Steady State Concentration for an Evolutionary Epidemic System

R. DJIDJOU DEMASSE
A. DUCROT
F. FABRE

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- The sustainable management of plant disease has two distinct but interdependent goals:

  - ***Immediate epidemiological*** → reducing severity and frequency of disease epidemics

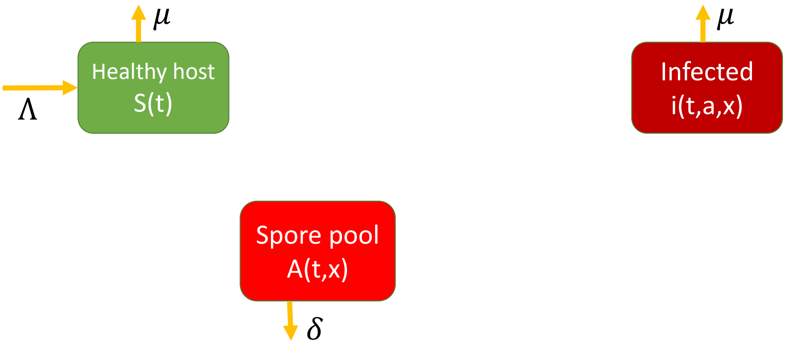
  - ***Longer-term evolutionary*** → reducing the rate of evolution of new patho-types (*i.e.* preserving the efficiency of disease resistance genes)

- Here, we model epidemiological and evolutionary dynamics of spore-producing pathogens in a host population.

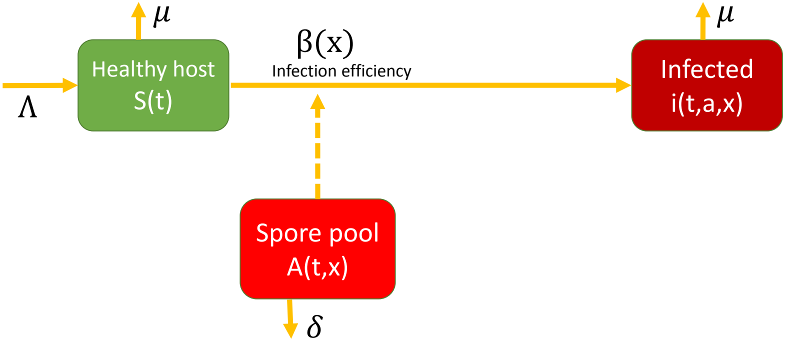
- The host population did not represent individual plants, but rather leaf area densities (leaf surface area per m^2).

Zhan J. et al., *Annu Rev Phytopatol* (2015)

Model *(Host homogeneity)*



Model (*Host homogeneity*)



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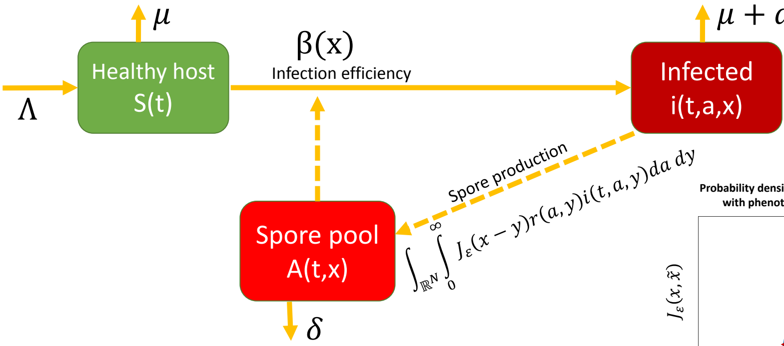
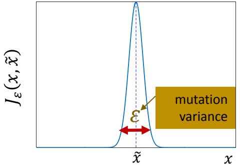


Probability density function that a spore with phenotype $\tilde{x}$ mutates to x



$$r(a,x) = p(x)\chi_{[\tau(x),\tau(x)+l(x)]}(a)$$

$$J_\varepsilon(x) = \frac{1}{\varepsilon^N}J\left(\frac{x}{\varepsilon}\right);\ \varepsilon \ll 1$$

