Traps and Patches:

(I) Berg-Purcell Problem: Narrow Capture by Small Boundary Traps

(II) Optimization of the Persistence Threshold in Patchy Landscapes.

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Outline

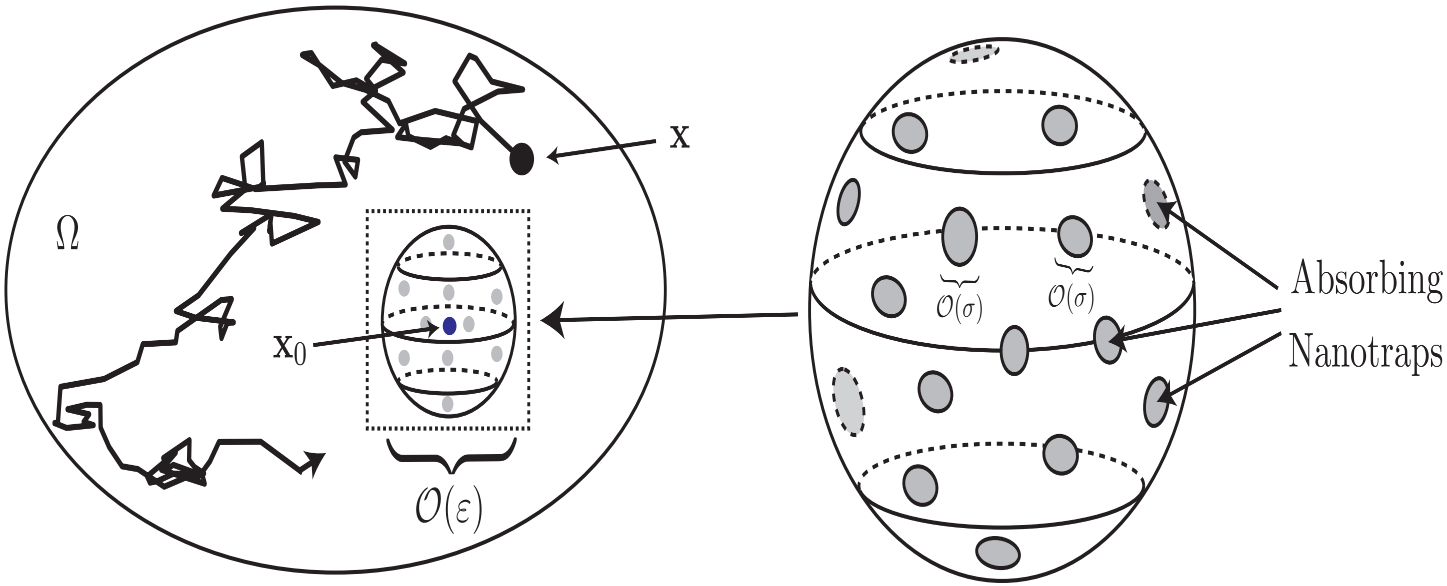
Two distinct applications of Strong Localized Perturbation theory (SLPT) in biology. Diffusive processes in domains containing small obstacles; either small boundary traps or interior patches.

Two Specific Problems:

- **Topic I:** Berg-Purcell Problem Revisited. Determination of effective capacitance of a sphere with N small "traps" on the boundary. The homogenized limit and the mean first capture time. (Lindsay, Bernoff)
- **Topic II:** Persistence threshold for diffuse logistic model in a 2-D spatial environment with highly patchy food resources. Mathematically: Optimize the principal eigenvalue of an indefinite weight eigenvalue problem.

Online Notes (SLPT): M. J. Ward, *Asymptotics for Strong Localized Perturbations and Applications*, lecture notes for Fourth Winter School in Applied Mathematics, CityU of Hong Kong, Dec. 2010. (99 pages).

Topic I: Narrow Capture in 3-D

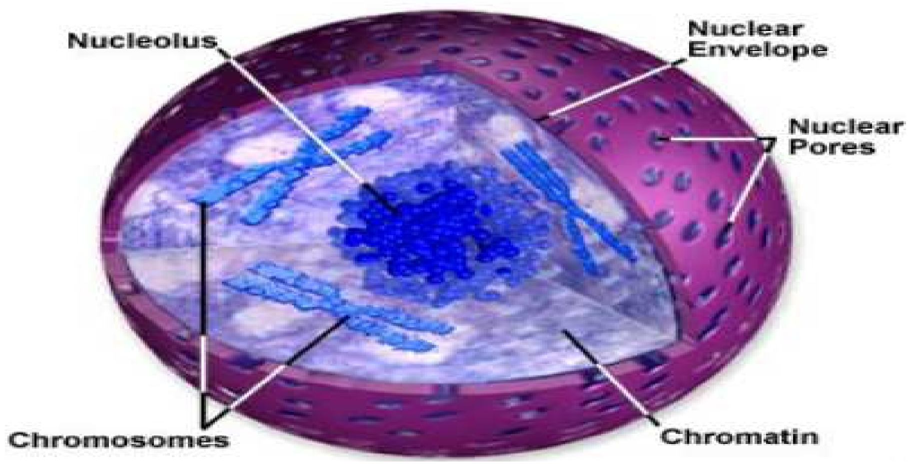


Caption: spherical target of radius $\varepsilon \ll 1$ centered at $\mathbf{x}_0 \in \Omega$, with N locally circular absorbing surface nanotraps (nanopores) of radii $\sigma \ll \varepsilon$ modeled by homogeneous Dirichlet condition.

- A particle (protein etc..) undergoes Brownian walk ($dX_t = DdW_t$) until captured by one of the N small absorbing surface nanotraps.
- Q1: How long on average does it take to get captured? (MFPT).
- Q2: What is the effect on the MFPT of the spatial distribution $\{\mathbf{x}_1, \ldots, \mathbf{x}_N\}$ of the surface nanotraps? (Capacitance).

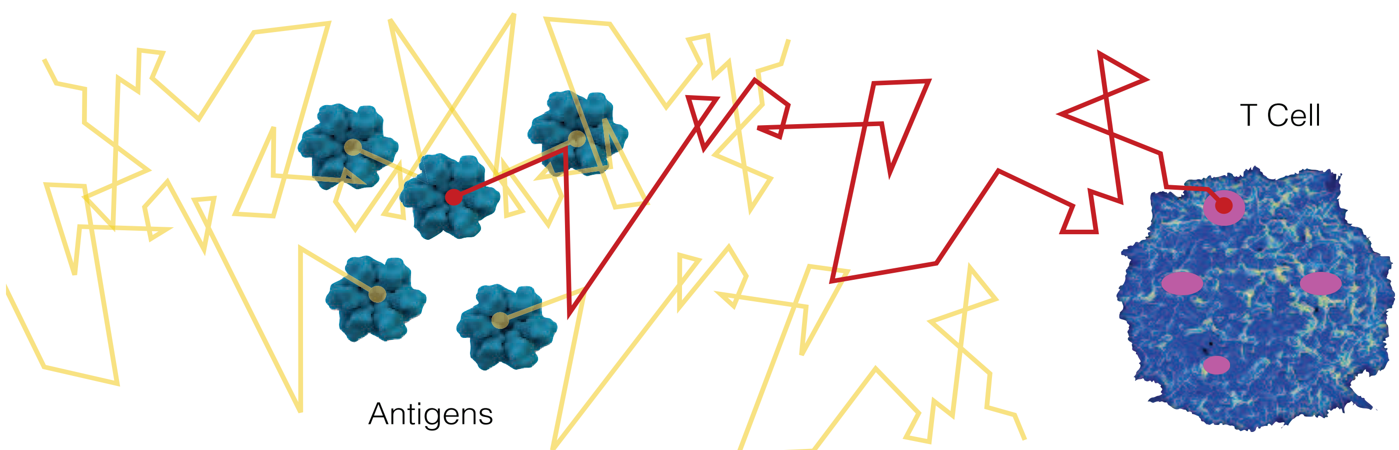
Applications of Narrow Capture

Nuclear Pores: Genetic material enters nucleus via small pores.



Scaling: Nucleus $\approx 10\%$ of cell volume ($\varepsilon = 0.1$). Roughly, $N = 2000$ pores that occupy 2% of the surface area. (Eilenberg et al. Science 341(6146), 2013).

Cell Signalling: How long does it take an antigen to bind to a receptor on a T-cell to produce antibodies?



The MFPT PDE for Narrow Capture

The Mean First Passage Time (MFPT) T satisfies

$$\Delta T = -\frac{1}{D}\,, \quad \mathbf{x} \in \Omega \backslash \Omega_\varepsilon\,; \qquad \partial_n T = 0\,, \quad \mathbf{x} \in \partial\Omega\,,$$
$$T = 0\,, \quad \mathbf{x} \in \partial\Omega_{\varepsilon a}\,; \quad \partial_n T = 0\,, \quad \mathbf{x} \in \partial\Omega_{\varepsilon r}\,,$$

where $\partial\Omega_{\varepsilon a}$ and $\partial\Omega_{\varepsilon r}$ are the absorbing and reflecting part of the surface of the small sphere Ω_ε within the 3-D cell Ω.

- Calculate the averaged MFPT $\bar{T}$ for capture of a Brownian particle.
- $\bar{T}$ depends on the capacitance C_0 of the structured target (related to the Berg-Purcell problem, 1977). This is the inner or local problem.
- Derive new discrete optimization problems characterizing the optimal MFPT and determine how the fragmentation of the trap set affects $\bar{T}$.

Ref: [LBW2017] Lindsay, Bernoff, MJW, *First Passage Statistics for the Capture of a Brownian Particle by a Structured Spherical Target with Multiple Surface Traps*, SIAM Multiscale Mod. and Sim. **15**(1), (2017), pp. 74–109.

Asymptotic Result for the Average MFPT

Using strong localized perturbation theory, for $\varepsilon \to 0$ the average MFPT is

$$\bar{T} \equiv \frac{1}{|\Omega \backslash \Omega_\varepsilon|} \int_{\Omega \backslash \Omega_\varepsilon} T \, d\mathbf{x} = \frac{|\Omega|}{4\pi C_0 D \varepsilon} \left[1 + 4\pi\varepsilon C_0 R(\mathbf{x}_0) + \mathcal{O}(\varepsilon^2) \right],$$

where $R(\mathbf{x}_0)$ is the regular part of the Neumann Green's function for Ω:

$$\Delta G = \frac{1}{|\Omega|} - \delta(\mathbf{x} - \mathbf{x}_0), \quad \mathbf{x} \in \Omega; \quad \partial_n G = 0, \quad \mathbf{x} \in \partial\Omega,$$

$$G(\mathbf{x}; \mathbf{x}_0) = \frac{1}{4\pi|\mathbf{x} - \mathbf{x}_0|} + R(\mathbf{x}_0), \quad \text{as} \quad \mathbf{x} \to \xi; \qquad \int_\Omega G \, d\mathbf{x} = 0.$$

Capacitance Problem: "exterior" problem in potential theory. C_0 satisfies

$$\Delta v = 0, \quad \mathbf{y} \in \mathbb{R}^3 \setminus \Omega_0; \quad v = 0, \quad \mathbf{y} \in \Gamma_a, \quad \partial_n v = 0, \quad \mathbf{y} \in \Gamma_r,$$

$$\lim_{R \to \infty} \int_{\partial\Omega_R} \partial_n v \, ds = -4\pi; \quad v \sim -\frac{1}{C_0} + \frac{1}{|\mathbf{y}|} + \mathcal{O}(|\mathbf{y}|^{-2}), \quad |\mathbf{y}| \to \infty.$$

