TRINITY UNIVERSITY

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Wave Propagation and Global Dynamics of Invasion via Lattice Difference Equations

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Motivation

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Motivation

- The motivation comes from the spatial dynamics of Wolbachia invasion.
- Wolbachia is an endosymbiotic bacterium that infects a wide range of arthropods.
- It is used as a biological control agent for vector-borne diseases such as dengue, Zika, chikungunya, and malaria. [Hoffmann and et al., 2011, Werren et al., 2008]
- It manipulates host reproductive mechanism (through cytoplasmic incompatibility) (CI) by reducing the competence of mosquitoes to transmit pathogens.
- It is therefore deployed in urban (dense) as well as in rural (spread-out) areas of suspected infection.

- Classical ODE models have offer foundational insights into Wolbachia dynamics based on maternal transmission and fitness trade-offs. [Dobson and et al., 2002, Hancock and et al., 2011]

- They lack spatial resolution and cannot capture heterogeneities in landscape structure or dispersal patterns, which play a crucial role in the success or failure of biological invasions.

Existing models

- Classical ODE models have offer foundational insights into Wolbachia dynamics based on maternal transmission and fitness trade-offs. [Dobson and et al., 2002, Hancock and et al., 2011]

- They lack spatial resolution and cannot capture heterogeneities in landscape structure or dispersal patterns, which play a crucial role in the success or failure of biological invasions.

- Spatial models (reaction-diffusion equations and integro-difference equations (IDE)) have addressed this gap. [Kot et al., 1996, Lewis and Kareiva, 1993, Murray, 2002]

- However, they still over-simplify population structure in fragmented or patchy environments, where mosquito habitats are inherently discrete.

- To address this limitation, we introduce a lattice difference equation (LDE) framework for modeling the spatial spread of Wolbachia.
- LDEs represent spatial domains as a grid or lattice.
- They enable modeling of mosquito movement between discrete locations.
- They allow for a more faithful representation of local heterogeneity, habitat fragmentation, and non-uniform dispersal. [Weinberger, 1982, Li and Smith, 2020]

The goal is to rigorously study the dynamics of Wolbachia spread in lattice- based mosquito populations by

- Analyzing local stability near biologically meaningful fixed points.
- Proving the existence of traveling waves and wavefront propagation.
- Investigating how dispersal mechanisms interact with Allee effects to accelerate or inhibit invasion.

Integro-Difference Equation models

Consider the integro-difference equation of the form (see [Kot et al., 1996]):

$$\boxed{v(t+1,x) = \int_{-\infty}^{\infty} K(x,y) f(y, v(t,y))dy,}$$

where

- $v(t,y)$ = infection frequency at location y and time or generation t,
- $K(x,y) = K(x-y)$ =the dispersal kernel capturing mosquitoes movements (relative distance from x to y). More specifically, it is the probability of moving from location y to x.
- $f(x, v(t,x))$= the local growth function determined by cytoplasmic incompatibility and fitness costs.

- IDEs provide a powerful framework for modeling the spatial spread.

↪↪ They incorporate both local reproductive dynamics and long-range dispersal.

- They account for the fact that mosquito populations undergo generational turnover with discrete time steps t.

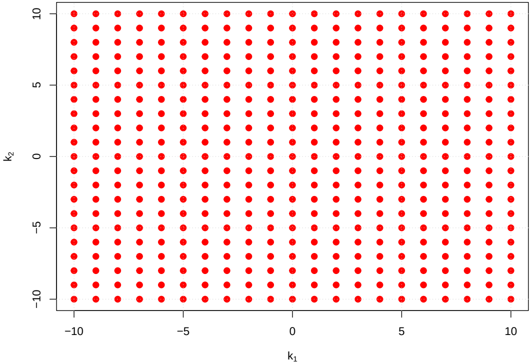
↪↪ This makes them well-suited for studying wavefront propagation in heterogeneous environments.

