Effect of habitat fragmentation on persistence and spreading of populations

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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

Δu: 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

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

Linearized operator near the steady state $u \equiv 0$:

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

The operator $\mathcal{L}$ admits unique principal eigenelements $\big(\phi, k_0(\mu)\big)$ 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

$$\mu = f'(0), \quad \phi \equiv 1 \quad \text{and} \quad k_0(\mu) = -f'(0).$$

Characterization of extinction/persistence II

$$\partial_t u - \Delta u = f(x,u) \quad (0,\infty)\times\Omega$$

Theorem

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

$$\textit{if} \quad u_0 \not\equiv 0, \quad \textit{then} \quad \lim_{t\to+\infty} u(t,x) = p(x) \quad \textit{loc. } x\in\Omega.$$

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

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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 μ_2.

What is the dependence of $\mu \mapsto k_0(\mu)$?
How to measure the "fragmentation of the habitat" through μ?

The patch model in 1d

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

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 μ ?

The Schwarz periodic rearrangement

$\mu = 1_A$: $\mu^\star := 1_{A^\star}$ with $A^\star := (-\frac{|A|}{2}, \frac{|A|}{2})$ centered interval of length $|A|$.

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

$$\mu^\star := \sum_{i=1}^{m} \alpha_i 1_{A_i^\star}$$

With a density argument...

Definition

μ periodic measurable bounded: $\exists!$ periodic measurable $\mu^\star$, called the **Schwarz periodic rearrangement** *of μ,*

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

Definition of the Schwarz rearrangement

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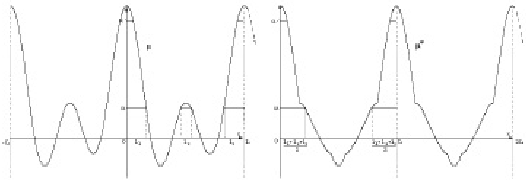

A continuous function μ and its Schwarz rearrangement $\mu^\star$.

Observation (Berestycki-Hamel-Roques 05): "less fragmented" habitat is associated with the growth rate $\mu^\star$.

A Faber-Krahn inequality

Proposition

(Berestycki-Hamel-Roques 05)

$$k_0(\mu^\star) \le k_0(\mu).$$

Corollary: There exist some μ's such that if

$$\partial_t u = \Delta u + \mu(x)u - u^2, \quad \partial_t v = \Delta v + \mu^\star(x)v - v^2,$$

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)

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

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

$$k_0(\mu) = \min_{\alpha \in \mathcal{C}^1_{per}} \frac{< -\mathcal{L}\alpha, \alpha >_{L^2}}{< \alpha, \alpha >_{L^2}} = \min_{\alpha \in \mathcal{C}^1_{per}} \frac{1}{\int_0^1 \alpha^2} \int_0^1 (\alpha'^2 - \mu(x)\alpha^2)$$

Two classical properties of rearrangement:

$\int_0^1 \mu^\star(\alpha^\star)^2 \geq \int_0^1 \mu\alpha^2$	Hardy-Littlewood inequality
$\int_0^1 (\alpha^\star)'^2 \leq \int_0^1 \alpha'^2$	Polya-Szego inequality

□

A Faber-Krahn inequality

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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.

What happens when the species persists in both environments?

The spreading property in homogeneous media

$f = f(u)$ does not depend on x

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

u_0 compactly supported

Theorem

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

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

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

Interpretation: The population “spreads” with speed w^*.

The spreading property in periodic media

$f = f(x, u)$ periodic in x

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

u_0 compactly supported

Theorem

(Gartner-Freidlin 79, Weinberger 02, Berestycki-Hamel-N. 08)
If $k_0(\mu) < 0$, $\exists w^* = w^*(\mu)$ s. t.

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

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

Characterization of the spreading speed

$$\mathcal{L}\varphi := \partial_{xx}\varphi + \mu(x)\varphi$$

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

L_p admits a unique **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

μ periodic measurable bounded: $\exists!$ periodic measurable $\mu^\star$, called the **Schwarz periodic rearrangement** *of μ,*

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

Theorem

[N. 09]

$$w^*(\mu^\star) \geq w^*(\mu)$$

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

Corollary for the patch model

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

Corollary

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

Proof.

- $w^*(\mu_A^\star) \geq w^*(\mu_A)$ for all A
- $\mu_A^\star = \mu_{A^\star}$, where $A^\star$ 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.

$\Rightarrow$ If $k_p(\mu^\star) \le k_p(\mu)$ for all p, then $w^*(\mu^\star) \ge w^*(\mu)$.

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

$$k_p(\mu^\star) \le k_p(\mu)$$

where $\mu^\star$ is the Schwarz rearrangement of μ.

Comparison with the Faber-Krahn inequality ($p = 0$)

Proposition

(Berestycki-Hamel-Roques 05)

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

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

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

An integral characterization of $k_p(\mu)$

Proposition

(N. 09) $k_p(\mu) = \max_{\alpha \in \mathcal{C}^1_{per}} \frac{1}{\int_0^1 \alpha^2} \Big(\int_0^1 \alpha'^2 - \int_0^1 \mu(x)\alpha^2 - p^2 \frac{1}{\int_0^1 \frac{1}{\alpha^2}} \Big)$

Corollary

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

Proof. Follows from the two classical properties of rearrangement:

$$\int_0^1 \mu^\star (\alpha^\star)^2 \geq \int_0^1 \mu\alpha^2 \quad \text{and} \quad \int_0^1 (\alpha^\star)'^2 \leq \int_0^1 \alpha'^2,$$

and from $\int_0^1 \frac{1}{\alpha^2} = \int_0^1 \frac{1}{(\alpha^\star)^2}$ since the rearrangement preserves the distribution function. □

A general characterization of principal eigenvalue for non-symetric operators

$\mathcal{L}\phi := div(A(x)\nabla\phi) + q(x)\cdot\nabla\phi + \mu(x)\phi$
$k_0(A, q, \mu)$: periodic principal eigenvalue of $-\mathcal{L}$

Theorem

(N. 09)
$k_0(A, q, \mu) = \min_{\beta \ periodic} k_0(A, 0, \mu + \nabla\beta A\nabla\beta + q\cdot\nabla\beta - divq/2)$

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.
$\Rightarrow$ 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** $\mu^\star$ of μ. 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.* $w^*(\mu^\star) < w^*(\mu)$.

Open problems

1. $\mu_A = \mu^+$ in A, μ^- in $(0,1)^2 \backslash A$. 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"? μ_1 and μ_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.