Djidjou Demasse *et al., Math. Models Meth. Appl. Sci., 2017*

Model equations (*Host homogeneity*)

$$\begin{cases} \partial_t S(t) = \Lambda - \mu S(t) - S(t) \displaystyle\int_{\mathbb{R}^N} \beta(y) A(t,y) \mathrm{d}y \\ (\partial_t + \partial_a)\, i(t,a,x) = -\mu i(t,a,x), \\ i(t,0,x) = \beta(x) S(t) A(t,x), \\ \partial_t A(t,x) = \displaystyle\int_{\mathbb{R}^N} \int_0^\infty J(x-y) r(a,y) i(t,a,y) \mathrm{d}a \mathrm{d}y - \delta A(t,x). \end{cases}$$

with

$$\begin{aligned} & S(t=0) \in \mathbb{R}_+, \\ & i(t=0,.,.) \in L^1_+\left((0,\infty) \times \mathbb{R}^N\right) \\ & A(t=0,.) \in L^1_+\left(\mathbb{R}^N\right). \end{aligned}$$

Evolutionary Attractor (EA)

The EAs are characterized by the following fitness function:

Infection efficiency

$$\Psi(x) := \frac{\beta(x)}{\delta} \int_0^{\infty} r(a,x)\, e^{-\mu a} \mathrm{d}a$$

$$r(a,x) := p(x)\chi_{[\tau(x),\tau(x)+l(x)]}(a)$$

Sporulation rate

Latent period

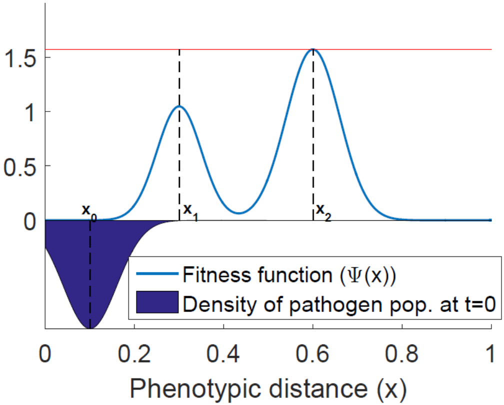
Infectious period

The phenotype x^* *is EA if* x^* *maximize* Ψ

$$\mathrm{MAX}_x\ \Psi(x) = \Psi(x_2)$$

one EA

$\{x_2\}$



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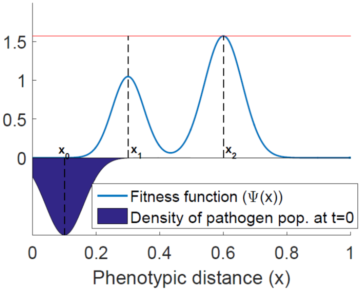
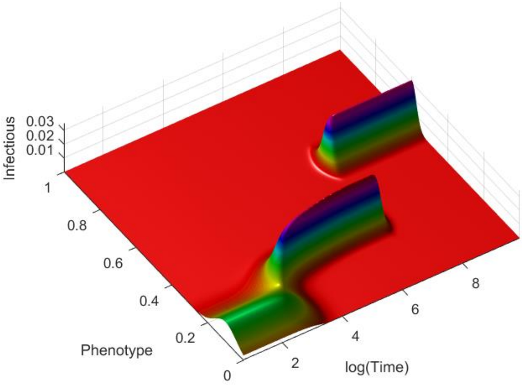
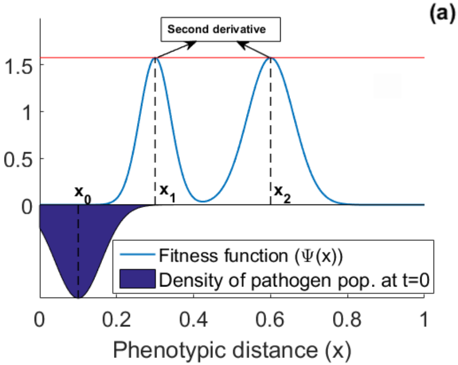




$$\mathrm{MAX}_x\ \Psi(x) = \Psi(x_1) = \Psi(x_2)$$

two EAs

$\{x_1; x_2\}$



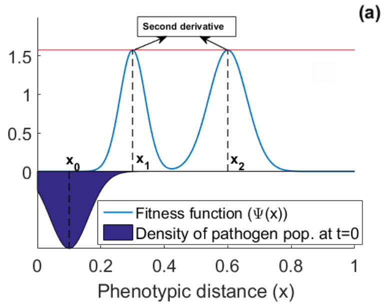
Which *EA* will asymptotically persist?:

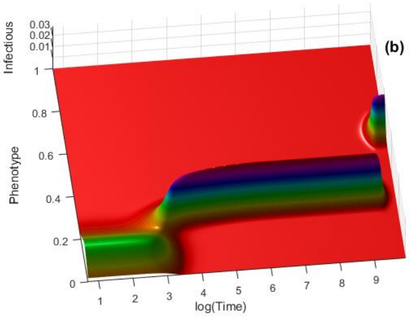
Globally Stable Evolutionary Attractor (GSEA)

$$\mathrm{MAX}_x\,\Psi(x) = \Psi(x_1) = \Psi(x_2)$$

two EAs

$$\{x_1; x_2\}$$



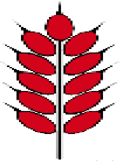


***Metastable behavior*.**
Before the system concentrates around the GSEA x_2, it persists on the EA x_1 for a relatively long time interval, whose size depends on ε and diverges to $+\infty$ as $\varepsilon \to 0$.

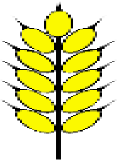
Host heterogeneity

♣ Context:

Two cultivars:



sensitive (S)



quantitative resistant (R)

♣ Objectives:

- ❑ Reducing the severity of disease epidemics.
- ❑ Preserving the efficiency of disease R genes.

Host heterogeneity

- Each environment induced a specific fitness function:

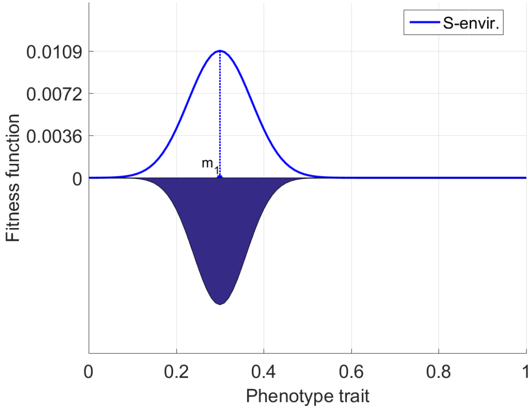
$$\text{S envir.} \hookrightarrow \ \Psi_S := G(m_1, \sigma)$$

$$\text{R envir.} \hookrightarrow \ \Psi_R := G(m_2, \sigma)$$

- The fitness function of S and R envir.:

$$\text{S} + \text{R envir.} \hookrightarrow \ \Psi := P_S \Psi_S + (1 - P_S)\Psi_R$$

Host heterogeneity



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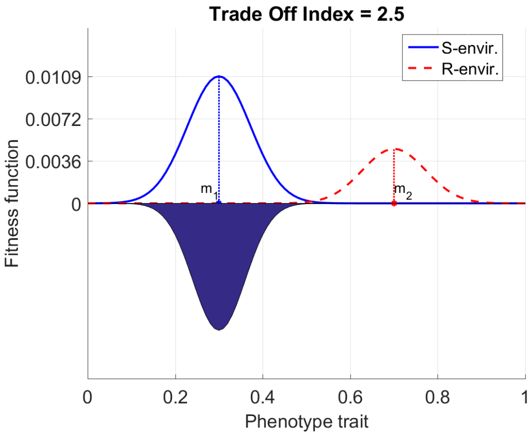