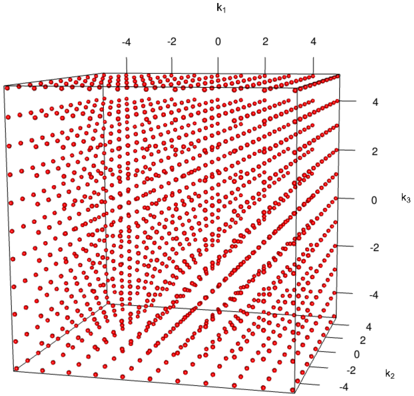
- Despite the usefulness of IDEs, they may not fully capture population dynamics in environments where mosquito habitats are highly fragmented, leading to naturally discrete population distributions.

- An alternative approach is to use **lattice difference equations (LDE)**, which allows for a more granular, spatially structured model.
- **What is a Lattice?**

Let d be a positive integer and $i, j \in \mathbb{Z}^d$. A **d-dimensional integer lattice** is defined as

$$\boxed{\mathbb{Z}^d = \{(k_1, k_2, \cdots, k_d) : k_\ell \in \mathbb{Z}, \ell \in \{1, 2, 3, \cdots, d\}\} \ .}$$





Lattice Difference Equation

For $i, j \in \mathbb{Z}^d$, put

$$\begin{aligned} \delta_i &= \delta(x_i) \ , \\ K_{ij} &= K(x_i, y_j) \ , \\ v_i(t) &= v(t, x_i) \ , \\ f_i(v_i(t)) &= f(x_i, v(t, x_i)) \ . \end{aligned}$$

- Consider the autonomous lattice difference equation (LDE) given as

$$\boxed{v_i(t+1) = (1-\delta_i) f_i(v_i(t)) + \sum_{j \in \mathbb{Z}^d} \delta_j K_{ij} f_j(v_j(t)), \quad \text{for } i \in \mathbb{Z}^d \ ,}$$

where δ_i= the proportion of the population that disperses at location x_i.

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- Consider $\delta_i = \delta =$constant. The fixed points of the above LDE satisfy $v_i(t+1) = v_i(t)$ for all $i \in \mathbb{Z}^d$. This amounts to

$$\boxed{v_i(t) = (1-\delta)f(v_i(t)) + \delta \sum_{j\in\mathbb{Z}^d} K_{ij} f(v_j(t)) \ .}$$

- If $v_i(t)$ is also a fixed point of f, then

$$\boxed{v_i(t) = \sum_{j\in\mathbb{Z}^d} K_{ij} v_j(t) \ .}$$

- In vector form, this amounts to

$$\boxed{Kv = v, \quad \text{where } K = (K_{ij})_{i,j\in\mathbb{Z}^d}}$$

Theorem

Let $\widehat{K}$ be the Fourier transform of the dispersal kernel K. Then we have the following:

1. If $\sup_{k\in(\mathbb{Z}^+)^d} |f'(v_k^*)||(1-\delta)+\delta\widehat{K}(k)| < 1$, then the fixed point $v = (v_k^*)$ is locally asymptotically stable (LAS).
2. If $\sup_{k\in(\mathbb{Z}^+)^d} |f'(v_k^*)||(1-\delta)+\delta\widehat{K}(k)| > 1$, then fixed point $v = (v_k^*)$ is unstable (UNS).

- First, linearize around the fix point $v = v^*$:

$$v_i(t+1) \approx (1-\delta)[v_i^* + f'(v_i^*)(v_i(t) - v^*)] + \delta \sum_{j \in \mathbb{Z}^d} K_{ij}[v_j^* + f'(v_j^*)(v_j(t) - v^*)].$$