Capacitance C_0 of Structured Target

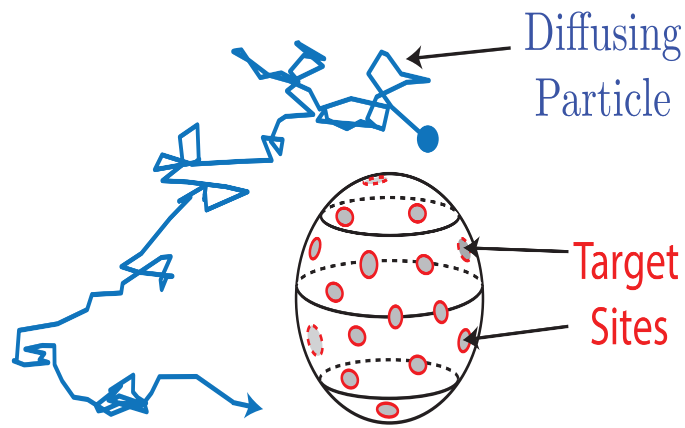
The inner problem for the capacitance C_0 is equivalent to finding the probability $w(\mathbf{y})$ that a particle is captured starting at $\mathbf{y} \in \mathbb{R}^3 \setminus \Omega_0$:

$$\Delta w = 0\,, \quad \mathbf{y} \in \mathbb{R}^3 \setminus \Omega_0 \text{ (outside unit ball)}$$

$$w = 1\,, \quad \mathbf{y} \in \Gamma_a \text{ (absorbing pores)}$$

$$\partial_n w = 0\,, \quad \mathbf{y} \in \Gamma_r \text{ (reflecting surface)}$$

$$w \sim \frac{C_0}{|\mathbf{y}|} + \mathcal{O}\left(\frac{1}{|\mathbf{y}|^2}\right)\,, \quad \text{as} \quad |\mathbf{y}| \to \infty\,.$$

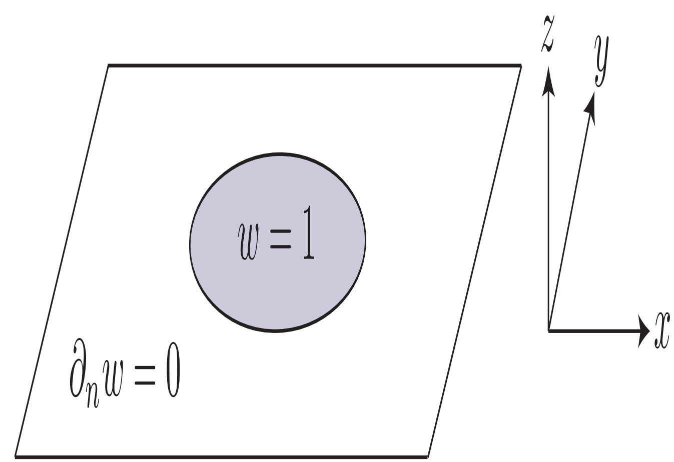


Remarks:

- $C_0 = 1$ if entire surface is absorbing.
- The diffusive flux J into the sphere is

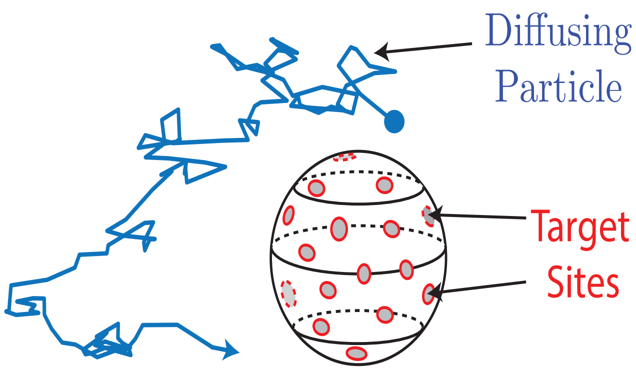
$$J = D \int_{\Gamma_a} \partial_n w \, dS = 4\pi D C_0\,.$$

- The sub-inner problem near a pore is the classic electrified disk problem.



Berg-Purcell Problem: I

This is the Berg-Purcell (BP) problem (Physics of Chemoception, Biophysics, **20**(2), (1977)) ≈ 1500 citations)



BP assumed

- $N \gg 1$ disjoint equidistributed small pores.
- common pore radius $\sigma \ll 1$.
- dilute fraction limit, i.e. $f \equiv N\sigma^2/(4\pi) \ll 1$.

Using a "physically-isnpired" derivation, BP postulated that

$$C_{0\text{bp}} = \frac{N\sigma}{N\sigma + \pi}, \qquad J_{\text{bp}} = 4\pi D \frac{N\sigma}{N\sigma + \pi} = 4DN\sigma + \mathcal{O}(\sigma^2) .$$

Suggests that J is proportional to the total pore perimeter when $\sigma \ll 1$.

Our Goal: Calculate C_0, and the flux J, systematically for a collection of disjoint pores centered at $\{\mathbf{y}_1, \ldots, \mathbf{y}_N\}$ over the surface. Study the effect of the location of the pores and fragmentation. For equidistributed pores derive the BP result and the asymptotic corrections to it.

Berg-Purcell Problem: II

BP analysis revisited by Shoup-Szabo (Biophysical J. 1982). Replace trap set by effective trapping parameter k, so that for a sphere of radius R

$$\Delta u = 0 \,, \quad r \geq R \,; \quad D u_r = k u \,, \quad r = R \,.$$

Then, the flux $J = \int_\Omega D \partial_u r|_{r=R}$ into the sphere is $J = 4\pi D C$, where

$$u = 1 - \frac{C}{r} \,, \quad \text{with} \quad \frac{1}{C} = \frac{1}{R} + \frac{D}{kR^2} \,.$$

Now estimate k: On an infinite plane with a single trap of radius a

$$J_{\text{disk}} = \int_{\text{disk}} D u_z|_{z=0} \, d\boldsymbol{x} = 2\pi D c_{\text{disk}} \,, \qquad c_{\text{disk}} = \frac{2a}{\pi} \,.$$

Thus $J_{\text{disk}} = k_{\text{disk}} = 4aD$. Now estimate

$$k \approx k_{\text{disk}} \left(\frac{N}{4\pi R^2} \right) = \frac{4D}{\pi R \sigma} f \,, \quad \text{where} \quad f \equiv \frac{N \pi \sigma^2}{4\pi}$$

and $\sigma \equiv a/R$. Finally, this yields the BP capacitance and BP flux

$$\frac{1}{C_{\text{bp}}} = \frac{1}{R} \left(\frac{\pi}{N\sigma} + 1 \right) \,, \qquad J_{\text{bp}} = 4\pi D R \left(\frac{N\sigma}{N\sigma + \pi} \right) \,.$$

Main Result for C_0 and flux J: I

Main Result: For $\sigma \to 0$, [LBW2017] derived that

$$\frac{1}{C_0} = \frac{\pi}{N\sigma}\left[1 + \frac{\sigma}{\pi}\left(\log\left(2e^{-3/2}\sigma\right) + \frac{4}{N}\mathcal{H}(\mathbf{y}_1,\ldots,\mathbf{y}_N)\right) + \mathcal{O}(\sigma^2\log\sigma)\right],$$

$$J = 4DN\sigma\left[1 + \frac{\sigma}{\pi}\log(2\sigma) + \frac{\sigma}{\pi}\left(-\frac{3}{2} + \frac{2}{N}\mathcal{H}(\mathbf{y}_1,\ldots,\mathbf{y}_N)\right) + \cdots\right]^{-1}.$$

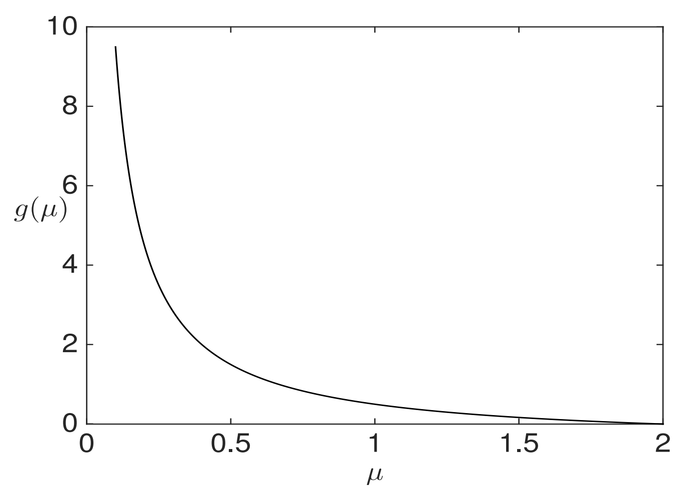
The interpore interaction energy $\mathcal{H}$, subject to $|\mathbf{y}_j| = 1 \ \forall j$, is

$$\mathcal{H}(\mathbf{y}_1,\ldots,\mathbf{y}_N) \equiv \sum_{j=1}^{N}\sum_{k=j+1}^{N} g(|\mathbf{y}_j - \mathbf{y}_k|)\,; \quad g(\mu) \equiv \frac{1}{\mu} + \frac{1}{2}\log\mu - \frac{1}{2}\log(2+\mu)\,.$$

Here $\mathbf{y}_j$ for $j = 1,\ldots,N$ are the nanopore centers with $|\mathbf{y}_j| = 1$.

Remarks:

- Flux J minimized when $\mathcal{H}$ minimized
- $g(\mu)$ is monotone decreasing, positive, and convex.
- Indicates that optimal configuration should be (roughly) equidistributed.



Main Result for C_0 and flux J: II

Here $g(|\mathbf{y}_j - \mathbf{y}_k| = 2\pi G_s(\mathbf{y}_j;\mathbf{y}_k)$, G_s is the surface-Neumann G-function

$$G_s(\mathbf{y}_j;\mathbf{y}_k) = \frac{1}{2\pi}\left[\frac{1}{|\mathbf{y}_j - \mathbf{y}_k|} - \frac{1}{2}\log\left(\frac{1 - \mathbf{y}_j{\cdot}\mathbf{y}_k + |\mathbf{y}_j - \mathbf{y}_k|}{|\mathbf{y}_j| - \mathbf{y}_j{\cdot}\mathbf{y}_k}\right)\right].$$

Key steps in singular perturbation analysis for C_0:

- Asymptotic expansion of global (outer) solution and local (inner) solutions near each pore (using tangential-normal coordinates).
- The surface G_s-function has a subdominant logarithmic singularity on the boundary (related to surface diffusion). This fact requires adding "logarithmic switchback terms in σ" in the outer expansion.
- The leading-order local solution is the tangent plane approximation and yields electrified disk problem in a half-space, with (local) capacitance $c_j = 2\sigma/\pi$.
- **Key:** Need corrections to the tangent plane approximation in the inner region near the pore. This higher order term in the inner expansion satisfies a Poisson-type problem, with monopole far-field behavior.
- Asymptotic matching and solvability conditions yield $1/C_0$.

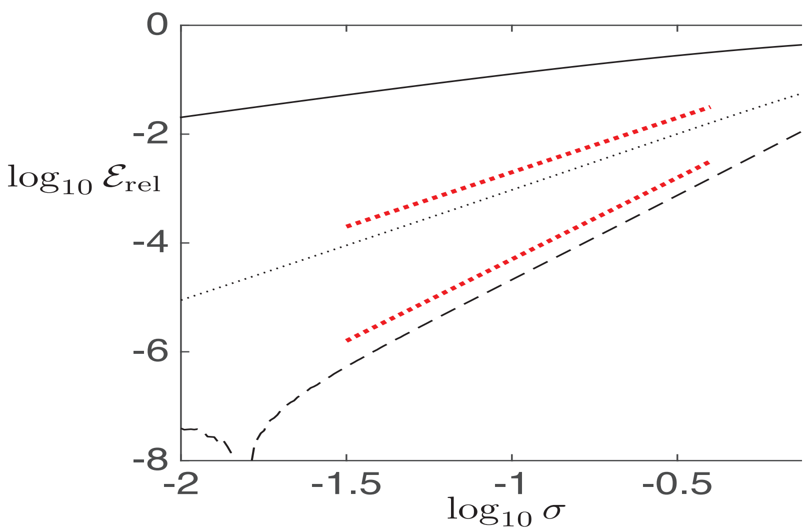
Asymptotics versus Numerics (Small N)