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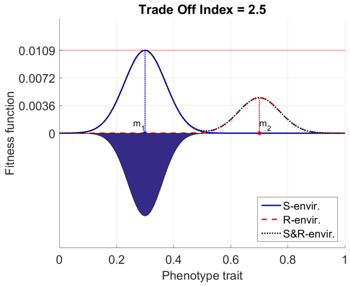
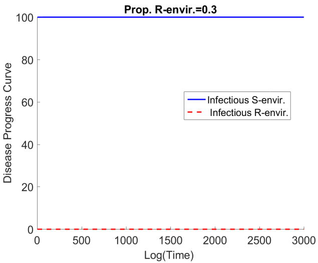
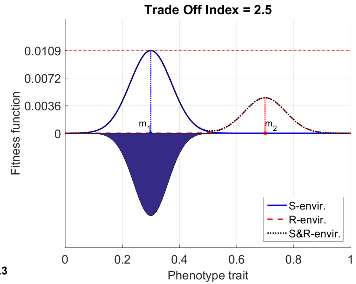
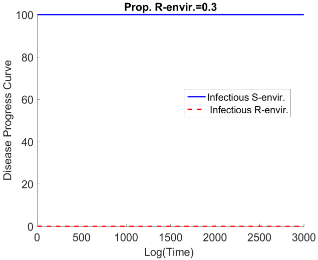




Preserving the efficiency of R genes

Host heterogeneity





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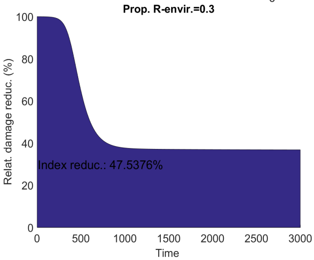
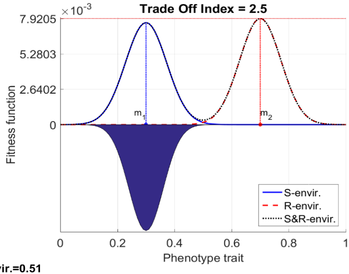
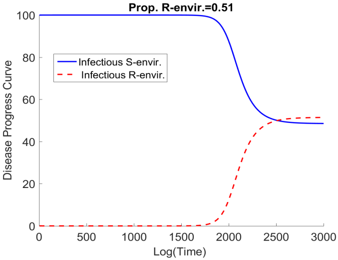


Reducing the epidemics severity

Host heterogeneity





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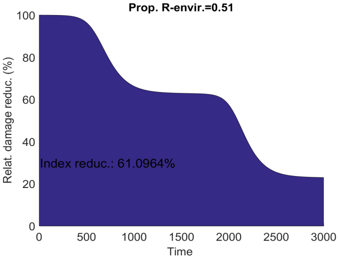

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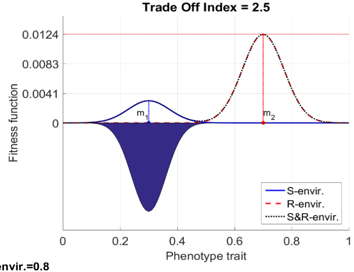

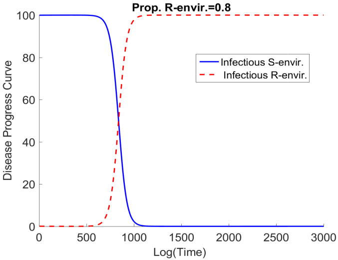

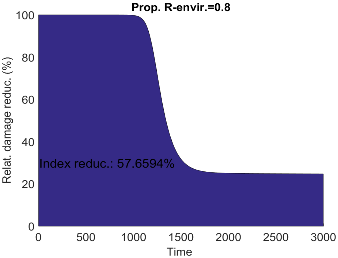

Preserving the efficiency of R genes

Reducing the epidemics severity

Some technical materials

$$
\begin{cases}
\partial_t S(t) = \Lambda - \mu S(t) - S(t) \int_{\mathbb{R}^N} \beta(y) A(t,y) \mathrm{d}y \\
(\partial_t + \partial_a)\, i(t,a,x) = -\mu i(t,a,x), \\
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&S(t=0) \in \mathbb{R}_+, \\
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$$

A unique non-trivial stationary state...