- Second, obtain the Jacobian:

$$J_{ij} = \left.\frac{\partial v_i(t+1)}{\partial v_j(t)}\right|_{v(t)=v^*} ,$$

so that

$$J_{ij} = (1-\delta) f'(v_i^*)\delta_{ij} + \delta K_{ij} f'(v_j^*),$$

- Third, write the Jacobian in Matrix form:

$$J = f'(v^*) \left[(1-\delta)I + \delta K\right].$$

- Fourth, use DFT to calculate the eigenvalues:

$$\widehat{Jv}(k) = f'(v^*)[(1-\delta)\widehat{v}(k) + \delta\widehat{Kv}(k)] = \lambda\widehat{v}(k) \ .$$

- Hence

$$\lambda_k = f'(v_k^*)\left[1-\delta+\delta\widehat{K}(k)\right], \quad k \in (\mathbb{Z}^+)^d \ .$$

Dispersal Kernel Choices

In practice, one may use one of the kernels in Table 1 below, with their corresponding Fourier Transform ($d = 2$)

Name	Kernel	DFT
Cauchy	$C(m,n) = \dfrac{\gamma}{\pi(\gamma^2 + m^2 + n^2)}$, for some $\gamma > 0$	$\widehat{C}(k,l) = \dfrac{\exp\left(-2\pi\gamma\sqrt{k^2+l^2}\right)}{1+e^{-2\pi\gamma}}$
Power Law	$P(m,n) = \dfrac{c}{(1+m^2+n^2)^{\gamma/2}}$	$\widehat{P}(k,l) \approx \dfrac{c}{(1+\frac{k^2}{M^2}+\frac{l^2}{N^2})^{\gamma/2}}$
Gaussian	$G(m,n) = \dfrac{1}{2\pi\sigma^2}\exp\left(-\dfrac{m^2+n^2}{2\sigma^2}\right)$	$\widehat{G}(k,l) = \exp\left(-2\pi^2\sigma^2\left(\dfrac{k^2}{M^2}+\dfrac{l^2}{N^2}\right)\right)$
Uniform	$U(m,n) = \dfrac{1}{MN}$, for $0 \le m < M,\ 0 \le n < N$	$\widehat{U}(k,l) = \begin{cases} \dfrac{1}{MN}\left(e^{-\pi\hat{j}\frac{k}{M}}e^{\pi\hat{j}\frac{l}{N}}\dfrac{\sin\pi k}{\sin\frac{\pi k}{M}}\cdot\dfrac{\sin\pi l}{\sin\frac{\pi l}{N}}\right) & \text{if } k \neq 0 \neq l \\ 1 & \text{if } k = 0 = l \end{cases}$
Laplace	$L(m,n) = \begin{bmatrix} 0 & 1 & 0 \\ 1 & -4 & 1 \\ 0 & 1 & 0 \end{bmatrix}$, for $0 \le m \le M,\ \ 0 \le n \le N$	$\widehat{L}(k,l) = -4 + 2\cos\left(\dfrac{2\pi k}{M}\right) + 2\cos\left(\dfrac{2\pi l}{N}\right)$

Table: Commonly used kernels and their respective Fourier Transform, where $\hat{j}^2 = -1$.

Growth Function Choices

In practice, one may use one of the following growth functions:

- The **Wolbachia growth function**:

$$\boxed{f(v(t,x)) = \frac{(1-s_f)v(t,x)}{s_h v^2(t,x) - (s_h + s_f)v(t,x) + 1},}$$

where

- s_h represents the cytoplasmic incompatibility (CI) intensity,
- s_f represents the relative fitness cost of infected females/males and $0 < s_f < s_h < 1$.
- $v(t)$ represents the infection frequency at time t and location x.

- The **logistic growth function**:

$$\boxed{f(v(t,x)) = rv((t,x)\left(1 - \frac{v(t,x)}{K}\right)\left(\frac{v(t,x)}{A} - 1\right),}$$

where

- r represents the intrinsic growth rate.
- K represents the carrying capacity,
- A represents the Allee threshold.