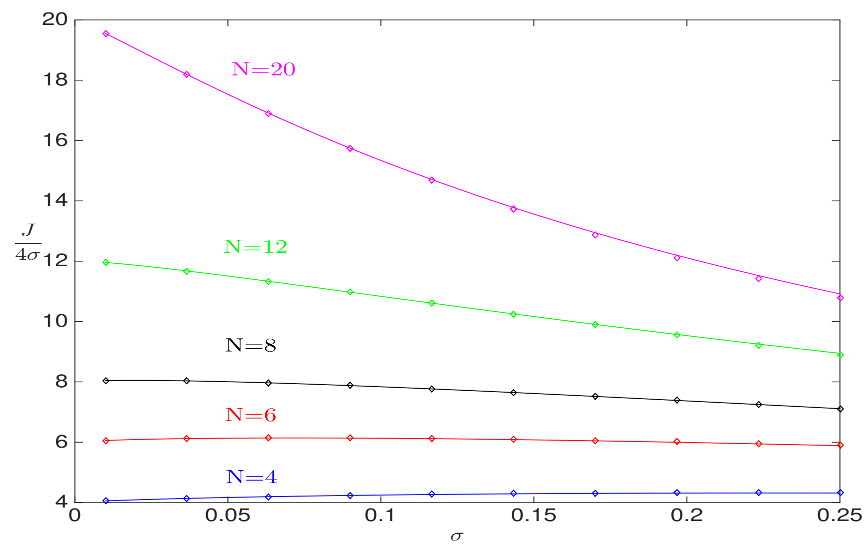
Asymptotic Results: For $\sigma \to 0$

$$J = 4D\sigma \left[1 + \frac{\sigma}{\pi} \left(\log(2\sigma) - \frac{3}{2} \right) - \frac{\sigma^2}{\pi^2} \left(\frac{\pi^2 + 21}{36} \right) + \cdots \right], \quad (N = 1),$$

$$J = 4DN\sigma \left[1 + \frac{\sigma}{\pi} \log(2\sigma) + \frac{\sigma}{\pi} \left(-\frac{3}{2} + \frac{2}{N} \mathcal{H}(\mathbf{y}_1, \ldots, \mathbf{y}_N) \right) + \cdots \right]^{-1}, \quad (N > 1).$$

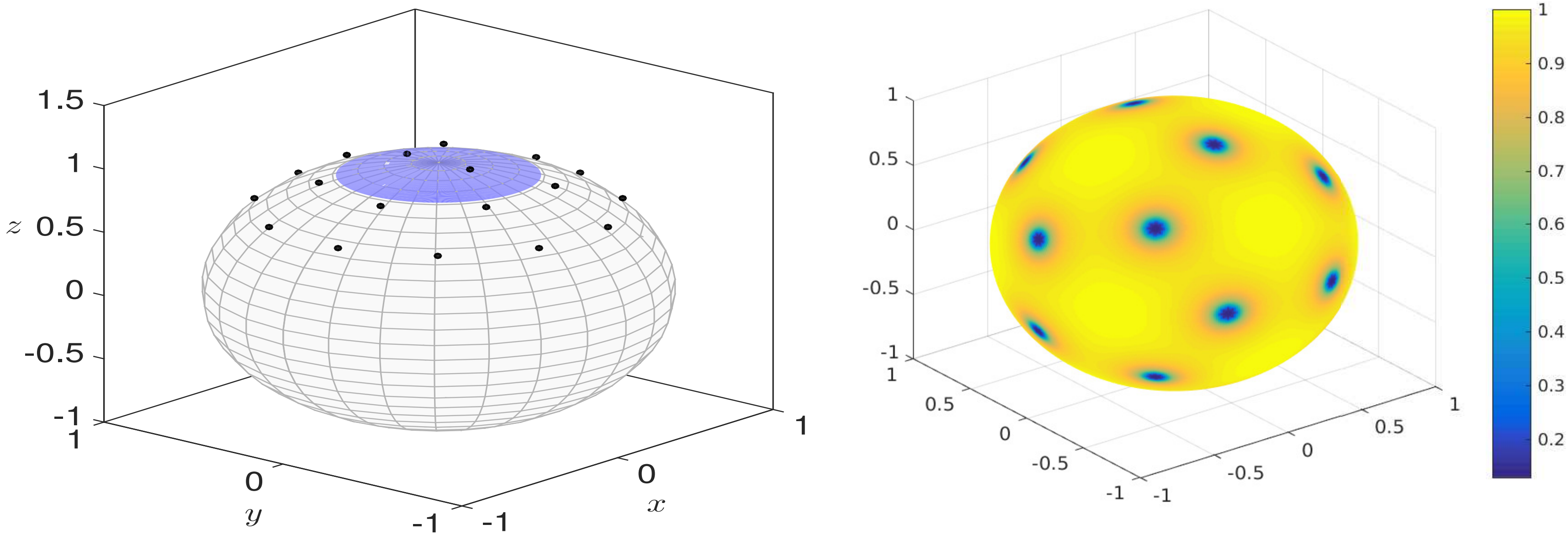
Numerics: Compare asymptotics with full numerics from fast multipole theory based on integral equations [Bernoff, Lindsay]





Left: One pore: log-log plot of relative error. Leading-order (solid), three-term (dotted), four-term (dashed). **Right:** Comparison of rescaled flux $J/(4\sigma)$ versus σ when pores are centered at vertices of platonic solids. Marked points are full numerics.

Clustering and Fragmenting the Pore Set



Left: $N = 20$ equally-spaced nanopores (centers shown only) clustered in the polar region $\theta \in (0, \frac{\pi}{3})$ with total absorbing fraction $f = 0.05$. Blue pore: is the equivalent area as a single nanopore. Nanopore radius is $\sigma = 2\sqrt{f/N}$. Right: optimal dodecahedron pattern.

$$\frac{1}{C_0} \approx 5.41 \;\; (\text{single Pore})\,; \qquad \frac{1}{C_0} \approx 2.79 \;\; (\text{clustered}); \qquad \frac{1}{C_0} \approx 1.98 \;\; (\text{optimal})\,.$$

Conclude I: subdividing a single nanopore into 20 smaller, but clustered, nanopores of same total area rougly halves the MFPT to the target.

Conclude II: The MFPT for 20 optimally distributed pores is significantly smaller than for 20 clustered pores.

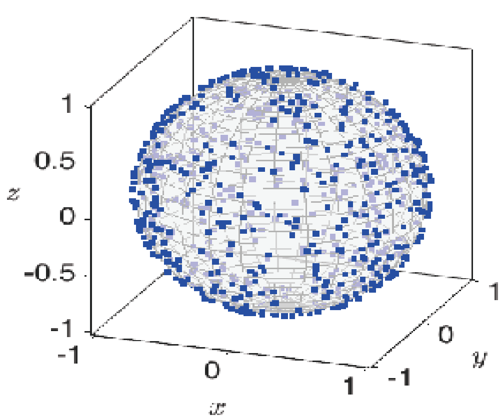
Discrete Energy: Equidistributed Points

Find global minimum $\mathcal{H}_{\min}$ of $\mathcal{H}$ when $N \gg 1$

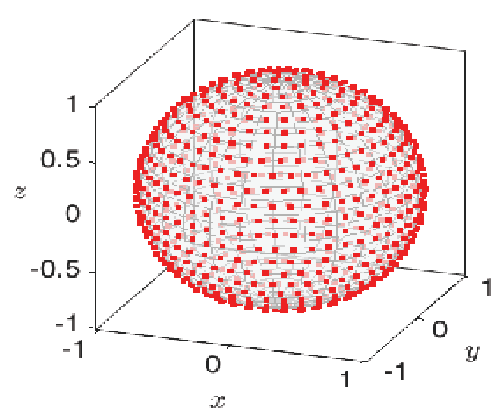
$$\mathcal{H} = \sum_{j} \sum_{k \neq j} g(|\mathbf{y}_j - \mathbf{y}_k|) \,, \quad \text{where} \quad g(\mu) \equiv \frac{1}{\mu} + \frac{1}{2} \log\left(\frac{\mu}{2+\mu}\right) \,.$$

- What is asymptotics of $\mathcal{H}_{min}$ as $N \to \infty$?
- For large N, many local minima, so finding global min is difficult.
- Cannot tile a spherical surface with hexagons (must have defects).
- Related to classic Fekete point problems of minimizing pure Coulombic energies on the sphere (Smale's 7th problem).

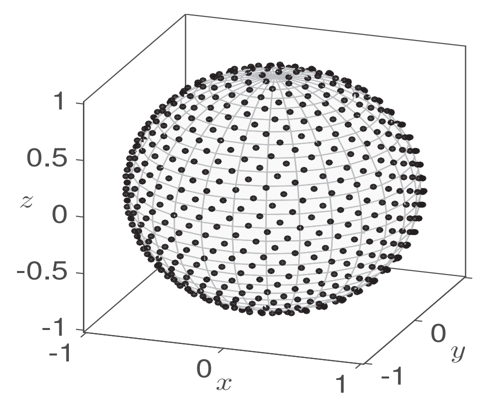
Three Coverings of $N = 800$ points



Uniform Random
Not Great



Equispaced in (θ, ϕ)
Better



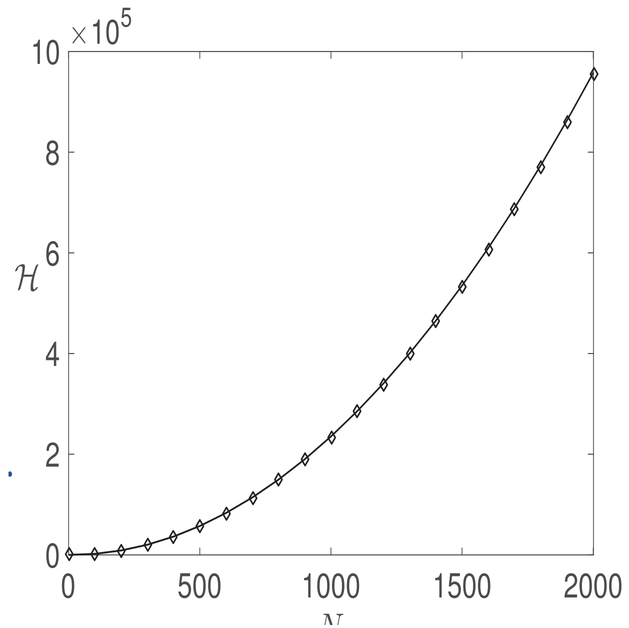
Fibonacci Spirals
Best (so far...)

Scaling Law: Equidistributed Points

Formal Large N Limit: For N large and "equidistributed points", we have

$$\mathcal{H}_{min} \sim \frac{N^2}{4} - d_1 N^{3/2} + \frac{N}{8}\log N + d_2 N + d_3 N^{1/2} + \cdots ,$$

with $d_1 = 1/2$, $d_2 = 1/8$ and $d_3 = 1/4$. Better to use $d_1 = 0.55230$ for "pure" Coulombic interactions [Saff].



