psi|^2}{\psi^2} + \int(m-\tilde{v})^2 + \lambda_1\int m = 0.$

Since $\tilde{v} \neq m$, we have $\lambda_1 < 0$. #.

Related Works

$$\mathcal{L}u = \Delta\left(\frac{u}{m}\right)$$

[Korobenko - Braverman JMB (2014)]

$$\mathcal{L}u = \Delta\left(\gamma\left(\frac{m}{u}\right)u\right), \quad s \mapsto \gamma(s) \text{ is decreasing.}$$

[Y.-J. Kim - Kwon - F. Li JMB (2013)].

Discrete diffusion / Patch models [Cantrell et al. JMB (2012)]

Integro-differential models [Cantrell et al. CAMQ (2012)]

[Cosner - Dávila - Martinez JBD (2012)]

Integro-difference model [Cantrell - Cosner - Y. Zhou (preprint)]

Ideal Free Distribution in Time-Periodic Environment.

Consider

$$\begin{cases} u_t = \mu \nabla\cdot(\nabla u - u\nabla P(x,t)) + u(m(x,t)-u-v) & \Omega\times(0,\infty) \\ v_t = \nu \nabla\cdot(\nabla v - v\nabla Q(x,t)) + v(m(x,t)-u-v) & \Omega\times(0,\infty) \\ \text{no-flux b.c.} & \partial\Omega\times(0,\infty) \\ u(x,0)=u_0(x), \quad v(x,0)=v_0(x) & \Omega. \end{cases}$$

where $m(x,t)$ is a given T-periodic function.

and we consider dispersal strategy (μ,P) (ν,Q) that are periodic.

Q. Does resource matching $\Rightarrow$ ESS ?

A. Yes, provided

(*) $m(x,t)>0$ and $\int_\Omega m(x,t)\,dx$ is const. in time.

Thm [Cantrell-Cosner, Math. Biosci (2018)]

If (*) hold, $E_1=(m,0)$ and $E_2 \neq (0,m)$,

then $(u(\cdot,t),v(\cdot,t)) - (m(\cdot,t),0) \longrightarrow 0$ as $t\to\infty$.

But in general, resource matching is not possible! What is IFD?

- Ideal : individual has complete information.
- Free : no cost to travel

Pathwise fitness

Given a periodic curve $\gamma : \mathbb{R} \to \Omega$,

Define $\tilde{F}(\gamma) = \int_0^1 F(\gamma(t), t)\, dt$.

If each individual has ideal knowledge, and can move freely without cost, then $\tilde{F}(\gamma)$ should by independent of γ.

This is equivalent to

$F(x,t)$ being independent of x.

In a static environment, each individual chooses a specific location as habitat choice.

In a periodic environment, each individual chooses a full periodic path as habitat choice!

[Cantrell - Cosner - L. S.I.A.P. (2021)] 7

Let $\theta(x,t)$ be a single species distribution

It is an IFD if $\underbrace{F(x,t) = m(x,t) - \theta(x,t)}_{\text{fitness fcn.}}$ is independent of x.

Thm [CCL] Given (μ, P) and (ν, Q).
If (μ, P) produce IFD but (ν, Q) do not,
then $(u,v) - (\tilde{u}, 0) \longrightarrow 0$ as $t \to \infty$.

Thm If (μ, P) does not produce IFD, then it is not ESS, i.e. $\exists (\nu, Q)$ such that $(\tilde{u}, 0)$ is unstable.

Thm $\exists\, m(x,t) > 0$ such that IFD is impossible.

In fact In such an environment, no T-periodic solution consisting of any number of species can be ESS
(it is always invadable)

$\Rightarrow$ An ecological attractor is ESS
$\Rightarrow$ it must consist of 3 or more species.
(because attractor of 1 or 2 species is necessarily periodic, by monotone dynamical system's result.)

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By a transformation $\varphi(x,t) = e^{-Q}\phi(x,t)$,

$$\begin{cases} \partial_t \varphi = \Delta\varphi + \nabla Q \cdot \nabla\varphi + F(x,t)\varphi + \lambda_1 \varphi & \Omega \times [0,1] \\ n \cdot \nabla\varphi = 0 & \partial\Omega \times [0,1] \\ \varphi(x,0) = \varphi(x,1) & \Omega \end{cases}$$

Sine $Q = -\alpha|x-\gamma(t)|^2$, <u>Lemma A</u> implies

$$\limsup_{\alpha\to\infty} \lambda_1 \leq -\int_0^1 F(\gamma(t),t)\,dt < 0.$$

i.e. $(\theta^*, 0)$ is destabilized by the mutant invader with strategy <u>$Q(x,t)$</u>.

$\Rightarrow$ $(\theta^*, 0)$ is not an ESS.

Lemma Let λ_1 be the p.e.v. of

$$\begin{cases} \partial_t \varphi - \Delta\varphi + \alpha \nabla q(x,t)\cdot\nabla\varphi = V(x,t)\varphi + \lambda_1\varphi & \text{in } \Omega\times[0,1] \\ n\cdot\nabla\varphi = 0 & \partial\Omega\times[0,1] \\ \varphi(x,0) = \varphi(x,1) & \Omega \end{cases}$$

where $q(x,t) = |x - \gamma(t)|^2$ for some 1-periodic γ.

then $\limsup\limits_{\alpha\to\infty} \lambda_1 \leq -\int_0^1 V(\gamma(t),t)\,dt$.