Growth Function Choices

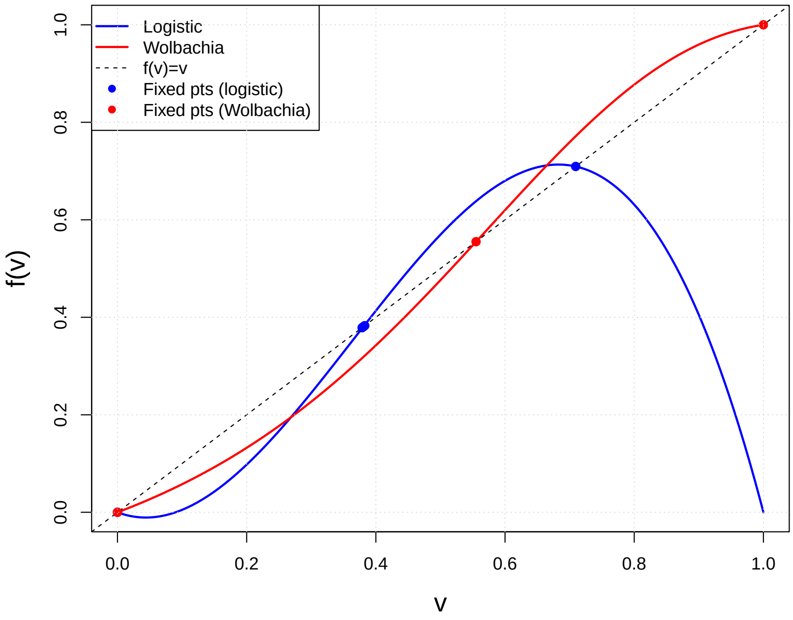
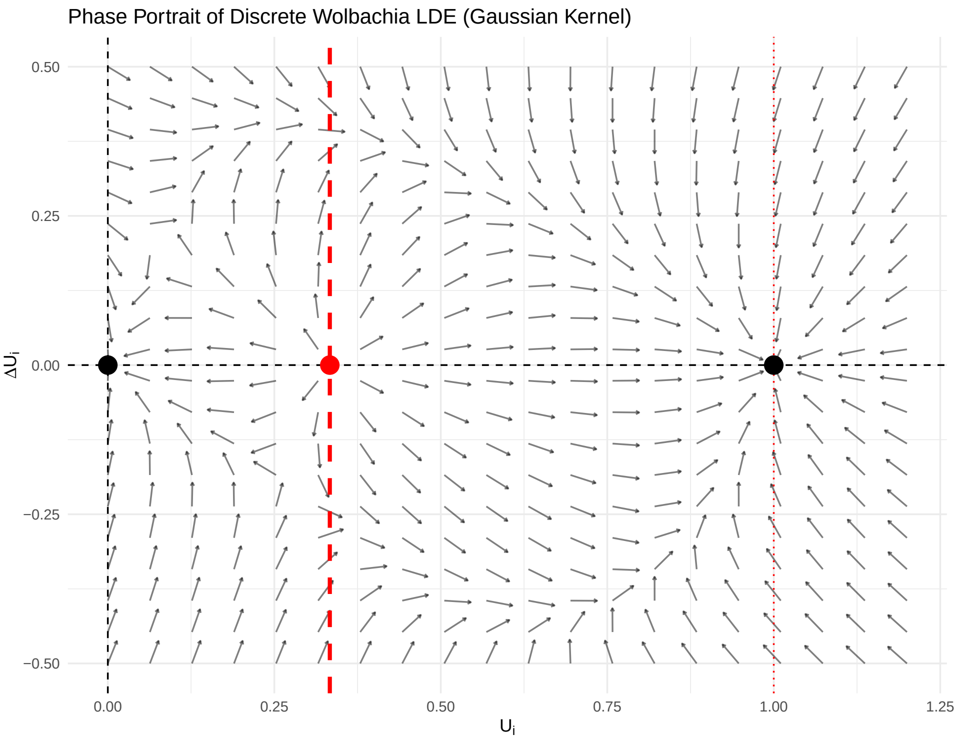


