Effect of habitat fragmentation on persistence and spreading of populations

Grégoire Nadin

Laboratoire Jacques-Louis Lions, université Paris 6

Miami, december 2012
Habitat fragmentation

Habitat loss $\Rightarrow$ emergence of discontinuities (*fragmentation*) in an organism’s preferred environment (*habitat*).

**Causes:**
- Natural: geological processes, climate change.
- Human: agriculture, urban areas.

**Effects:** One of the main cause of *extinction* of species
- increased competition in remaining habitats
- size effects
- impossible immigration and rescue effects

Characterization of the “fragmentation“? Optimization of conservation strategies?
A reaction-diffusion model

\[ \partial_t u - \Delta u = f(x, u) \]

- \( u \): population density
- \( \Delta u \): diffusion term
- \( f(x, u) \): growth rate, depends on the space variable \( x \)
- \( \mu(x) := f'_u(x, 0) \): growth rate per capita at small density
- \( \mu(x) > 0 \): favourable area / habitat
- \( \mu(x) < 0 \): unfavourable area
A reaction-diffusion model

\[ \partial_t u - \Delta u = f(x, u) \]

Hypotheses:

- \( f(x, 0) = 0 \)
- \( u \mapsto f(x, u)/u \) decreasing (intraspecific competition)
- \( \exists M > 0 \mid \forall x, \ f(x, M) \leq 0 \) (saturation)

Example: logistic growth rate \( f(x, u) = \mu(x) - u^2 \)

Additional hypothesis: \( x \mapsto f(x, u) \) periodic \( \forall u \geq 0 \)
Characterization of extinction/persistence \( I \)

\[
\begin{cases}
\partial_t u - \Delta u = f(x, u) & (0, \infty) \times \mathbb{C}, \\
u(0, x) = u_0(x) \geq 0 & \{0\} \times \mathbb{C}.
\end{cases}
\]

Linearized operator near the steady state \( u \equiv 0 \):

\[-\mathcal{L}\phi := -\Delta\phi - \mu(x)\phi \quad \text{where} \quad \mu(x) := f'_u(x, 0)\]

The operator \( \mathcal{L} \) admits unique principal eigenelements \((\phi, k_0(\mu))\) s.t.

\[
\begin{cases}
-\mathcal{L}\phi = k_0(\mu)\phi & \Omega, \\
\phi > 0 & \Omega, \\
\phi \text{ periodic} & \end{cases}
\]

**Example:** If \( f = f(u) \) does not depend on \( x \), then

\[\mu = f'(0), \quad \phi \equiv 1 \quad \text{and} \quad k_0(\mu) = -f'(0).\]
\[ \partial_t u - \Delta u = f(x, u) \quad (0, \infty) \times \Omega \]

**Theorem**

If \( k_0(\mu) < 0 \), then there exists a unique positive steady state \( p \), which is globally attractive, that is,

\[
\text{if } \ u_0 \neq 0, \quad \text{then} \quad \lim_{t \to +\infty} u(t, x) = p(x) \quad \text{loc. } x \in \Omega.
\]

If \( k_0(\mu) \geq 0 \), then 0 is globally attractive.

- Ludwig-Aronson-Weinberger 79 (dim 1)
- Cantrell-Cosner 89 (dim \( N \))
- Berestycki-Hamel-Roques 05 (periodic, general \( f \))
Characterization of extinction/persistence III

**Theorem**
*If* $k_0(\mu) < 0$, *then there exists a unique positive steady state* $p$, *which is globally attractive*, *that is,*

$$
\text{if } u_0 \neq 0, \text{ then } \lim_{t \to +\infty} u(t, x) = p(x) \text{ loc. } x \in \Omega.
$$

*If* $k_0(\mu) \geq 0$, *then* $0$ *is globally attractive.*

**Interpretation:**
- The stability of $0$ determines the persistence of the population.
- It only depends on the growth rate at small density $\mu(x) = f'_u(x, 0)$.
- $k_0(\mu_1) \leq k_0(\mu_2)$ $\Rightarrow$ $\mu_1$ "better environment" than $\mu_2$.