Observe that $(S^*, i^*, A^*) \in (0,\infty) \times L^1_+\left((0,\infty)\times\mathbb{R}^N\right) \times L^1_+(\mathbb{R}^N)$ is a stationary state of the model iff

$$\begin{cases} L[A^*](x) = \dfrac{1}{S^*}A^*(x), \\ \Lambda - \mu S^* = S^* \displaystyle\int_{\mathbb{R}^N} \beta(y)A^*(y)\mathrm{d}y \text{ and } i^*(a,x) = \beta(x)S^*A^*(x)e^{-\mu a}. \end{cases}$$

with

$$L[u](x) := \int_{\mathbb{R}^N} J(x-y)\Psi(y)u(y)\mathrm{d}y$$

and

$$\Psi(x) = \frac{\beta(x)}{\delta}\int_0^\infty r(a,x)e^{-\mu a}\mathrm{d}a. (\text{ fitness function})$$

Therefore the study of the stationary state of the model strongly relies on the spectral properties of L.

Model assumptions

Assumption 1 (Fitness function):

- The fitness function $\Psi : \mathbb{R}^N \to \mathbb{R}_+$ is assumed to be continuous on $\mathbb{R}^N$ and $\lim_{\|x\|\to\infty} \Psi(x) = 0$.
- There exists a finite number of points $\{x_1, .., x_M\} \subset \mathbb{R}^N$;

$$\left\{x \in \mathbb{R}^N : \ \Psi(x) = \|\Psi\|_\infty\right\} = \{x_1, .., x_M\},$$

and $\forall k$, the Hessian $-D^2\Psi\left(x_k\right)$ is positive definite.

Assumption 2 (Mutation kernel):

- J is non-negative, $J(-x) = J(x)$ and $\int_{\mathbb{R}^N} J(x)\mathrm{d}x = 1$.
- There exist some constants $M_0 > 0$, $\eta_0 > 0$ and $\gamma_0 \in (0, 1)$ such that

$$J(x) \le M_0 \exp\left(-\eta_0 \|x\|^{\gamma_0}\right), \ a.e. \ x \in \mathbb{R}^N.$$

(J decays faster without being a thin-tailed kernel)

- The covariance matrix $\Sigma[J]$ of the probability measure $J(x)\mathrm{d}x$ is positive definite.

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A unique non-trivial stationary state...

Theorem

Let Assumption **1** *and* **2** *be satisfied. Define the number* $\mathcal{T}_0$ *by*

$$\mathcal{T}_0 = \frac{\Lambda}{\mu} \sup_{\substack{\varphi \in L^2(\mathbb{R}^N) \\ \|\varphi\|_{L^2(\mathbb{R}^N)}=1}} \iint_{\mathbb{R}^N \times \mathbb{R}^N} \Psi^{\frac{1}{2}}(x)\Psi^{\frac{1}{2}}(y)J(x-y)\varphi(x)\varphi(y)\mathrm{d}x\mathrm{d}y.$$

- *When* $\mathcal{T}_0 \leq 1$, *then the model has a unique equilibrium point* $\left(S^0, i^0, A^0\right) := \left(\frac{\Lambda}{\mu}, 0, 0\right)$.
- *When* $\mathcal{T}_0 > 1$, *then the model has two different equilibrium points* $\left(S^0, i^0, A^0\right)$ *and* (S^*, i^*, A^*)*:*

$$0 < S^* < S^0, \ A^* \in L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N) \text{ with } A^* > 0 \ a.e.,$$
$$\text{and } i^*(a,x) = \beta(x)S^*A^*(x)e^{-\mu a}.$$

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Next...

[Reed M., Simon B.(1979). Helffer B., Sjöstrand J.(1984). Klein M., Rosenberger E. (2008)]

We now assume that the mutation kernel J depends upon a small parameter $0 < \varepsilon << 1$ and takes the form

$$J_\varepsilon(x) := \varepsilon^{-N} J\left(\frac{x}{\varepsilon}\right), \ \forall x \in \mathbb{R}^N.$$

We aim at describing the behaviour of the endemic equilibrium point $(S_\varepsilon^*, i_\varepsilon^*, A_\varepsilon^*)$ of the model as $\varepsilon \to 0$.
A_ε^* arises as the principle eigenvector of the linear operator

$$L^\varepsilon[u](x) := \Psi^{\frac{1}{2}}(x) \int_{\mathbb{R}^N} J_\varepsilon(x-y)\Psi^{\frac{1}{2}}(y)u(y)\mathrm{d}y.$$

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Asymptotic expansion of the principal eigenvalue of L^ε...