Figure: $r = 0.5, K = 1, A = 0.09, s_f = 0.5, s_h = 0.9$

If we choose the dispersal kernel K such that $\sup_{k\in(\mathbb{Z}^+)^d} \widehat{K}(k) = 1$, then

Function	Fixed point	Stability
	$v^* = 0$	$\lvert f'(0)\rvert = \lvert 1 - s_f\rvert < 1 \implies$ **LAS**
Wolbachia	$v^* = 1$	$\lvert f'(1)\rvert = \left\lvert \frac{1-s_f}{1-s_h} \right\rvert < 1 \implies$ **LAS**
	$v^* = \dfrac{s_f}{s_h}$	$f'\left(\dfrac{s_f}{s_h}\right) = \dfrac{s_h - s_f^2}{s_h - s_h s_f} > 1 \implies$ **UNS**
	$v^* = 0$	$\lvert f'(0)\rvert = \lvert r\rvert < 1 \implies$ **LAS if** $\lvert r\rvert < 1$
Logistic	$v^* = v_1 = \dfrac{A + K + \sqrt{(A+K)^2 - 4AK\left(1 + \frac{1}{r}\right)}}{2}$	$\lvert f'(v_1)\rvert < 1 \implies$ **LAS**
	$v^* = v_2 = \dfrac{A + K - \sqrt{(A+K)^2 - 4AK\left(1 + \frac{1}{r}\right)}}{2}$	$\lvert f'(v_2)\rvert > 1 \implies$ **UNS**



Phase Portrait of Discrete Wolbachia LDE (Gaussian Kernel)
0.50
0.25
0.00
−0.25
−0.50
ΔU_i
0.00
0.25
0.50
0.75
1.00
1.25
U_i

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▶ Traveling waves represent a spatially structured invasion where infected population spreads steadily across a habitat.

▶ These waves determine how fast and under what conditions the infection propagates, which has biological and epidemiological significance in disease control.

Definition

A traveling wave for the LDE is a solution written using the ansatz

$$v_i(t) = U(\xi), \quad \xi = i - ct \ ,$$

where

- $U(\xi)$ is called the wave profile,
- $\xi = i - ct$ is the traveling wave coordinate,
- c is the wave speed.

That is,

$$\boxed{U(\xi + c) = (1-\delta)f(U(\xi)) + \delta \sum_{j \in Z^d} K_{ij} f(U(\xi + i - j)) \ .}$$

Theorem

Suppose the following are true:

A_1 Suppose $f(0) = 0$ and $f(1) = 1$, there exists $0 < \xi < 1$ s.t. $f(\xi) = \xi$ and f'' changes signs at ξ.

A_2 : For all $i \in \mathbb{Z}^d$, we have $\sum_{i \in \mathbb{Z}^d} K_{ij} = 1$.

A_3: $\lim_{\xi \to \infty} U(\xi) = 0$. This means that the leading edge of the wave $\xi \to \infty$ corresponds to the uninfected mosquito population.

A_4: $\lim_{\xi \to -\infty} U(\xi) = 1$. This means that the trailing edge of the wave $\xi \to -\infty$ corresponds to a fully established *Wolbachia*-infected population.

Then the LDE defined above possesses traveling waves.