What is the dependence of $\mu \mapsto k_0(\mu)$?
How to measure the "fragmentation of the habitat" through $\mu$?
The patch model in 1d

\[ \mu_A(x) = \begin{cases} \mu^+ & \text{in } A \text{ "habitat"}, \\ \mu^- & \text{in } (-\frac{1}{2}, \frac{1}{2}) \setminus A. \end{cases} \text{ with } \mu^+ > \mu^- \]

**Theorem**

The sets A minimizing \( k_0(\mu_A) \) (over sets of length \(|A|\)) are the intervals.

- Cantrell-Cosner 91 when \((-\frac{1}{2}, \frac{1}{2}) \setminus A\) interval and Neumann BC
- Berestycki-Hamel-Roques 05 over arbitrary A’s

**Interpretation:** The habitat A giving the higher chance of persistence is the unfragmented one.

For the patch model in dim 1, unfragmented habitat \(\equiv\) intervals. More general \(\mu\) ?
The Schwarz periodic rearrangement

\[ \mu = 1_A : \mu^* := 1_{A^*} \text{ with } A^* := \left(-\frac{|A|}{2}, \frac{|A|}{2}\right) \text{ centered interval of length } |A|. \]

\[ \mu = \sum_{i=1}^{m} \alpha_i 1_{A_i}, \text{ with } A_1 \subset \ldots \subset A_m \subset (-L/2, L/2) \text{ and } \alpha_i \geq 0: \]

\[ \mu^* := \sum_{i=1}^{m} \alpha_i 1_{A_i^*} \]

With a density argument...

**Definition**

\( \mu \) periodic measurable bounded: \( \exists! \) periodic measurable \( \mu^* \), called the **Schwarz periodic rearrangement** of \( \mu \),

- with the same distribution function,
- even
- nonincreasing on \((0, L/2)\).
Definition of the Schwarz rearrangement

**Definition**

\(\mu\) periodic measurable bounded: \(\exists!\) periodic measurable \(\mu^*\), called the **Schwarz periodic rearrangement** of \(\mu\),

- with the same distribution function,
- even
- nonincreasing on \((0, L/2)\).

A continuous function \(\mu\) and its Schwarz rearrangement \(\mu^*\).

**Observation (Berestycki-Hamel-Roques 05):** "less fragmented" habitat is associated with the growth rate \(\mu^*\).
A Faber-Krahn inequality

**Proposition**

(Berestycki-Hamel-Roques 05)

\[ k_0(\mu^*) \leq k_0(\mu). \]

**Corollary:** There exist some \( \mu \)'s such that if

\[ \partial_t u = \Delta u + \mu(x)u - u^2, \quad \partial_t v = \Delta v + \mu^*(x)v - v^2, \]

with \( u(0, x) = v(0, x) = u_0(x) \), then

\[ \lim_{t \to +\infty} u(t, x) = 0 \] while \( v \) converges to a positive steady state.

**Interpretation:** The habitat \( A \) giving the higher chance of persistence is the unfragmented one.
A Faber-Krahn inequality

**Proposition**  
*(Berestycki-Hamel-Roques 05)*

\[ k_0(\mu^*) \leq k_0(\mu). \]

**Proof.**  \( k_0(\mu) \) periodic principal eigenvalue of \(-L\phi = -\phi'' - \mu(x)\phi\) self-adjoint. Thus \( k_0(\mu) \) is a *Rayleigh quotient*:

\[
k_0(\mu) = \min_{\alpha \in C^1_{\text{per}}} \frac{\langle -L\alpha, \alpha \rangle_{L^2}}{\langle \alpha, \alpha \rangle_{L^2}} = \min_{\alpha \in C^1_{\text{per}}} \frac{1}{\int_0^1 \alpha^2} \int_0^1 (\alpha''^2 - \mu(x)\alpha^2)
\]

Two classical properties of rearrangement:

\[
\int_0^1 \mu^*(\alpha^*)_2 \geq \int_0^1 \mu \alpha^2 \quad \text{Hardy-Littlewood inequality}
\]

\[
\int_0^1 (\alpha^*)_2 \leq \int_0^1 \alpha'^2 \quad \text{Polya-Szego inequality}
\]
A Faber-Krahn inequality

**Proposition**
(Berestycki-Hamel-Roques 05)

\[ k_0(\mu^*) \leq k_0(\mu). \]

**Corollary:** There exist some \( \mu \)'s such that if

\[ \partial_t u = \Delta u + \mu(x)u - u^2, \quad \partial_t v = \Delta v + \mu^*(x)v - v^2, \]

with \( u(0, x) = v(0, x) = u_0(x) \), then

\[
\lim_{t \to +\infty} u(t, x) = 0 \text{ while } v \text{ converges to a positive steady state.}
\]