Main Result (Scaling Law): For $N \gg 1$, but small pore surface area fraction $f = \mathcal{O}(\sigma^2 \log \sigma)$ and with equidistributed pores, the optimal C_0 and J are

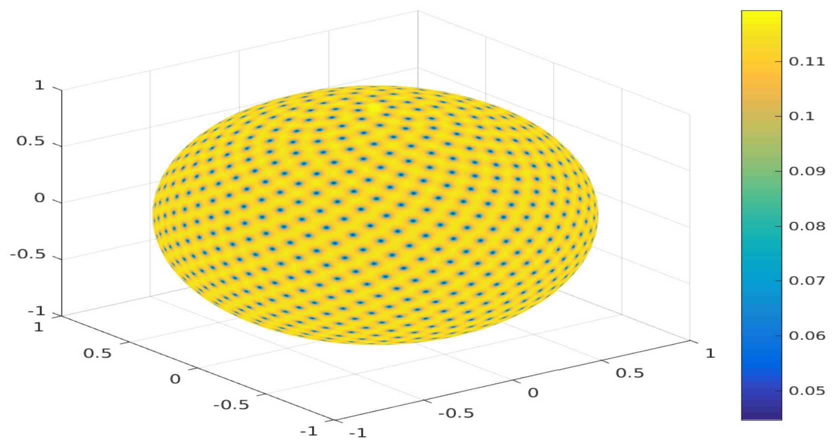
$$\frac{1}{C_0} \sim 1 + \frac{\pi\sigma}{4f}\left(1 - \frac{8d_1}{\pi}\sqrt{f} + \frac{\sigma}{\pi}\log\left(\beta\sqrt{f}\right) + \frac{2d_3\sigma^2}{\pi\sqrt{f}}\right), \quad \beta \equiv 4e^{-3/2}e^{4d_2},$$

$$J \sim 4\pi D\left[1 + \frac{\pi\sigma}{4f}\left(1 - \frac{8d_1\sqrt{f}}{\pi} + \frac{\sigma}{\pi}\log\left(\beta\sqrt{f}\right) + \frac{2d_3\sigma^2}{\pi\sqrt{f}}\right)\right]^{-1}.$$

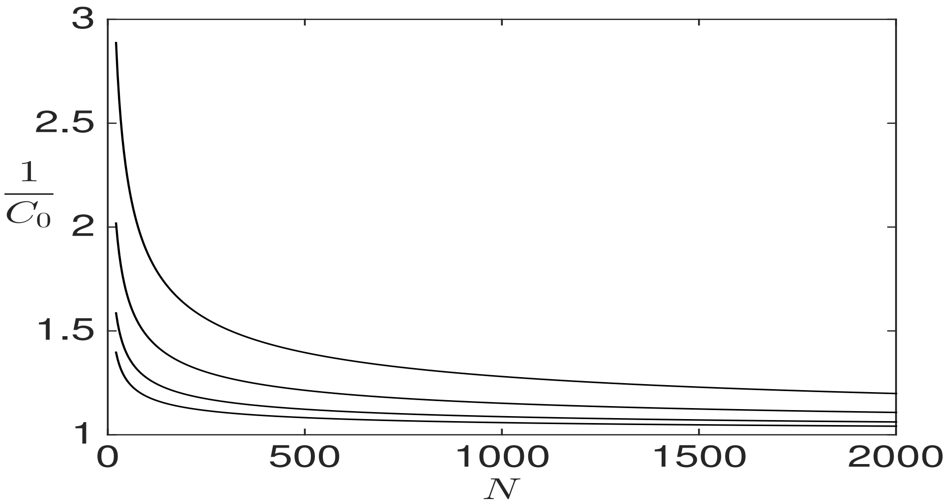
BP Result is the leading-order term. Our analysis yields correction terms for the sphere. Most notable is the $\sqrt{f}$ term, where $f \equiv N\sigma^2/4$.

Fragmentation Effects

Effect of Fragmentation: fix pore fraction f, increase N, and obtain σ from $f = N\pi\sigma^2/[4\pi]$. Locate pores centered at spiral Fibonacci points.



Caption: 1001 Nanopores at vertices of the spiral Fibonacci points.



Caption: From top to bottom: $f = \{0.02, 0.05, 0.1, 0.15\}$ For $N = 2000$, $f = 0.02$, full numerics gives $C_{0n}^{-1} = 1.1985$ and $C_0^{-1} = 1.2028$ (scaling law).

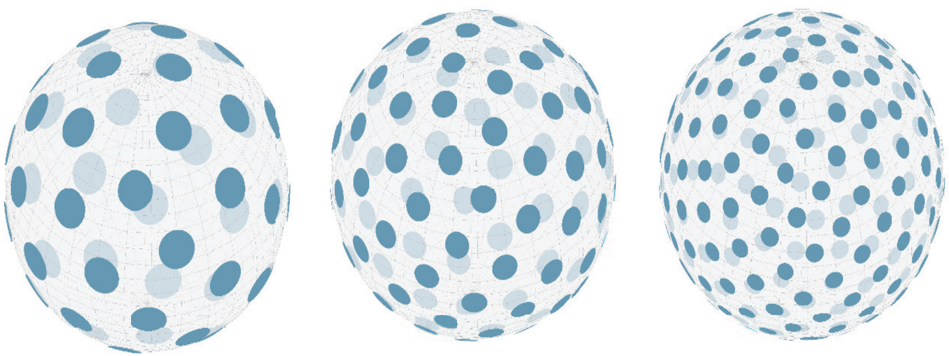
Conclusion: Fragmentation effects are significant until N becomes large.

Compare Scaling Law with Full Numerics

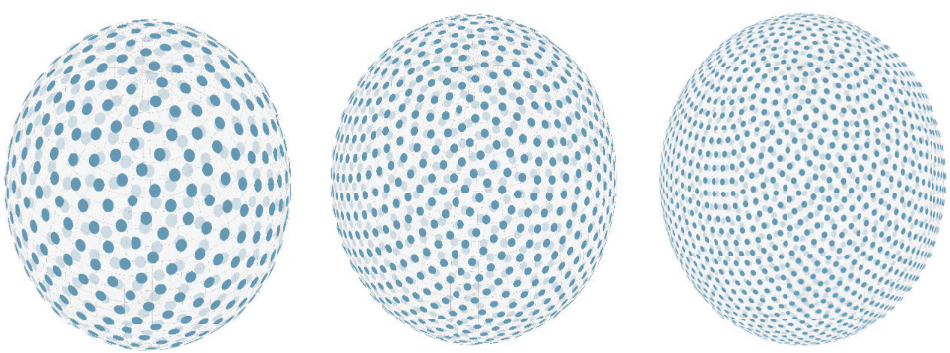
Compare full numerics with the asymptotic scaling law

$$J \sim 4\pi D \left[1 + \frac{\pi\sigma}{4f} \left(1 - \frac{8d_1\sqrt{f}}{\pi} + \frac{\sigma}{\pi} \log\left(\beta\sqrt{f}\right) + \frac{2d_3\sigma^2}{\pi\sqrt{f}} \right) \right]^{-1} .$$

Fix 2% pore coverage ($f = 0.02$) and choose spiral Fibonacci points.



$N = 51$ $N = 101$ $N = 201$

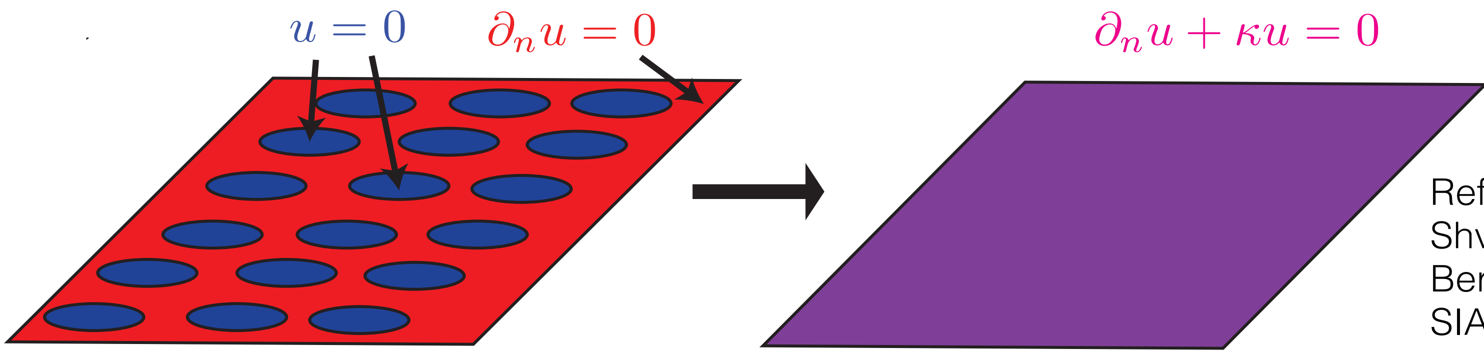


$N = 501$ $N = 1001$ $N = 2001$

N	$\mathcal{E}_{\text{rel}}$
51	1.02%
101	0.90%
201	0.76%
501	0.58%
1001	0.37%
2001	0.34%

Caption: $f = 0.02$ (2% pore coverage). Scaling law accurately predicts the flux to the target for the biological parameters $f = 0.02$ and $N = 2001$.

Effective Robin Condition: Leakage κ_h: I



Ref: Muratov, Shvartsmam, Berezhkovskii, SIAM MMS 2006.

Consider the planar case with σ pore radius and f coverage. Previous empirical laws (Berezhkovskii 2013) for a hexagonal arrangement

$$\kappa = \frac{4Df}{\pi\sigma}\chi(f)\,, \qquad \chi(f) = \frac{1 + 1.37\sqrt{f} - 2.59 f^2}{(1-f)^2}\,,$$

Our homogenized Robin condition: use scaling law for C_0 and find κ_h from

$$\Delta v_h = 0\,, \quad |\mathbf{y}| > 1\,; \quad \partial_n v_h + \kappa_h v_h = 0\,, \quad |\mathbf{y}| = 1\,; \quad v_h(\mathbf{y}) \sim \frac{1}{|\mathbf{y}|} - \frac{1}{C_0}\,, \quad |\mathbf{y}| \to \infty\,.$$

For the unit sphere, and in terms of d_1, d_2, d_3 and $\beta \equiv 4e^{-3/2}e^{4d_2}$, we get

$$\kappa_h \sim \frac{4Df}{\pi\sigma}\left[1 - \frac{8d_1}{\pi}\sqrt{f} + \frac{\sigma}{\pi}\log\left(\beta\sqrt{f}\right) + \frac{2d_3\sigma^2}{\pi\sqrt{f}}\right]^{-1} \approx \frac{4Df}{\pi\sigma}\left[1 + 1.41\sqrt{f} + \cdots\right]\,.$$

Effective Robin Condition: Leakage κ_h: II

Is homogenized leakage parameter κ_h still accurate at smallish N? Take nanopores centered at the spiral Fibonacci points. Choose $f = 0.02$.

N	κ_0	κ_h	$\kappa_{\rm t}$
10	0.36817	0.36303	0.34723
20	0.50909	0.50784	0.49105
40	0.71202	0.71190	0.69446
80	1.0108	1.0000	0.98211
160	1.4275	1.4071	1.3889

Comparison of leakage parameter in Robin condition: Full discrete energy (second column) $\kappa_0 = [-1 + 1/C_0]^{-1}$; The new scaling law κ_h (third column); The truncated scaling law (last column) $\kappa_{\rm t} \sim \frac{4f}{\pi\sigma}\left[1 - \frac{8d_1}{\pi}\sqrt{f}\right]^{-1}$ with $d_1 = 0.552$ (which neglects the curvature of the sphere). With $f = 0.02$, the nanopore radius is $\sigma = 2\sqrt{f/N}$.

Conclusion I: The correction due to curvature is less significant as N increases.

Conclusion II: The $\sqrt{f}$ correction to leading-order (classic) BP result is key.

Further Directions

- Rigorus results for the large N behavior of $\mathcal{H}$.
- Not just MFPT, but full time-dependent probability density.
- Potential theoretic methods (fast) to compute capacitance (L. Greengard, J. Kaye, preprint archive)
- Derive an explicit formula for the capacitance of a bumpy sphere containing N nanopores
  - Local analysis near a pore is possible, but no explicit globally-defined surface Neumann Green's function.
  - Needed for asymptotics: computation of surface Neumann Green's function and its local behavior near the singularity.
  - Full numerical computations based on integral equations challenging.
- A spherical Helmholtz resonator with many small apertures with an incoming plane wave. Determine the quasifrequencies with large amplitude and the effect of the spatial distribution of apertures.
  - Replace nanopores with a transmission condition between the outside and inside of the sphere.
  - Surface Neumann Green's function for the Helmholtz operator is available.

Topic II: Persistence Problem (One Species)

The diffusive logistic equation for a population density $u(\mathbf{x},t)$ is

$$u_t = D\Delta u + u\left[m_\varepsilon(\mathbf{x}) - c(\mathbf{x})u\right], \quad \mathbf{x} \in \Omega \in \mathbb{R}^2; \quad \partial_n u = 0, \quad \mathbf{x} \in \partial\Omega.$$

Here $D > 0$. A favorable habitat is a sub-region of Ω where $m_\varepsilon(\mathbf{x}) > 0$, while unfavorable habitats are where $m_\varepsilon(\mathbf{x}) < 0$. Assume that such habitats are patchy with spatial scale ε.