Existence of traveling waves

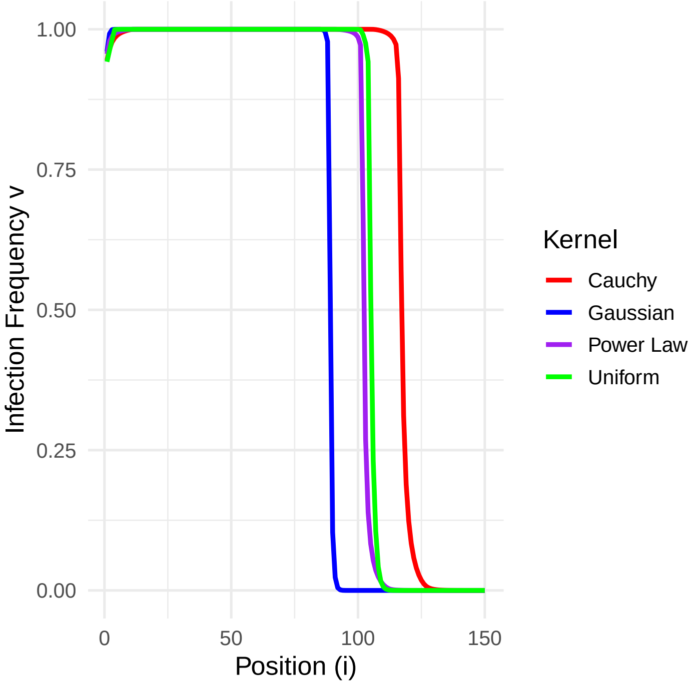

Figure. This figure was obtained on 1-dimensional lattice with width 150 and for $\phi = 0.8$, $\Lambda = 0.4$, $\delta = 0.1$, and over a discrete

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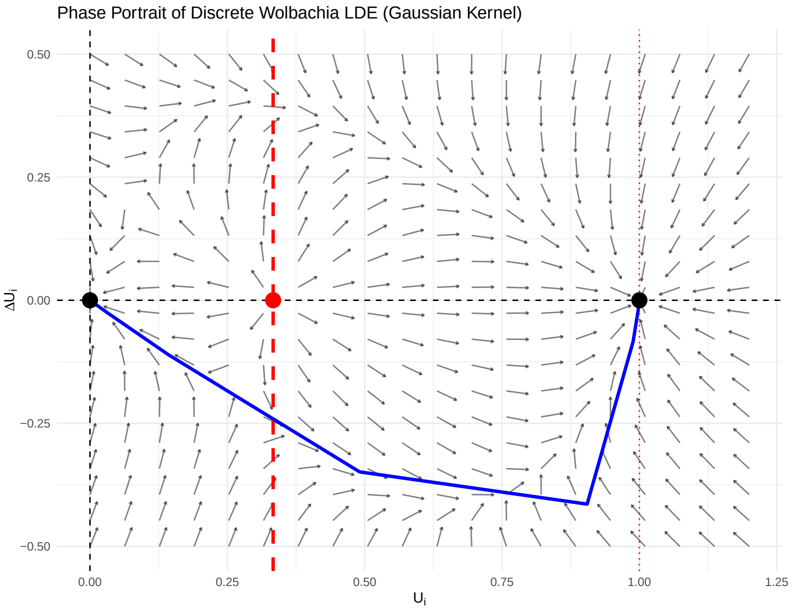

Remark: Spatial coupling versus ODE/DE flow

- In a pure DE or local map $V_{t+1} = f(v_t)$, the flow in **one-dimensional and monotonic**, that is, trajectories cannot jump over an unstable fixed point.
- The Allee threshold A blocks spread from infinitesimal introduction.
- However in spatial system like the Wolbachia-LDE, **non-local dispersal** that couples space allows spatial invasion.
- If the invasion **exceeds A** over a sufficiently wide region, the wave can self-propagate, creating a heteroclinic connection in function space.

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- We recall that $v(x_i, t)$ represents the infection frequency at location x_i and time t, that is, the ratio of infected female or males relatively to the whole population at time t and location x_i.
- Define

$$Y_{it} = \begin{cases} 1 & \text{if there is an infected individual at location } x_i \text{ and time } t \\ 0 & \text{otherwise} \end{cases}.$$

- Therefore, we have that

$$\boxed{\begin{cases} \mathbb{P}(Y_{it} = 1) = v(x_i, t) \\ \mathbb{P}(Y_{it} = 0) = 1 - v(x_i, t) \end{cases}.}$$