Problem (*): $L^\varepsilon \psi^\varepsilon(x) = \lambda^\varepsilon \psi^\varepsilon(x),$ on $L^1(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N)$.

$\forall x_j \in \{x_1, .., x_M\} := \left\{x \in \mathbb{R}^N : \ \Psi(x) = \|\Psi\|_\infty\right\}$; find a *formal* solution of (*) of the form

$$\psi_j^\varepsilon(x) := \sum_{k=0}^{\infty} \varepsilon^{\frac{k}{2}} \varphi_{k,j}\left(\frac{x - x_j}{\varepsilon^{\frac{1}{2}}}\right) \text{ and } \lambda_j^\varepsilon := \|\Psi\|_\infty \left(1 + \sum_{k=0}^{\infty} \varepsilon^{1+\frac{k}{2}} \lambda_{k,j}\right),$$

where $\{\varphi_{k,j}\}_{k\geq 0} \subset L^2(\mathbb{R}^N)$ and $\{\lambda_{k,j}\}_{k\geq 0} \subset \mathbb{R}$ are determined by using:

- a recurrence relation,
- the elliptic operator $P_j := -\Delta + \| \left(-D^2\Psi(x_j)\right)^{\frac{1}{2}} x\|$.

Note that

$$\varphi_{0,j}(x) = (2\pi)^{-\frac{N}{2}} \sqrt{\det(\mathrm{A_j})} \exp\left(-\frac{\|A_j x\|^2}{2}\right) \text{ and } \lambda_{0,j} = -\mathrm{tr}(A_j).$$

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Asymptotic expansion of the principal eigenvalue of L^ε...

Order relation in the set of maximum points: $\{x_1, .., x_M\} := \{x : \Psi(x) = \|\Psi\|_\infty\}$;

- Define the order $\trianglelefteq$ on the set $\{1, .., M\}$:

$$i \trianglelefteq j \;\Leftrightarrow\; \{\lambda_{k,i}\}_{k\geq 0} \preceq \{\lambda_{k,j}\}_{k\geq 0}\,.$$

- Consider the set $\mathcal{M} \subset \{1, .., M\}$ defined by

$$\mathcal{M} = \max\left(\{1, .., M\}, \trianglelefteq\right).$$

- If $i \neq j$ belongs to $\mathcal{M}$ then $\lambda_{k,i} = \lambda_{k,j}$ for all $k \geq 0$.
- In the case $N = 1$:

$$i, j \in \mathcal{M} \Longleftrightarrow (\Psi)^{(n)}(x_j) = (\Psi)^{(n)}(x_i)\,, \;\forall n \in \mathbb{N}.$$

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$$i \trianglelefteq j \;\Leftrightarrow\; \{\lambda_{k,i}\}_{k\geq 0} \preceq \{\lambda_{k,j}\}_{k\geq 0}\,.$$

- Consider the set $\mathcal{M} \subset \{1,..,M\}$ defined by

$$\mathcal{M} = \max\left(\{1,..,M\}, \trianglelefteq\right).$$

- If $i \neq j$ belongs to $\mathcal{M}$ then $\lambda_{k,i} = \lambda_{k,j}$ for all $k \geq 0$.
- In the case $N = 1$:

$$i, j \in \mathcal{M} \Longleftrightarrow (\Psi)^{(n)}(x_j) = (\Psi)^{(n)}(x_i)\,,\ \forall n \in \mathbb{N}.$$

Asymptotic expansion of the principal eigenvalue of L^{ε}...

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$$L^\varepsilon[u](x) := \Psi^{\frac{1}{2}}(x)\int_{\mathbb{R}^N} J_\varepsilon(x-y)\Psi^{\frac{1}{2}}(y)u(y)\mathrm{d}y.$$

Theorem

- *Let Assumptions* **1** *and* **2** *be satisfied.*
- *Let* λ^ε *denotes the principal eigenvalue of operator* L^ε*.*

Then λ^ε *admits the following asymptotic series expansion as* $\varepsilon \to 0$, *for any* $j \in \mathcal{M}$,

$$\frac{1}{\|\Psi\|_\infty}\lambda^\varepsilon = 1 + \sum_{k=0}^{p} \varepsilon^{1+k}\lambda_{2k,j} + O\left(\varepsilon^{p+2}\right) \text{ as } \varepsilon \to 0.$$

for any $p \geq 0$*; and where*

- $\{\lambda_{k,j}\}_{k\geq 0}$ *is a unique well defined sequence for each* j*;*
- $\lambda_{2k+1,j} = 0$ *for all* k*.*

Concentration of the principal eigenvector ψ^ε of L^ε...

