A Moving-Boundary Model for Biological Invasion and Recession in Two Dimensions

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Invading and Receding Biological Populations

- Invading/receding populations common in cell biology 1 and ecology.
 - Invading: region occupied grows, population establishes.
 - Receding: region occupied shrinks, population might become extinct.

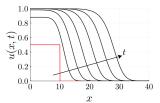


- Seek prototype models for range of phenomena:
 - Invasion and/or recession.
 - Constant speed invasion/recession.
 - Well-defined interface between occupied and unoccupied regions.
 - 1D/2D populations.
- Continuum, single-species population represented by density $u(\mathbf{x}, t)$.

¹P. K. Maini, D. L. S. McElwain, and D. I. Leavesley, Tissue Eng. (2004).

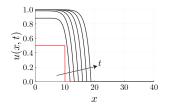
Reaction–Diffusion Models

- Reaction-diffusion equations often used for populations.
 - Travelling-wave solutions capture constant invasion speed.
 - Few parameters: helps fit models to data.
- Dimensionless Fisher–KPP (FKPP) equation: $u_t = u_{xx} + u(1 u)$.



- Travelling waves, speed $c \ge 2$
- Non-compact support
- Local density cannot decrease

• Porous-Fisher's (PF) equation: $u_t = (uu_x)_x + u(1-u)$.



- Travelling waves, speed $c \ge 1/\sqrt{2}$
- Compact support
- Local density cannot decrease

One-Phase Stefan Problem

- PDE moving-boundary problem involving the heat/diffusion equation.
- Models change of phase, e.g. ice melting, water solidification.

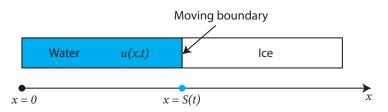
$$u_t = u_{xx} \quad \text{on} \quad 0 < x < S(t),$$

$$u(0, t) = 1,$$

$$u(S(t), t) = 0,$$

$$\beta S_t = -u_x(S(t), t),$$

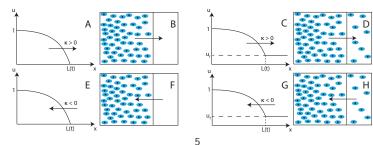
$$u(x, 0) = U(x) \quad \text{on} \quad 0 < x < S(0).$$



1D Fisher-Stefan Model

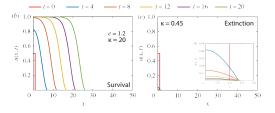
- Solve FKPP model with Stefan-like condition.
- κ represents population loss/gain at interface.
 - $\kappa > 0$: population invades. $\kappa < 0$: population recedes.

$$\begin{split} u_t &= u_{xx} + u(1-u) \quad \text{on} \quad 0 < x < L(t), \\ u_x(0, t) &= 0, \\ u(L(t), t) &= u_f, \\ L_t &= -\kappa u_x(L(t), t), \\ u(x, 0) &= U(x) \quad \text{on} \quad 0 < x < L(0). \end{split}$$



Travelling Waves and 1D Survival/Extinction Results

- Fisher–Stefan model first proposed by Du and Lin².
- Survival/extinction for 1D³ and radially-symmetric⁴ geometry.
 - Population survives if region it occupies becomes sufficiently large.
 - 1D planar: $L(t) > L_c$. Radially-symmetric: $L(t) > R_c$.
- Admits travelling wave solutions for $-\infty < c < \infty$.
 - Unlike FKPP, which only admits feasible solutions for $c \ge 2$.

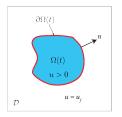




²Y. Du and Z. Lin, <u>SIAM J. Math. Anal.</u> (2010).
³M. El-Hachem et al., <u>Proc. Royal Soc. A</u> (2019).
⁴M. J. Simpson, <u>ANZIAM J.</u> (2020).

2D Fisher–Stefan Model and Research Questions

• Fisher–Stefan model on general 2D region $\Omega(t)$, with boundary $\partial \Omega(t)$.



I

$$u_t = u_{xx} + u_{yy} + u(1 - u) \quad \text{on} \quad \mathbf{x} \in \Omega(t),$$

$$u = u_f \quad \text{on} \quad \mathbf{x} \in \partial \Omega(t),$$

$$V = -\kappa \nabla u \cdot \hat{\boldsymbol{n}} \quad \text{on} \quad \mathbf{x} \in \partial \Omega(t),$$

$$u(x, y, 0) = U(x, y) \quad \text{on} \quad \mathbf{x} \in \Omega(0).$$

Research Questions:

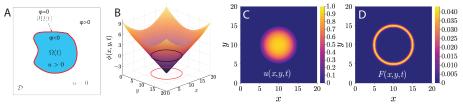
- 1. How does the geometry of Ω affect survival/extinction in 2D? Under what conditions will an initially-rectangular population survive?
- 2. Are planar fronts stable or unstable to shape perturbations? Can we predict patterns wavelength for unstable solutions?