**Interpretation:** The habitat \( A \) giving the higher chance of persistence is the unfragmented one.

What happens when the species persists in both environments?
The spreading property in homogeneous media

\[ f = f(u) \text{ does not depend on } x \]

\[ \partial_t u - \partial_{xx} u = f(u) \]

\[ u_0 \text{ compactly supported} \]

**Theorem**
*(Kolmogorov-Petrovsky-Piskunov 37, Aronson-Weinberger 78)*

\[ u(t, wt) \rightarrow \begin{cases} 
1 & \text{if } w \in [0, w^*), \\
0 & \text{if } w > w^*,
\end{cases} \quad \text{as } t \to +\infty \]

where \( w^* = 2\sqrt{f'(0)}. \)

**Interpretation:** The population “spreads” with speed \( w^*. \)
The spreading property in periodic media

\[ f = f(x, u) \text{ periodic in } x \]

\[ \partial_t u - \partial_{xx} u = f(x, u) \]

\[ u_0 \text{ compactly supported} \]

**Theorem**

(Gartner-Freidlin 79, Weinberger 02, Berestycki-Hamel-N. 08)

If \( k_0(\mu) < 0 \), \( \exists w^* = w^*(\mu) \) s. t.

\[ u(t, wt) \rightarrow \begin{cases} 1 & \text{if } w \in [0, w^*) \\ 0 & \text{if } w > w^* \end{cases} \text{ as } t \rightarrow +\infty \]

Dependence \( \mu \mapsto w^*(\mu) \)? Influence of the “fragmentation of the habitat” on the spreading speed \( w^* \)?
Characterization of the spreading speed

\[ L \varphi := \partial_{xx} \varphi + \mu(x) \varphi \]

\[ \forall p \in \mathbb{R}, \quad L_p \varphi := e^{px} L(e^{-px} \varphi) = \partial_{xx} \varphi - 2p \partial_x \varphi + \left(p^2 + \mu(x)\right) \varphi. \]

\(L_p\) admits a unique \textbf{periodic principal eigenvalue} \(k_p(\mu)\), def. by:

\[
\begin{cases}
- L_p \varphi = k_p(\mu) \varphi \text{ in } \mathbb{R}, \\
\varphi > 0, \\
\varphi \text{ is periodic}.
\end{cases}
\]

**Proposition**

If \(k_0(\mu) < 0\), then

\[
w^*(\mu) = \min_{p > 0} \frac{-k_p(\mu)}{p}.
\]
Statement of the result

**Definition**

\( \mu \) periodic measurable bounded: \( \exists! \) periodic measurable \( \mu^* \), called the Schwarz periodic rearrangement of \( \mu \),
- with the same distribution function,
- even
- nonincreasing on \((0, L/2)\).

**Theorem**

[N. 09]

\[ w^*(\mu^*) \geq w^*(\mu) \]

**Interpretation:** The unfragmented habitat gives the higher spreading speed for the species when it persists.
Corollary for the patch model

\[
\mu_A(x) = \begin{cases} 
\mu^+ & \text{in } A \text{ "habitat"}, \\
\mu^- & \text{in } (-\frac{1}{2}, \frac{1}{2}) \setminus A.
\end{cases}
\text{ with } \mu^+ > \mu^-
\]

**Corollary**

The sets \( A \) maximizing \( w^*(\mu_A) \) (over sets of length \( |A| \)) are the intervals.

**Proof.**

- \( w^*(\mu_A^*) \geq w^*(\mu_A) \) for all \( A \)
- \( \mu_A^* = \mu_A^* \), where \( A^* \) is the centered interval of length \( |A| \)
A related nonsymmetric eigenvalue optimization pbm

\[ w^*(\mu) = \min_{p > 0} \frac{-k_p(\mu)}{p} \]

where \( k_p(\mu) = \) periodic principal eigenvalue of \( L_p \).

\[ \Rightarrow \text{If } k_p(\mu^*) \leq k_p(\mu) \text{ for all } p, \text{ then } w^*(\mu^*) \geq w^*(\mu). \]

**Reformulation of our problem** Prove that for all \( p \in \mathbb{R} \):

\[ k_p(\mu^*) \leq k_p(\mu) \]

where \( \mu^* \) is the Schwarz rearrangement of \( \mu \).
Comparison with the Faber-Krahn inequality ($p = 0$)

**Proposition**  
(Berestycki-Hamel-Roques 05)

$$k_0(\mu^*) \leq k_0(\mu).$$

Issues when $p \neq 0$:

- No Rayleigh quotient since $L_p$ is not symmetric.

  $$L_p\phi = \phi'' - 2p\phi' + (p^2 + \mu(x))\phi.$$

- Rearrangement properties are integral ones.