We linearize around the zero solution with $u = e^{\mu D t}\phi(\mathbf{x})$ and set $\mu = 0$:

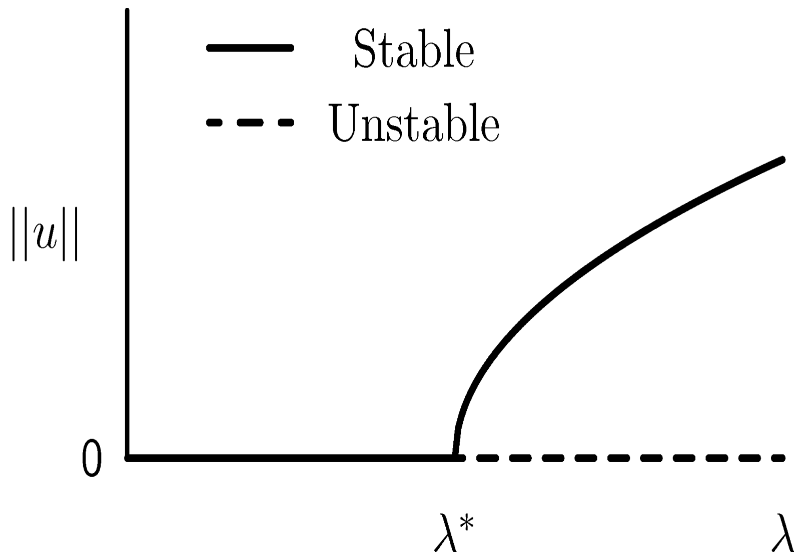
$$\Delta\phi + \lambda m_\varepsilon(\mathbf{x})\phi = 0, \quad \mathbf{x} \in \Omega; \quad \partial_n \phi = 0, \quad \mathbf{x} \in \partial\Omega; \quad \lambda = \frac{1}{D}.$$

- The extinct solution $u = 0$ exists $\forall \lambda \geq 0$. Depending on the choice for the growth rate $m_\varepsilon(\mathbf{x})$, at some critical value of λ there can be a transcritical bifurcation to a spatially dependent solution. This leads to the idea of a persistence threshold.
- **Key feature:** Growth rate m_ε changes sign in Ω. This is an indefinite weight eigenvalue problem (no standard oscillation theory, or standard variational characterization of eigenvalues, etc..).

Previous Results

Key Previous Result I: Assume that $\int_\Omega m_\mathcal{E}\, d\mathbf{x} < 0$, but that $m_\mathcal{E} > 0$ on a set of positive measure. Then, there exists a positive principal eigenvalue $\lambda_1 = \lambda^\star$, i.e. the persistence or extinction threshold, with corresponding eigenfunction $\phi > 0$ (Brown and Lin, (1980)).

Key Previous Result II: Transcritical bifurcation: $u \to u_\infty(\mathbf{x}) \neq 0$ as $t \to \infty$ if $\lambda > \lambda^\star$, while $u \to 0$ as $t \to \infty$ if $0 < \lambda < \lambda^\star$. (many authors; Cantrell, Cosner, Berestycki, etc..)

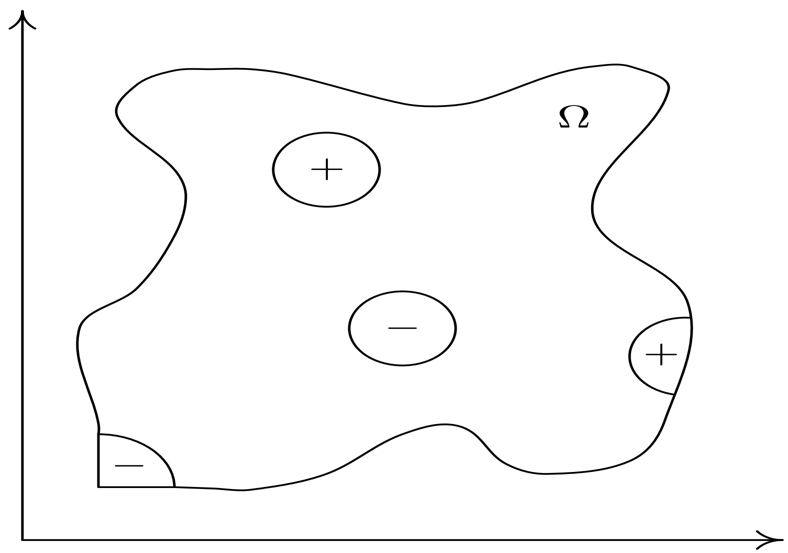


Key Previous Result III: The optimal growth rate $m_\mathcal{E}(\mathbf{x})$ is of bang-bang type.
(Theorem 1.1 of Lou and Yanagida, JJAM, 2006, for 2-D).

Optimization of Persistence Threshold

<u>Main Goal:</u> Minimize λ_1 wrt $m_\varepsilon(\mathbf{x})$, subject to a fixed $\int_\Omega m_\varepsilon \, d\mathbf{x} < 0$: i.e. determine the largest D that allows for the persistence of the species.

Long-standing open problem for the optimal shape of $m_\varepsilon(\mathbf{x})$ in a 2-D domain. (Cantrell and Cosner 1990's, Lou and Yanagida, (2006); Kao, Lou, and Yanagida, (2008); Roques and Stoica, (2007); Berestycki, Hamel, (2005,2006)).



- $\pm$ indicates favorable (+) and unfavorable (-) habitats.
- Localized habitats vary on ε spatial scale.
- $\exists$ a constant background (possibly neutral) habitat.

Remark: $\exists$ solution in a 1-D domain (Lou and Yanagida, JJAM (2006)). The optimal $m_\varepsilon(\mathbf{x})$ in 1-D is to concentrate favorable resources near one of the endpoints of the domain, and to have only one favorable patch. What about 2-D?

Patch Model I

Our Patch Model: The eigenvalue problem for the persistence threshold is

$$\Delta\phi + \lambda\, m_\varepsilon(\mathbf{x})\phi = 0\,, \quad \mathbf{x} \in \Omega; \quad \partial_n \phi = 0\,, \quad \mathbf{x} \in \partial\Omega\,; \quad \int_\Omega \phi^2\, d\mathbf{x} = 1\,.$$

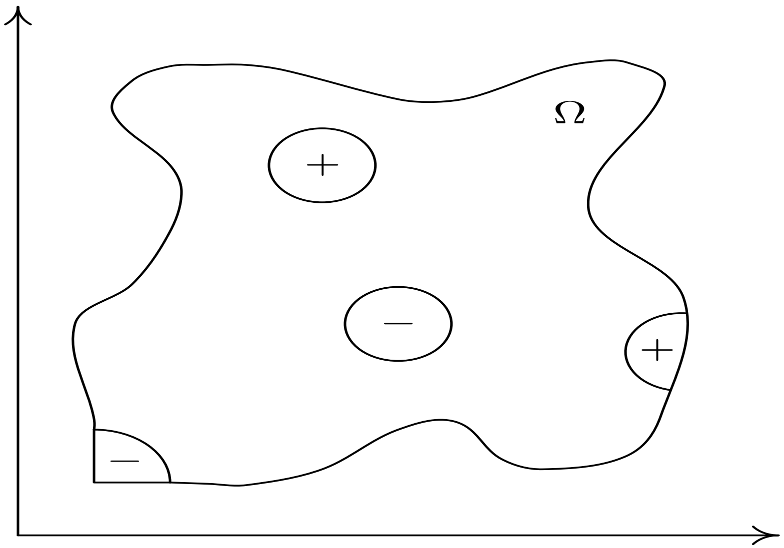
The piecewise-constant growth rate $m_\varepsilon(\mathbf{x})$ is chosen as

$$m_\varepsilon(\mathbf{x}) = \begin{cases} m_j/\varepsilon^2\,, & \mathbf{x} \in \Omega_{\epsilon_j} \equiv \{\mathbf{x}\,|\,|\mathbf{x}-\mathbf{x}_j| = \varepsilon\rho_j\, \cap\, \Omega\}\,, \quad j = 1,\ldots,n\,, \\ -m_b\,, & \mathbf{x} \in \Omega \backslash \bigcup_{j=1}^{n} \Omega_{\varepsilon_j}\,. \end{cases}$$

- Assume that at least one $m_j > 0$, and $\int_\Omega m_\varepsilon\, d\mathbf{x} < 0$. Then, there is a positive principal eigenvalue $\lambda_1 > 0$.
- **Biologically:** On the whole the environment is hostile, but there is at least one region that can support growth.
- **No immigration or emigration:** reflecting boundary condition on $\partial\Omega$.

Ref [LW]: A. Lindsay, M. J. Ward, *An Asymptotic Analysis of the Persistence Threshold for the Diffusive Logistic Model in Spatial Environments with Localized Patches*, DCDS-B, **14**(3), (2010), pp. 1139–1179.

Patch Model II



Assumptions in the Patch Model:

- Patches Ω_{ε_j} of radius $\mathcal{O}(\varepsilon)$ are portions of small circular disks strictly inside Ω. Circular patches are *locally* optimal (Hamel, Roques, 2007).
- The constant m_j is the local growth rate of the j^{th} patch, with $m_j > 0$ for a favorable habitat and $m_j < 0$ for a non-favorable habitat.
- The constant m_b is the background bulk decay rate.
- The boundary $\partial\Omega$ is piecewise smooth, with possible corner points.
- Overall, environment is unfavorable, i.e. $\int_\Omega m_\varepsilon(\mathbf{x})\, d\mathbf{x} < 0$.

Patch Model III

- Define $\Omega^I \equiv \{\mathbf{x}_1, \ldots, \mathbf{x}_n\} \cap \Omega$ to be the set of the centers of the interior patches, while $\Omega^B \equiv \{\mathbf{x}_1, \ldots, \mathbf{x}_n\} \cap \partial\Omega$ is the set of the centers of the boundary patches. Assume patches are well-separated, i.e. $|\mathbf{x}_i - \mathbf{x}_j| \gg \mathcal{O}(\varepsilon)$ for $i \neq j$ and $\text{dist}(\mathbf{x}_j, \partial\Omega) \gg \mathcal{O}(\varepsilon)$ if $\mathbf{x}_j \in \Omega^I$.
- We assign for each $\mathbf{x}_j$ for $j = 1, \ldots, n$, an angle $\pi\alpha_j$ representing the angular fraction of a circular patch that is contained within Ω.

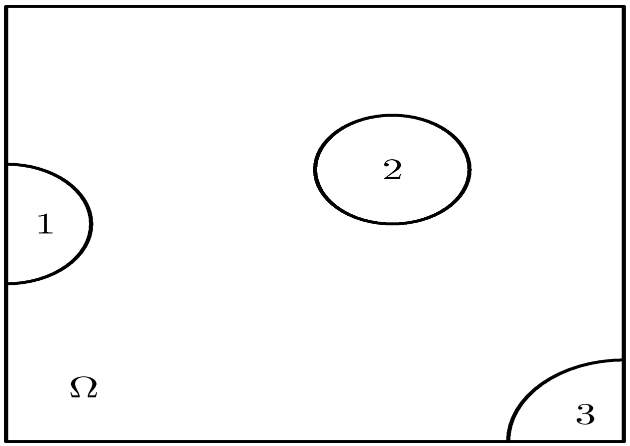


Illustration:

- Patch 1: $\mathbf{x}_1 \in \Omega^B$ (smooth): $\alpha_1 = \pi$
- Patch 2: $\mathbf{x}_2 \in \Omega^I$ (interior): $\alpha_2 = 2\pi$
- Patch 3: $\mathbf{x}_3 \in \Omega^B$ (right angle): $\alpha_3 = \frac{\pi}{2}$.

- The condition $\int_\Omega m_\varepsilon \, d\mathbf{x} < 0$ is equivalent for $\varepsilon \to 0$ to

$$\int_\Omega m_\varepsilon \, d\mathbf{x} = -m_b|\Omega| + \frac{\pi}{2} \sum_{j=1}^{n} \alpha_j m_j \rho_j^2 + \mathcal{O}(\varepsilon^2) = C < 0 \, .$$

Assume this condition holds and that one m_j is positive.