Level-Set Method

- Embed interface as zero level-set of signed-distance function $\phi(x, y, t)$.
- Level-set method for each time step:
 - 1. Solve FKPP equation on $\Omega(t)$.
 - 2. Calculate extension velocity field: F(x, y, t) such that F = V on $\partial \Omega$.
 - 3. Evolve position of interface ($\phi = 0$) by solving level-set equation:

$$\frac{\partial \phi}{\partial t} + F \left| \nabla \phi \right| = 0.$$

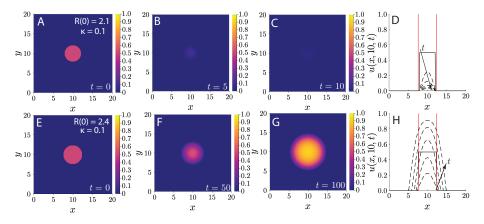
4. Reinitialise ϕ as a signed-distance function.



• Open-source Julia code available on GitHub: alex-tam.

Survival/Extinction in Circular Geometry

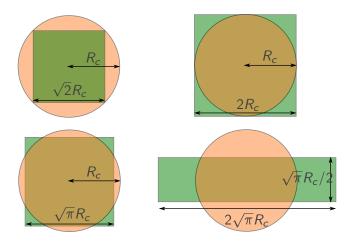
• Circular populations survive if ever $R(t) > R_c$.⁵



⁵M. J. Simpson, ANZIAM J. (2020).

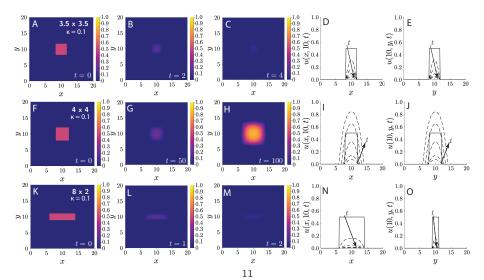
Problem 1: Survival/Extinction in 2D

- Survival/extinction in general 2D geometry unexplored.
- We consider survival/extinction in initially-rectangular regions.



Numerical Solutions for Rectangular Regions

- Initially-rectangular populations can survive or become extinct.
- Rectangle area alone cannot explain survival/extinction.



Analytical Results: Small u

- As $u \rightarrow 0$, will population recover or become extinct?
- Consider leading-order solution on fixed domain.

$$\begin{array}{c}
\hat{u}_{t} = \hat{u}_{xx} + \hat{u}_{yy} + \hat{u} \\
 \underbrace{\hat{u}_{t}}_{(0, 0)} \\
 \underbrace{X} \\
 \end{array}$$

$$\hat{u}(x, y, t) \sim A_{1,1} \sin\left(\frac{\pi x}{X}\right) \sin\left(\frac{\pi y}{Y}\right) e^{-\left(\frac{\pi^2}{X^2} + \frac{\pi^2}{Y^2} - 1\right)t}$$
 as $t \to \infty$.

• Survival requires

$$\underbrace{\int_{\Omega} \hat{u}(x, y, t)}_{\Omega \to \infty} > \underbrace{\int_{\partial \Omega} -\nabla \hat{u} \cdot \hat{\boldsymbol{n}}}_{\Omega \to \infty} \implies XY > \pi \sqrt{Y^2 + X^2}.$$

Population accumulation in Ω

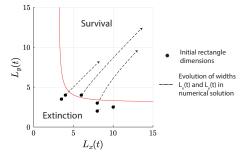
Loss through ∂Ω due to diffusion

Summary: Survival/Extinction in 2D

- Let $L_x(t)$, $L_y(t)$ be widths of $\Omega(t)$ in numerical solutions.
- Analysis suggests population survives if ever

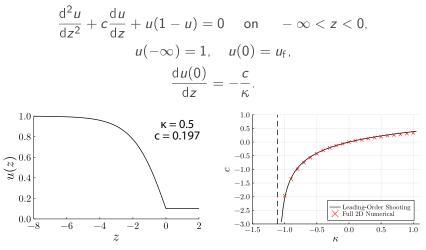
$$L_x > \pi$$
, and $L_y > \pi \sqrt{\frac{L_x^2}{L_x^2 - \pi^2}}$.

• Numerical solutions agree with analytical result.



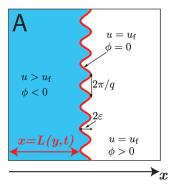
Travelling Wave Solutions

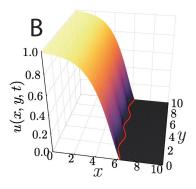
- 1D: Introduce travelling-wave co-ordinate z = x L(t) = x ct.
- Solution to boundary-value problem determines travelling wave profile.
 - Wavespeed c chosen to satisfy derivative BC at z = 0.



Problem 2: Front Stability for Planar Travelling Waves

- For a travelling wave, $\Omega(t) : 0 < x < L(y, t)$.
- Periodic BC on top and bottom in numerical solutions.
- Apply sinusoidal shape perturbations to L(t) and u(z).
 - Perturbations of form $\varepsilon e^{iqy+\omega t}$: Wave number q, growth rate ω .
- Stable: $\omega < 0$. Unstable: $\omega > 0$.