- Very few literature on the rearrangement of non-symmetric operators (Alvino-Trombetti-Lions 90-91, Hamel-Nadirashvili-Russ 05-07).

→ Find an integral characterization of $k_p(\mu)$. 
An integral characterization of $k_p(\mu)$

**Proposition**

(N. 09) $k_p(\mu) = \max_{\alpha \in C_{\text{per}}} \frac{1}{\int_0^1 \alpha^2} \left( \int_0^1 \alpha'^2 - \int_0^1 \mu(x) \alpha^2 - p^2 \frac{1}{\int_0^1 \frac{1}{\alpha^2}} \right)$

**Corollary**

$k_p(\mu^*) \leq k_p(\mu)$ for all $p$ and thus $w^*(\mu^*) \geq w^*(\mu)$.

**Proof.** Follows from the two classical properties of rearrangement:

\[
\int_0^1 \mu^*(\alpha^*)^2 \geq \int_0^1 \mu \alpha^2 \quad \text{and} \quad \int_0^1 (\alpha^*)'^2 \leq \int_0^1 \alpha'^2,
\]

and from $\int_0^1 \frac{1}{\alpha^2} = \int_0^1 \frac{1}{(\alpha^*)^2}$ since the rearrangement preserves the distribution function. □
A general characterization of principal eigenvalue for non-symmetric operators

\[ \mathcal{L}_\phi := \text{div}(A(x)\nabla \phi) + q(x) \cdot \nabla \phi + \mu(x)\phi \]

\( k_0(A, q, \mu) \): periodic principal eigenvalue of \(-\mathcal{L}\)

**Theorem**
(N. 09)

\[ k_0(A, q, \mu) = \min_{\beta \text{ periodic}} k_0(A, 0, \mu + \nabla \beta A \nabla \beta + q \cdot \nabla \beta - \text{div}q/2) \]

**Remark:** Similar formulas with different boundary conditions by Donsker-Varadhan (76), Holland (78).

Very useful to optimize principal eigenvalues of non-symmetric operators, like operators \( L_p \).

⇒ Other applications to reaction-diffusion equations in periodic media.
What happens in multidimensional media?

If $\mu = \mu(x_1, x_2)$, then

1. rearrange $x_1 \mapsto \mu(x_1, x_2)$ w.r.t to $x_1$ with $x_2$ fixed
2. do the same with $x_2$

$\Rightarrow$ one obtains the **Steiner symmetrization** $\mu^*$ of $\mu$. It is

- with the same distribution function,
- symmetric w.r.t $\{x_1 = 0\}$ and $\{x_2 = 0\}$
- nonincreasing w.r.t $x_1 \in (0, 1/2)$ and $x_2 \in (0, 1/2)$

**But**, it is not the unique function satisfying these properties. (Exple: rearrange first in $x_2$ and then in $x_1$)

**Proposition**

$(N. 09)$ $\exists \mu = \mu(x_1, x_2)$ s.t. $w^*(\mu^*) < w^*(\mu)$. 
Open problems

1. $\mu_A = \mu^+$ in $A$, $\mu^-$ in $(0, 1)^2 \setminus A$. Which $A$ minimizes $k_0(\mu_A)$ with $|A|$ prescribed?
   Conjecture in Hamel-Roques 07: $A=$ stripe, ball or complementary of a ball.

2. Does this $A$ maximizes $A \mapsto w^*(\mu_A)$?

3. Other notions of “fragmentation”? $\mu_1$ and $\mu_2$ given, which one is the “most fragmented”?
   Variations w.r.t the period: ElSmaily-Hamel-Roques 09, N. 09, Hamel-Fayard-Roques 10, Hamel-N.-Roques 12

4. Other classes of heterogeneities?
   Random stationary ergodic environment: N. in prep
Thank you for your attention.