Qualitative Questions

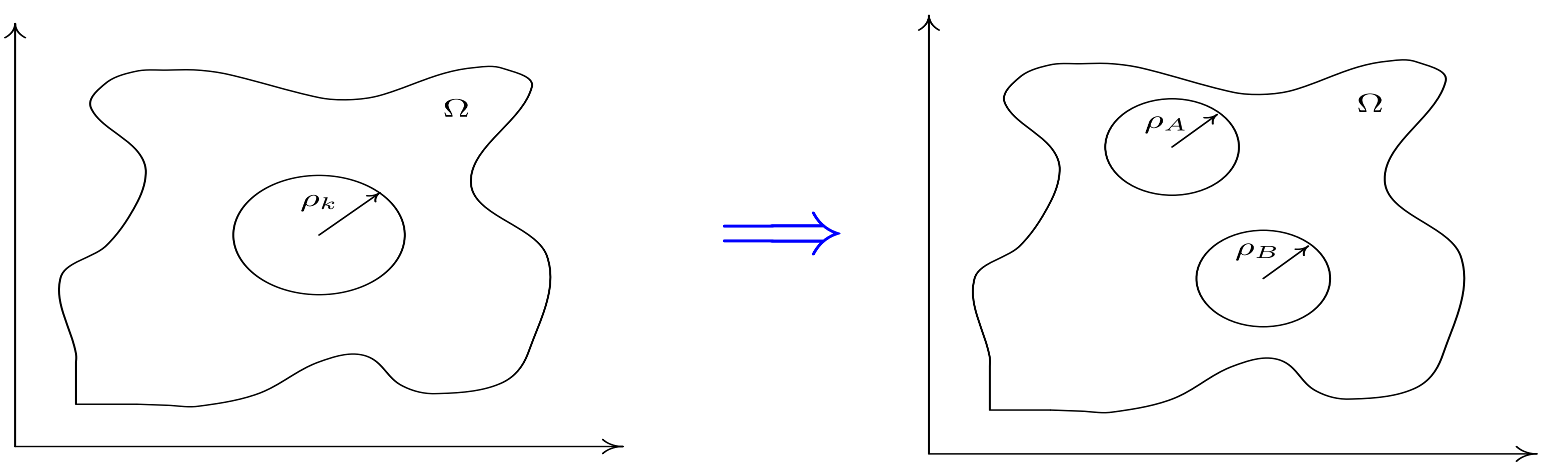
By Key Previous Result I, $\exists$ a positive principal eigenvalue λ_1.

- Calculate λ_1 as $\varepsilon \to 0$ using strong localized perturbation theory.
- Then, minimize λ_1 for a fixed $\int_\Omega m_\varepsilon \, d\mathbf{x} < 0$, over the parameter set $\{m_1, \ldots, m_n\}$, $\{\rho_1, \ldots, \rho_n\}$, $\{\mathbf{x}_1, \ldots, \mathbf{x}_n\}$, and $\{\alpha_1, \ldots, \alpha_n\}$.

Qualitative Questions

Q1: How do resource locations affect λ_1. Is the persistence threshold λ_1 smaller for boundary habitats than for interior habitats?

Q2: What is the effect of resource fragementation? Does fragmentation lead to larger persistence thresholds?. To maintain the value of $\int_\Omega m_\varepsilon \, d\mathbf{x}$, we need $m_k \rho_k^2 = m_A \rho_A^2 + m_B \rho_B^2$.



Main Result: Persistence Threshold

Principal Result: *In the limit $\varepsilon \to 0$, the positive principal eigenvalue λ_1 has the following two-term asymptotic expansion in terms of $\nu = -1/\log \epsilon$:*

$$\lambda_1 = \mu_0 \nu - \mu_0 \nu^2 \left(\frac{\kappa^T \left(\pi \mathcal{G}_m - \mathcal{P}\right) \kappa}{\kappa^T \kappa} + \frac{1}{4} \right) + \mathcal{O}(\nu^3) \,.$$

Here $\kappa = (\kappa_1, \ldots, \kappa_n)^T$ and $\mu_0 > 0$ is the first positive root of $\mathcal{B}(\mu_0) = 0$

$$\mathcal{B}(\mu_0) \equiv -m_b |\Omega| + \pi \sum_{j=1}^{n} \sqrt{\alpha_j} \kappa_j \,, \qquad \kappa_j \equiv \frac{\sqrt{\alpha}_j m_j \rho_j^2}{2 - m_j \rho_j^2 \mu_0} \,.$$

The $n \times n$ matrix $\mathcal{G}_m$ and diagonal matrix $\mathcal{P}$ are defined by

$$\mathcal{G}_{mij} = \sqrt{\alpha_i \alpha_j} G_{mij} \,, \quad i \neq j \,; \quad \mathcal{G}_{mjj} = \alpha_j R_{mj} \,; \quad \mathcal{P}_{jj} = \log \rho_j \,,$$

where $G_{mij} \equiv G_m(\mathbf{x}_i; \mathbf{x}_j)$ is the Green's function with regular part R_{mj}:

$$G_m(\mathbf{x}; \mathbf{x}_j) \equiv \begin{cases} G(\mathbf{x}; \mathbf{x}_j) \,, & \mathbf{x}_j \in \Omega \,, \\ G_s(\mathbf{x}; \mathbf{x}_j) \,, & \mathbf{x}_j \in \partial\Omega \,. \end{cases} \qquad G_m(\mathbf{x}; \mathbf{x}_j) \sim -\frac{1}{\alpha_j \pi} \log |\mathbf{x} - \mathbf{x}_j| + R_{mj} \,,$$

as $\mathbf{x} \to \mathbf{x}_j$. Here G (G_s) is the Neumann (surface Neumann) G-function.

Main Result: Remarks

The Neumann Green's function $G(\mathbf{x};\mathbf{x}_j)$ satisfies

$$\Delta G = \frac{1}{|\Omega|} - \delta(\mathbf{x}-\mathbf{x}_j)\,, \quad \mathbf{x}\in\Omega\,; \quad \partial_n G = 0\,, \quad \mathbf{x}\in\partial\Omega\,; \quad \int_\Omega G\, d\mathbf{x} = 0\,,$$

$$G \sim -\frac{1}{2\pi}\log|\mathbf{x}-\mathbf{x}_j| + R_j\,, \quad \text{as} \quad \mathbf{x}\to\mathbf{x}_j\,,$$

while the surface Neumann Green function $G_s(\mathbf{x};\mathbf{x}_j)$ satisfies

$$\triangle G_s = \frac{1}{|\Omega|}\,, \quad \mathbf{x}\in\Omega\,; \quad \partial_n G_s = 0\,, \quad \mathbf{x}\in\partial\Omega\backslash\{\mathbf{x}_j\}\,; \quad \int_\Omega G_s\, d\mathbf{x} = 0\,,$$

$$G_s(\mathbf{x};\mathbf{x}_j) \sim -\frac{1}{\alpha_j\pi}\log|\mathbf{x}-\mathbf{x}_j| + R_{sj}\,, \quad \text{as} \ \ \mathbf{x}\to\mathbf{x}_j\in\partial\Omega\,.$$

Remarks:

- The leading term μ_0 in the persistence threshold satisfies a nonlinear algebraic equation $\mathcal{B}(\mu_0)=0$, and is independent of patch locations.
- In contrast to the Laplacian eigenvalue problems for the MFPT, the leading-order term μ_0 does contain some key qualitative information.
- The $\mathcal{O}(\nu^2)$ term has spatial effects through the Green's matrix $\mathcal{G}_m$. Needed when the leading-order term cannot distinguish optimality.

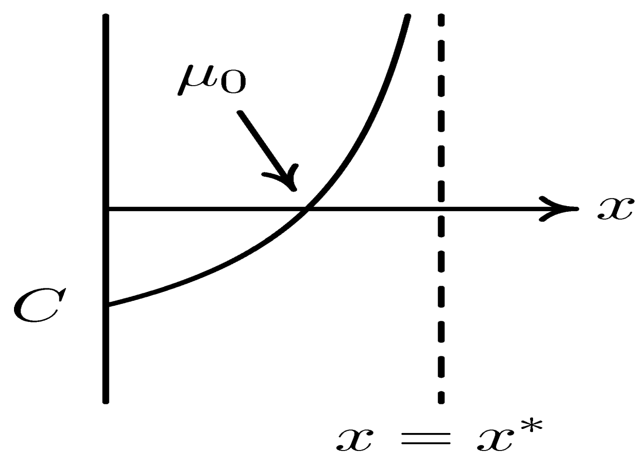
Existence of Leading-Order Threshold

Principal Result: *There exists a unique root* μ_0 *to* $\mathcal{B}(x) = 0$ *on the range* $0 < x < \mu_m \equiv 2/(m_J \rho_J^2)$, *where* $m_J \rho_J^2 = \max_{m_j > 0}\{m_j \rho_j^2 \,|\, j = 1, \ldots, n\}$. *The corresponding eigenfunction has one sign.*

Proof: $\mathcal{B}(0) = \int_\Omega m_\varepsilon(x)\, dx \sim C < 0$ by Assumption I. In addition,

$$\mathcal{B}'(x) = \sum_{j=1}^{n} \frac{\alpha_j m_j^2 \rho_j^4}{(2 - m_j \rho_j^2 x)^2} > 0\,, \quad 0 < x < \mu_m\,; \quad \mathcal{B}(x) \to +\infty\,, \text{ as } x \to \mu_m^-\,.$$

Here μ_m is the smallest vertical asymptote of $\mathcal{B}(x)$. Note: $\mu_m > 0$ since $m_j > 0$ for at least one j. Hence, $\exists$ a unique root $\mu_0 > 0$.



Goal: By rigorously optimizing μ_0 subject to $\int_\Omega m_\varepsilon dx < 0$, derive key qualititative results regarding the optimal resource distribution.

The positivity of ϕ_0 can be shown by constructing eigenfunction for $\varepsilon \to 0$.

Derivation of μ_0: I

We now derive μ_0 using strong localized perturbation theory.

We expand the positive principal eigenvalue λ_1 as

$$\lambda_1 \sim \mu_0 \nu + \mu_1 \nu^2 + \cdots \,, \quad \nu = -1/\log \varepsilon \,,$$

for μ_0 and μ_1 to be found.

In the outer region, away from an $\mathcal{O}(\varepsilon)$ neighborhoods of $\mathbf{x}_j$, we expand

$$\phi \sim \phi_0 + \nu \phi_1 + \nu^2 \phi_2 + \cdots \,.$$

We obtain that $\phi_0 = |\Omega|^{-1/2}$ is a constant, and that ϕ_1 satisfies

$$\Delta \phi_1 = \mu_0 m_b \phi_0 \,, \quad x \in \Omega \backslash \Omega^I \,;$$

$$\partial_n \phi_1 = 0 \,, \quad x \in \partial\Omega \backslash \Omega^B \,; \quad \int_\Omega \phi_1 \, dx = 0 \,.$$

Here $\Omega^I \equiv \{\mathbf{x}_1, \ldots, \mathbf{x}_n\} \cap \Omega$ is the set of the centers of the interior patches, while $\Omega^B \equiv \{\mathbf{x}_1, \ldots, \mathbf{x}_n\} \cap \partial\Omega$ is the set of the centers of the boundary patches.