Theorem

- *Let Assumptions* **1** *and* **2** *be satisfied.*
- *Consider the principal eigenvector* ψ^ε *of* L^ε*;* $\|\psi^\varepsilon\|_{L^1(\mathbb{R}^N)} = 1$.
- *Assume that* $\mathcal{M} = \{i\}$.

1. *Then, for each* $\nu \in (0, \gamma_0)$*, there exists* $\eta > 0$ *such that the following concentration property holds true:*

$$\int_{\mathbb{R}^N \setminus B(x_i, \varepsilon^\nu)} \psi^\varepsilon(x)\mathrm{d}x = O\left(\exp\left(-\eta\varepsilon^{\nu-\gamma_0}\right)\right) \text{ as } \varepsilon \to 0.$$

2. *In particular, one gets* $\psi^\varepsilon \to \delta_{x_i}$ *as* $\varepsilon \to 0$ *for the narrow topology:* $\forall f \in \mathcal{C}\left(\mathbb{R}^N\right)$ *ones has*

$$\lim_{\varepsilon \to 0} \int_{\mathbb{R}^N} f(x)\psi^\varepsilon(x)\mathrm{d}x = \int_{\mathbb{R}^N} f(x)\delta_{x_i}(\mathrm{d}x) = f(x_i).$$

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Concentration of the endemic steady state $(S_\varepsilon^*, i_\varepsilon^*, A_\varepsilon^*)$.

Corollary:

- Let Assumptions **1** and **2** be satisfied.
- $\lim_{\varepsilon\to 0} \mathcal{T}_0^\varepsilon = \mathcal{T}_0^0 := \frac{\Lambda}{\mu}\|\Psi\|_\infty > 1$,

$$\mathcal{T}_0^\varepsilon = \frac{\Lambda}{\mu} \sup_{\substack{\varphi\in L^2(\Omega)\\ \|\varphi\|_{L^2(\Omega)}=1}} \iint_{\Omega\times\Omega} \Psi^{\frac{1}{2}}(x)\Psi^{\frac{1}{2}}(y)J_\varepsilon(x-y)\varphi(x)\varphi(y)\mathrm{d}x\mathrm{d}y.$$

If $\mathcal{M} = \{i\}$ then the endemic steady state $(S_\varepsilon^*, i_\varepsilon^*, A_\varepsilon^*)$ satisfies :

1. $\lim_{\varepsilon\to 0} S_\varepsilon^* = \frac{1}{\mathcal{T}_0^0}$,
2. $\forall f \in \mathcal{C}(\mathbb{R}^N)$, $\lim_{\varepsilon\to 0} \int_{\mathbb{R}^N} f(x)A_\varepsilon^*(x)\mathrm{d}x = \frac{\mathcal{T}_0^0-1}{\mu\beta(x_i)} f(x_i)$,
3. $\lim_{\varepsilon\to 0} \int_{\mathbb{R}^N} f(x)i_\varepsilon^*(a,x)\mathrm{d}x = \frac{\mathcal{T}_0^0-1}{\mu\mathcal{T}_0^0} f(x_i)\, e^{-\mu a}$ in $L^1(0,\infty)\cap L^\infty(0,\infty)$.

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Concentration of the principal eigenvector ψ^ε of L^ε...

- If Ψ is symmetric; $\mathcal{M} = \{i, j\}$ with $i \neq j$ and $x_i = -x_j$ then, since the principle eingevector is also symmetric, the endemic stationary state (equally) concentrates on these two points yields to a dimorphic steady state.
- From a biological point of view, the condition $\mathcal{M} = \{i\}$ is a reasonable assumption.
  - In that case, when the dispersal in the phenotypic trait space is small, the unique endemic steady state of the model concentrates on a single trait.
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Thanks for your attention