Linear Stability Analysis

• Perturb front shape and population density.

$$L(y, t) = ct + \varepsilon e^{iqy + \omega t} + \mathcal{O}(\varepsilon^{2}),$$

$$\xi = x - L(y, t) = x - ct - \varepsilon e^{iqy + \omega t}$$

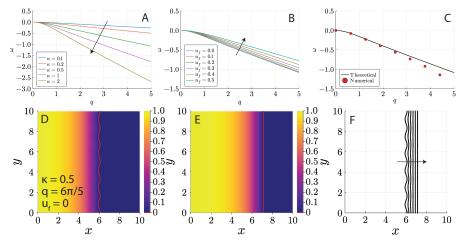
$$u(\xi, y, t) = u_{0}(\xi) + \varepsilon u_{1}(\xi) e^{iqy + \omega t} + \mathcal{O}(\varepsilon^{2}),$$

- Leading-order solution for $u_0(\xi)$ is planar travelling wave.
- First-order correction problem determines growth rate $\omega(q)$.

$$\frac{d^2 u_1}{d\xi^2} + c \frac{du_1}{d\xi} + \left[1 - \omega - q^2 - 2u_0(\xi)\right] u_1(\xi) = -\left(\omega + q^2\right) \frac{du_0}{d\xi},$$
$$u_1(-\infty) = 0, \quad u_1(0) = 0,$$
$$\frac{du_1(0)}{d\xi} = -\frac{\omega}{\kappa}.$$

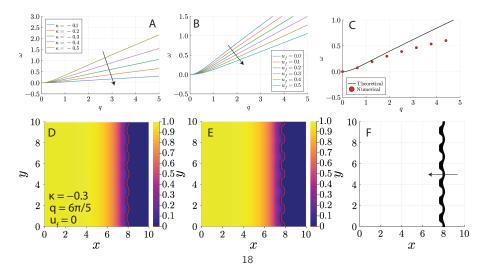
Linear Stability Results: Advancing Waves

- Advancing planar waves stable to perturbations of all wave numbers.
- Consistent with FKPP equation and planar melting in Stefan problem.



Linear Stability Results: Receding Waves

- Receding planar waves unstable to perturbations of all wave numbers.
- Consistent with planar solidification in Stefan problem.



Surface Tension Regularisation

- Modify interface condition to incorporate surface tension⁶.
 Surface tension might represent coll-coll adhesion⁷
- Surface tension might represent cell-cell adhesion⁷.

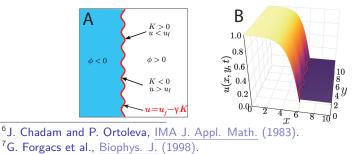
$$u_{t} = u_{xx} + u_{yy} + u(1 - u) \quad \text{on} \quad 0 < x < L(y, t),$$

$$u = 1 \quad \text{on} \quad x = 0,$$

$$u = u_{f} - \gamma K \quad \text{on} \quad x = L(y, t),$$

$$V = -\kappa \nabla u \cdot \hat{n} \quad \text{on} \quad x = L(y, t),$$

$$u(x, y, 0) = U(x, y) \quad \text{on} \quad 0 < x < L(y, 0).$$

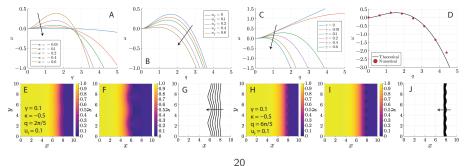


Linear Stability Results: Regularised Receding Waves

$$\frac{d^2 u_1}{d\xi^2} + c \frac{d u_1}{d\xi} + \left[1 - \omega - q^2 - 2u_0(\xi)\right] u_1(\xi) = -\left(\omega + q^2\right) \frac{d u_0}{d\xi},\\u_1(-\infty) = 0, \quad u_1(0) = -\gamma q^2,\\\frac{d u_1(0)}{d\xi} = -\frac{\omega}{\kappa}.$$

• Surface tension stabilises some previously unstable receding waves.

• Most unstable wave number indicates preferred pattern wavelength.



Summary

- Fisher-Stefan model involves solving FKPP equation on a moving boundary with Stefan condition.
- We considered 2 problems in 2D:
 - 1. Survival/extinction in initially-rectangular populations.
 - 2. Planar front stability and pattern formation.
- Aspect ratio influences survival/extinction for rectangular populations⁸.
- Receding planar fronts are unstable, and can generate patterns⁹.
- Open-source level-set method code in Julia on GitHub: alex-tam.
- Future work: Two-population model.

Acknowledgements:

- Mat Simpson.
- Seminar Organisers: Matthew Adams, Mat Simpson, Sarie Gould.
- QUT colleagues.

⁸A. K. Y. Tam and M. J. Simpson, Physica D (2022).

⁹A. K. Y. Tam and M. J. Simpson, arXiv (2022).