Derivation of μ_0: II

In the inner region near the j^{th} patch we introduce $\mathbf{y} = \varepsilon^{-1}(\mathbf{x} - \mathbf{x}_j)$ and $\psi(\mathbf{y}) = \phi(\mathbf{x}_j + \varepsilon \mathbf{y})$, and expand

$$\psi \sim \psi_{0j} + \nu \psi_{1j} + \nu^2 \psi_{2j} + \cdots \,,$$

where ψ_{0j} is a constant to be found. For $\mathbf{x}_j \in \Omega^I$, we find that

$$\Delta \psi_{1j} = \begin{cases} \mathcal{F}_{1j}\,, & |\mathbf{y}| \leq \rho_j\,, \\ 0\,, & |\mathbf{y}| \geq \rho_j\,, \end{cases} \qquad \mathcal{F}_{1j} \equiv -\mu_0 m_j \psi_{0j}\,.$$

The solution for ψ_{1j}, with $\rho = |\mathbf{y}|$, in terms of a constant $\bar{\psi}_{1j}$ is

$$\psi_{1j} = \begin{cases} A_{1j}\left(\frac{\rho^2}{2\rho_j^2}\right) + \bar{\psi}_{1j}\,, & 0 \leq \rho \leq \rho_j\,, \\ A_{1j} \log\left(\frac{\rho}{\rho_j}\right) + \frac{A_{1j}}{2} + \bar{\psi}_{1j}\,, & \rho \geq \rho_j\,. \end{cases}$$

For an interior or boundary patch, the divergence theorem yields A_{1j} as

$$A_{1j} = -\frac{\mu_0}{2} m_j \rho_j^2 \psi_{0j}\,.$$

Derivation of μ_0: III

The matching condition between the outer solution as $\mathbf{x} \to \mathbf{x}_j$ and the inner solution is $|\mathbf{y}| = \varepsilon^{-1}|\mathbf{x} - \mathbf{x}_j| \to \infty$ is

$$\phi_0 + \nu\phi_1 + \cdots \sim$$

$$\psi_{0j} + A_{1j} + \nu \left(A_{1j} \log|\mathbf{x} - \mathbf{x}_j| - A_{1j} \log \rho_j + \frac{A_{1j}}{2} + \bar{\psi}_{1j} + A_{2j} \right) + \cdots .$$

The leading-order matching condition (blue terms) yields

$$\phi_0 = \psi_{0j} + A_{1j} \,, \qquad j = 1, \ldots, n \,.$$

Solving for A_{ij} and ψ_{0j}, we get

$$\psi_{0j} = \frac{2\phi_0}{2 - m_j \rho_j^2 \mu_0} \,, \qquad A_{1j} = -\frac{m_j \rho_j^2 \mu_0 \phi_0}{2 - m_j \rho_j^2 \mu_0} \,, \qquad j = 1, \ldots, n \,.$$

The $\mathcal{O}(\nu)$ (red terms) yields the singularity behavior

$$\phi_1 \sim A_{1j} \log|\mathbf{x} - \mathbf{x}_j| - A_{1j} \log \rho_j + \frac{A_{1j}}{2} + \bar{\psi}_{1j} + A_{2j} \,, \quad \text{as} \quad \mathbf{x} \to \mathbf{x}_j \,.$$

Derivation of μ_0: IV

The problem for ϕ_1 is

$$\Delta\phi_1 = \mu_0 m_b \phi_0 \,, \quad \mathbf{x} \in \Omega \backslash \Omega^I \,;$$

$$\partial_n \phi_1 = 0 \,, \quad \mathbf{x} \in \partial\Omega \backslash \Omega^B \,; \quad \int_\Omega \phi_1 \, d\mathbf{x} = 0 \,.$$

$$\phi_1 \sim A_{1j} \log |\mathbf{x} - \mathbf{x}_j| - A_{1j} \log \rho_j + \frac{A_{1j}}{2} + \bar{\psi}_{1j} + A_{2j} \,, \quad \text{as} \quad \mathbf{x} \to \mathbf{x}_j \,.$$

From the divergence theorem we obtain that μ_0 satisfies

$$\mu_0 m_b |\Omega| = -\pi \sum_{j=1}^{n} \alpha_j \frac{A_{1j}}{\phi_0} = \sum_{j=1}^{n} \frac{\pi \alpha_j m_j \rho_j^2}{2 - m_j \rho_j^2 \mu_0} \,.$$

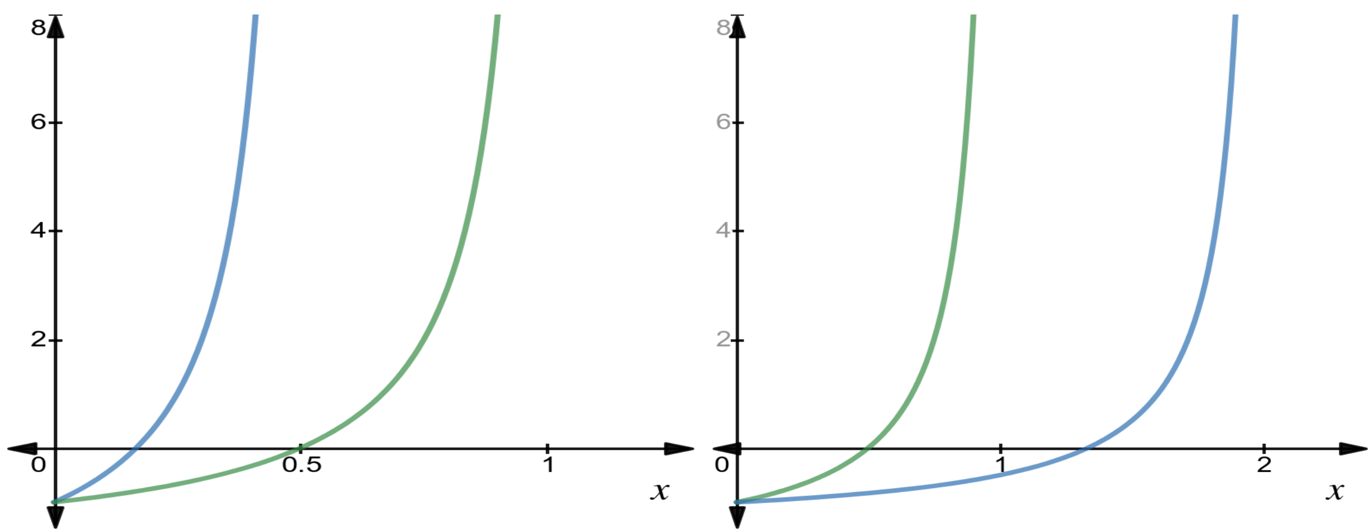
- This yields the nonlinear algebraic equation $\mathcal{B}(\mu_0) = 0$ for the leading-order term μ_0 in the expansion of λ_1.
- Calculating the $\mathcal{O}(\nu^2)$ is more involved. Through the Green's matrix it has the spatial information on the patch locations.
- Note: $\psi_{0j} > 0$ on $\mu_0 < \mu_{\text{m}} = 2/\max_j(m_J \rho_J^2)$. Implies positivity of principal eigenfunction.

A Simple Comparison Lemma

Lemma: *Let $\mathcal{B}(x)$ and $\mathcal{B}_{new}(x)$ be smooth and monotone increasing on $0 \le x < \mu_m$ and $0 \le x < \mu_m^{new}$, resp., and with $\mathcal{B}(0) = \mathcal{B}_{new}(0) < 0$, with a vertical asymptote at μ_m and μ_m^{new} resp. (see plot). Let μ_0 be the unique root to $\mathcal{B}(x) = 0$ on $0 < \mu_0 < \mu_m$ and μ_0^{new} be the unique root to $\mathcal{B}_{new}(x) = 0$ on $0 < \mu_0^{new} < \mu_m^{new}$. Then,*

- **CASE I**: If $\mu_m^{new} \le \mu_m$ and $\mathcal{B}_{new}(x) > \mathcal{B}(x)$ on $0 < x < \mu_m^{new}$, then $\mu_0^{new} < \mu_0$.
- **CASE II**: If $\mu_m^{new} \ge \mu_m$ and $\mathcal{B}_{new}(x) < \mathcal{B}(x)$ on $0 < x < \mu_m$, then $\mu_0^{new} > \mu_0$.

Schematic Plot: Blue curve: $\mathcal{B}_{new}(x)$ and Green curve: $\mathcal{B}(x)$.



CASE I **CASE II**

Habit Location

Qualitative Result I: *The movement of a single favorable habitat to the boundary of the domain is advantageous for species persistence.*

Proof: Move the j^{th} interior favorable patch with $m_j > 0$ of radius $\varepsilon\rho_j$ and angle 2π (i.e. $\alpha_j = 2$) to an unoccupied boundary location with patch radius $\varepsilon\rho_k$, "mass" $m_k > 0$, and angle $\pi\alpha_k$, with $\alpha_k < 2$.

To maintain $\int_\Omega m_\varepsilon \, d\mathbf{x}$, we need $m_j\rho_j^2 = \alpha_k m_k \rho_k^2/2$, which implies $m_k\rho_k^2 > m_j\rho_j^2$. We calculate $\Delta \equiv \mathcal{B}_{\text{new}}(\zeta) - \mathcal{B}(\zeta)$ as

$$\Delta = \frac{\pi\alpha_k m_k \rho_k^2}{2 - \zeta m_k \rho_k^2} - \frac{2\pi m_j \rho_j^2}{2 - \zeta m_j \rho_j^2} = \frac{2\pi m_j^2 \rho_j^4 \zeta}{\left(2 - \zeta m_j \rho_j^2\right)\left(2 - \zeta m_k \rho_k^2\right)} \frac{(2 - \alpha_k)}{\alpha_k} > 0 \,.$$

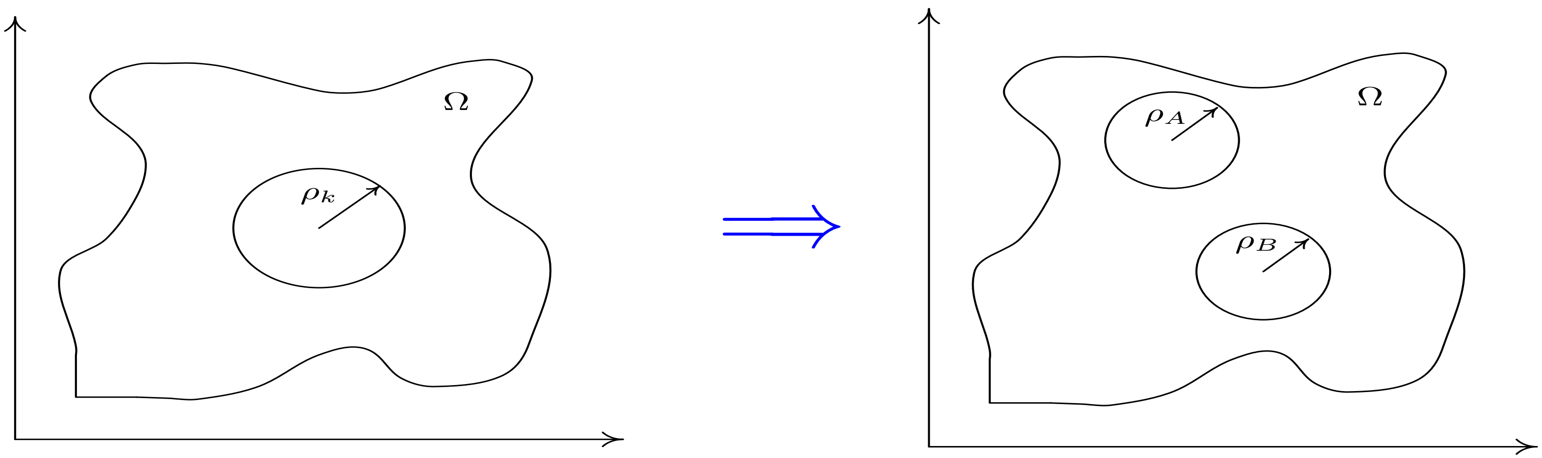
Recall that $\mathcal{B}(\zeta) = 0$ has a unique root on $0 < \zeta < \mu_{\text{m}} \equiv 2/(m_J\rho_J^2)$, where $m_J\rho_J^2 = \max_j m_j\rho_j^2$. Since $m_k\rho_k^2 > m_j\rho_j^2$, the first vertical asymptote for $\mathcal{B}_{\text{new}}(\zeta)$ cannot be larger than that of $\mathcal{B}(\zeta)$.

Thus, $\exists$ a unique root $\zeta = \mu_0^{\text{new}}$ to $\mathcal{B}_{\text{new}}(\zeta) = 0$ on $0 < \zeta < \mu_{\text{m}}^{\text{new}} \equiv 2/(m_K\rho_K^2)$, where $m_K\rho_K^2 \equiv \max\{m_J\rho_J^2, m_k\rho_k^2\}$. Since $\mu_{\text{m}}^{\text{new}} \leq \mu_{\text{m}}$, and $\mathcal{B}_{\text{new}}(\zeta) > \mathcal{B}(\zeta)$ for $0 < \zeta < \mu_{\text{m}}^{\text{new}}$, Case I of the Lemma yields $\mu_0^{\text{new}} < \mu_0$. ■

Habitat Fragmentation I

Qualitative Result II: *The fragmentation of one favorable interior habitat into two separate favorable interior habitats is not advantageous for species persistence. Similarly, the fragmentation of a favorable boundary habitat into two favorable boundary habitats, with each centered at a smooth point of $\partial\Omega$, is not advantageous.*

Proof: Suppose that we are fragmenting one favorable habitat (k) into two smaller favorable habitats (A) and (B). Then, $m_A > 0$, $m_B > 0$, and $m_k > 0$, and $\alpha_A = \alpha_B = \alpha_k$.