(In fact, equality holds.)

Pf. WLOG, assume $V(\gamma(t),t) \equiv 0$

by replacing $V(x,t)$ by $V(x,t) - V(\gamma(t),t)$

$\varphi(x,t)$ by $\varphi(x,t)\exp\left(-\int_0^t \left[V(\gamma(s),s) - \int_0^1 V(\gamma(\tau),\tau)\,d\tau\right] ds\right)$

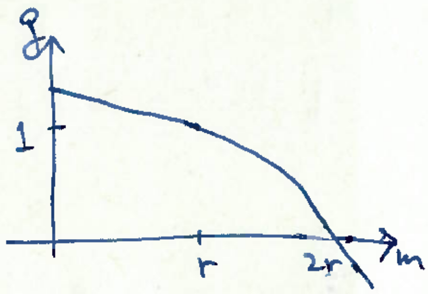
λ_1 by $\lambda_1 + \int_0^1 V(\gamma(\tau),\tau)\,d\tau$

Claim. For each $\varepsilon > 0$, $\limsup\limits_{\alpha\to\infty} \lambda_1 < \varepsilon$.

It suffices to construct, for each $\varepsilon>0$, a nonnegative nontrivial subsolution ψ such that

$$\begin{cases} \partial_t \psi - \Delta\psi + \alpha\nabla q\cdot\nabla\psi \leq V(x,t)\psi + \varepsilon\psi & \text{in } \Omega\times[0,1] \\ n\cdot\nabla\psi = 0 & \text{on } \partial\Omega\times[0,1] \\ \psi(x,0) = \psi(x,1) & \text{in } \Omega \end{cases}$$

Fix $r > 0$ small s.t. $|V(x,t)| < \frac{\varepsilon}{2}$ if $|x - \gamma(t)|^2 < 2r$



Define $\psi(x,t) = \max\{ g(|x-\gamma(t)|^2), 0 \}$

where $g : \mathbb{R} \to \mathbb{R}$ satisfies

$g'(s) < 0 \ \forall s, \quad g(2r) = 0, \quad g(s) = 1 + \delta(r-s)$ for $s \in [0,r]$

By choosing r small, $\psi \equiv 0$ near $\partial\Omega \times [0,1]$

$\Rightarrow \ n \cdot \nabla\psi \equiv 0 \quad \partial\Omega \times [0,1]$

When $g(q(x,t)) = g(|x-\gamma(t)|^2) = 1 + \delta(r - |x-\gamma(t)|^2)$,

$$\partial_t \psi - \Delta\psi + \alpha \nabla q \cdot \nabla\psi - (V+\varepsilon)\psi$$

$$= \delta(-\partial_t q + \Delta q - \alpha|\nabla q|^2) - \underbrace{(V+\varepsilon)}_{> \varepsilon/2} [\underbrace{1 + \delta g(q)}_{> 1}]$$

$\leq O(\delta) - \frac{\varepsilon}{2} < 0$ if δ chosen small relative to ε.

When $r \leq |x-\gamma(t)|^2 \leq 2r$,

$$\partial_t\psi - \Delta\psi + \alpha\nabla \cdot \nabla\psi - (V+\varepsilon)\psi$$

$$= \underbrace{g'(q)}_{<0} \Big[\underbrace{\partial_t q - \Delta q + \Big(-\frac{g''(q)}{g'(q)} + \alpha\Big)|\nabla m|^2}_{>0 \text{ if } \alpha \gg 1} \Big] \underbrace{- (V+\varepsilon) g(q)}_{\leq 0}.$$

Suppose $\theta^*(x,t)$ is not IFD we will show that it is not ESS.

<u>Claim</u> $F(x,t) = m(x,t) - \theta^*(x,t)$ satisfies

$$\int_0^1 \sup_{x\in\Omega} F(x,t)\,dt > 0.$$

Indeed, integrate eqn. of θ^*,

$$\frac{d}{dt}\int_\Omega \theta^* = \int_\Omega F(x,t)\theta^*(x,t)\,dx < \left(\sup_{x\in\Omega} F(x,t)\right)\int_\Omega \theta^*.$$

$$\Rightarrow \frac{d}{dt}\left(\log\int_\Omega \theta^*\right) < \sup_{x\in\Omega} F(x,t).$$

Integrate in t, we proved the claim.

Choose a smooth, periodic curve $\gamma : \mathbb{R} \to \operatorname{Int}\Omega$ s.t.

$$\int_0^1 F(\gamma(t),t)\,dt > 0.$$

Choose $Q(x,t) = -\alpha|x-\gamma(t)|^2$,

<u>Claim</u> For $\alpha \gg 1$, $(\theta^*, 0)$ is unstable.

$$\begin{cases} \partial_t\phi = \Delta\phi - \nabla\cdot(\phi\nabla Q(x,t)) + (m-\theta^*)\phi + \lambda_1\phi & \Omega\times[0,1] \\ n\cdot(\nabla\phi - \phi\nabla Q) = 0 & \partial\Omega\times[0,1] \\ \phi(x,0) = \phi(x,1) & \Omega \end{cases}$$

Indeed, <u>Lemma A</u> implies

$$\limsup_{\alpha\to\infty} \lambda_1 \le -\int_0^1 (m-\theta^*)(\gamma(t),t)\,dt < 0.$$