Split k^{th} patch as $m_k \rho_k^2 = m_A \rho_A^2 + m_B \rho_B^2$, so that $\int_\Omega m_\varepsilon(\mathbf{x})\, d\mathbf{x}$ is preserved. Determine how μ_0 changes under such a split. We will show that left figure always gives a smaller persistence threshold.

Habitat Fragmentation II

For the original patch distribution, $\mathcal{B}(\zeta) = 0$ has a unique root $\zeta = \mu_0$ on $0 < \zeta < \mu_{\text{m}} \equiv 2/(m_J\rho_J^2)$, where $m_J\rho_J^2 = \max_{m_j>0}(m_j\rho_j^2)$.

Since the first vertical asymptote for $\mathcal{B}_{\text{new}}(\zeta)$ cannot be smaller than that of $\mathcal{B}(\zeta)$ under this fragmentation, then $\mathcal{B}_{\text{new}}(\zeta) = 0$ has a positive root $\zeta = \mu_0^{\text{new}}$ on $0 < \zeta < \mu_{\text{m}}^{\text{new}}$ with $\mu_{\text{m}}^{\text{new}} \geq \mu_{\text{m}}$.

Setting $m_k\rho_k^2 = m_A\rho_A^2 + m_B\rho_A^2$, we calculate $\Delta \equiv \mathcal{B}_{\text{new}}(\zeta) - \mathcal{B}(\zeta)$ as

$$\begin{aligned}\Delta &= \frac{\alpha_k m_A\rho_A^2}{2 - m_A\rho_A^2\zeta} + \frac{\alpha_k m_B\rho_B^2}{2 - m_B\rho_B^2\zeta} - \frac{\alpha_k m_k\rho_k^2}{2 - m_k\rho_k^2\zeta} \\ &= \frac{-\zeta\alpha_k(m_A\rho_A^2 m_B\rho_B^2)[(2 - m_A\rho_A^2\zeta) + (2 - m_B\rho_B^2\zeta)]}{(2 - m_A\rho_A^2\zeta)(2 - m_B\rho_B^2\zeta)(2 - m_k\rho_k^2\zeta)} < 0\,.\end{aligned}$$

Hence, $\mathcal{B}_{\text{new}}(\zeta) < \mathcal{B}(\zeta)$ on $0 < \zeta < \mu_{\text{m}} \equiv 2/(m_J\rho_J^2)$. Since, $\mu_{\text{m}}^{\text{new}} \geq \mu_{\text{m}}$, it follows from Case II of the Lemma that $\mu_0^{\text{new}} > \mu_0$. ■

Implication: Fragmenting an interior favorable habitat into two separate favorable interior habitats is deleterious to survival of the species.

Partial Fragmentation

Q3: What about a partial fragmentation scenario, whereby an interior favorable habitat is fragmented into a boundary habitat and a smaller interior favorable habitat?

Qualitative Result III: *The fragmentation of one favorable interior habitat into a new smaller interior favorable habitat (j) together with a favorable boundary habitat (k), is advantageous for species persistence when the boundary habitat is sufficiently strong in the sense that*

$$m_k \rho_k^2 > \frac{4}{2-\alpha_k} m_j \rho_j^2 \,, \qquad \text{(Bound 1)}\,.$$

Such a fragmentation of a favorable interior habitat is not advantageous when the new boundary habitat is too weak in the sense that

$$m_k \rho_k^2 < m_j \rho_j^2 \,, \qquad \text{(Bound 2)}\,.$$

Finally, the clumping of a favorable boundary habitat and an unfavorable interior habitat into one single interior habitat is not advantageous for species persistence when the resulting interior habitat is still unfavorable.

Remark: These bounds give sufficient but not necessary conditions.

Qualitative Result III: Example

Example 1: Let Ω be the unit disk and set $m_b = 2$: Fragment a single interior patch of radius ε centered at the origin into a favorable boundary patch of radius $\varepsilon\rho_0$ together with a smaller favorable interior patch of radius $\varepsilon\rho_1$. Take $m_j = 1$ for each patch WLOG.

To maintain $\int_\Omega m_\varepsilon \, d\mathbf{x} = -\pi$, we require that ρ_0 and ρ_1, with $0 < \rho_1 < 1$, satisfy $1 = \rho_1^2 + \frac{1}{2}\rho_0^2$. For the new configuration, μ_0^{new} is the root of

$$\mathcal{B}_{\text{new}}(\mu_0) \equiv -2\pi + \pi \left(\frac{\rho_1^2}{2 - \rho_1^2 \mu_0} - \frac{\rho_0^2/2}{2 - \rho_0^2 \mu_0} \right) = 0 \,, \quad \text{with} \quad \rho_1^2 = 1 - \frac{\rho_0^2}{2} \,,$$

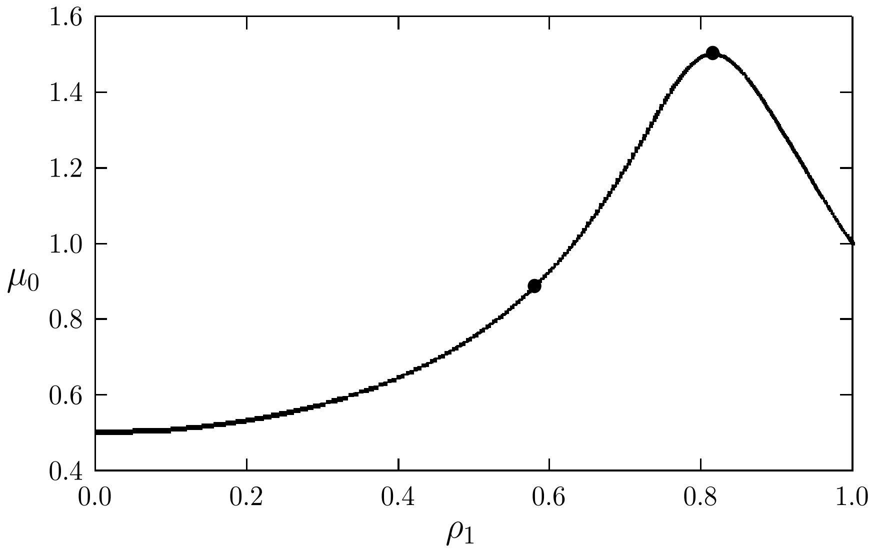
which yields the quadratic equation for μ_0:

$$\mu_0^2 \rho_1^2 \left(1 - \rho_1^2\right) + \mu_0 \left(-2 + \frac{5}{2}\rho_1^2 - \frac{3}{2}\rho_1^4 \right) + 1 = 0 \,.$$

Note: $\mu_0 = 1$ when $\rho_1 = 1$ (original configuration of one interior patch), and $\mu_0 = 1/2$ when $\rho_1 = 0$ (only a boundary patch).

Find the range of ρ_1 for which $\mu_0 < 1$, i.e. so that this fragmentation is desirable.

Qualitative Result III: Example



Caption: μ_0 vs. the (normalized) radius ρ_1 of the new interior patch after fragmenting an interior patch of radius 1 into a smaller interior patch and a boundary patch.

The (sufficient condition) bounds in Qualitative Result III state that:

- fragmentation of an interior patch into a boundary patch is undesirable when $\rho_1 > \rho_0$, which yields $\rho_1 > \sqrt{2/3}$. (Bound 2).
- such a fragmentation is advantageous when $\rho_1 < 1/\sqrt{3}$. (Bound 1).

For this simple two-patch case, we obtain that $\mu_0 = 1$ when $\rho_1 = \sqrt{2/5}$, or equivalently $\rho_0 = \sqrt{6/5}$. Thus, fragmentation is advantageous when $\rho_1 < \sqrt{2/5}$, or equivalently $\rho_0 > \sqrt{6/5}$.

Optimal Allocation of New Resources

Consider a pre-existing distribution of one favorable and one unfavorable interior patch. What is the optimal way to allocate additional resources?

By analyzing the equation for μ_0:

- inserting a new favorable boundary patch is preferable only when it has a sufficiently large size.
- if only a limited amount of an additional favorable resource is available, it is preferable to re-enforce the pre-existing favorable habitat.
- It is never optimal to use the additional favorable resource to mitigate the effect of the unfavorable interior patch.

Overall: This shows that, given some fixed amount of favorable resources to distribute, the optimal strategy is to clump them together at a point on the boundary of the domain, and more specifically at the corner point of the boundary (if any are present) with the smallest angle $\leq 90^\circ$. This minimizes μ_0, thereby maximizing the persistence of the species.

Remark: These qualitative results regarding habitat location and fragmentation are rigorous results based on manipulating the formula for μ_0, which was derived only formally by SLPT.

Optimization at Second Order

Remark: To mimimize the persistence threshold we typically need only consider μ_0. However, in certain particular cases, we must examine the μ_1 term. Recall that μ_0 is independent of patch location.

Result: *For a single boundary patch centered at $\mathbf{x}_0$ on a smooth boundary $\partial\Omega$, the persistence threshold is minimized at the global maximum of the regular part $R_s(\mathbf{x}_0)$ of the surface Neumann Green function.*

Recall that on a smooth boundary $R_s(\mathbf{x}_0)$ is defined via

$$\triangle G_s = \frac{1}{|\Omega|}\,, \quad \mathbf{x} \in \Omega\,; \qquad \partial_n G_s = 0\,, \quad \mathbf{x} \in \partial\Omega \backslash \{\mathbf{x}_0\}\,; \quad \int_\Omega G_s \, d\mathbf{x} = 0\,,$$

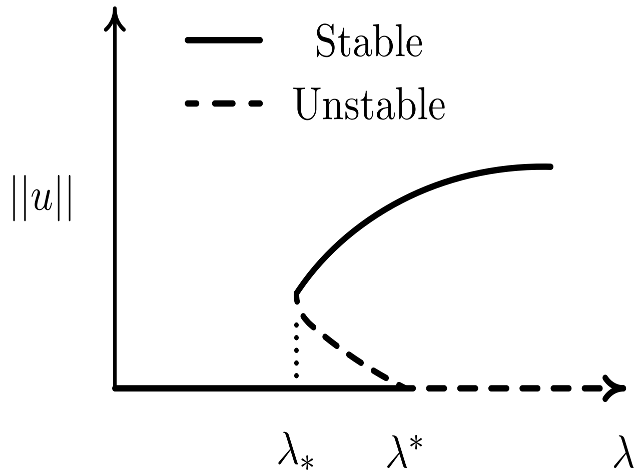
$$G_s(x; x_0) \sim -\frac{1}{\pi} \log|\mathbf{x} - \mathbf{x}_0| + R_s(\mathbf{x}_0)\,, \quad \text{as } \mathbf{x} \to \mathbf{x}_0 \in \partial\Omega\,.$$

Remark: For $\partial\Omega$ smooth, local maxima of $R_s(\mathbf{x}_0)$ and the boundary curvature do not necessarily coincide.

Remark: Given a pre-existing patch distribution, finding the optimal location of a new favorable habitat may also require optimizing the $\mathcal{O}(\nu^2)$ term.

Persistence Problem: Further Directions

- Give a rigorous PDE proof for the asymptotic expansion of the persistence threshold.
- Consider including the weak Allee effect



$$D\Delta u + u\left[m_\varepsilon(\mathbf{x}) - u\right](a+u) = 0\,, \quad \mathbf{x} \in \Omega\,,$$
$$\partial_n u = 0 \quad \mathbf{x} \in \partial\Omega\,.$$

The extinction threshold is now a saddle node bifurcation point.

- Extend single species analysis to multi-species systems.
- Consider the effect of a predator v, modeled in Ω by

$$u_t = D\Delta u + u\left[m_\varepsilon(\mathbf{x}) - u\right] - \beta uv\,, \qquad v_t = \Delta v - \sigma v + \beta uv\,,$$

with $\partial_n u = \partial_n v = 0$ for $\mathbf{x} \in \partial\Omega$. One might guess that a predator has an advantage when its prey is concentrated in favorable habitats. Does the optimal strategy for the prey still remain the same as for the single species problem?

Thanks For Your Attention!