Theorem

Define, for all $x_i \in \mathbb{R}$, $N_i = \min\{t \in \mathbb{Z}^+ : v(t+1, x_i) = v(t, x_i)\}$.
Let

$$Y_i|N_i = \sum_{t=0}^{N_i-1} Y_{it} \quad \text{be the outbreak size.}$$

Then $Y_i|N_i$ has a **Poisson-Binomial distribution**. More over, there exists $0 < q_i < 1$ such that

$$\boxed{\mathbb{P}(Y_i = k) = \sum_{m=0}^{\infty} \mathbb{P}(Y_i = k|N_i = m)(1-q_i)^m q_i \ ,}$$

where

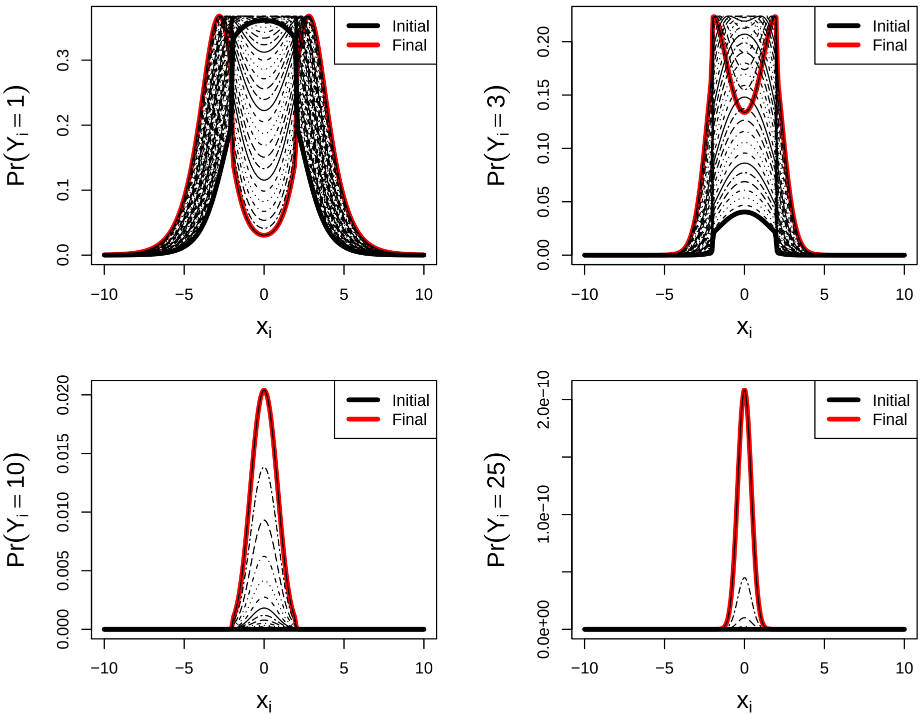
$$\boxed{\mathbb{P}(Y_i = k|N_i = m) = \sum_{U \in \Lambda_k} \prod_{j \in U} p_{ij} \prod_{i \in U^c} (1-p_{ij}) \ ,}$$

and

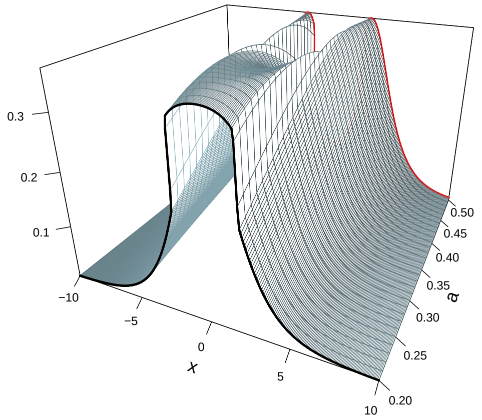
$$\Lambda_k = \{S_k : S_k \subseteq \{1, 2, \cdots, m\} \ , \ |S_k| = k\} \ , \quad \text{where } |A| \text{ is the cardinality of the set } A \ .$$

- Suppose $p_{i0} = v(x_i, 0) = a \cdot 1_{|x|<L}$ (Pulse function) for a given $L = 2$ and $N_i = 400$.
- Take equidistant values of a between 0.2 and 0.5.
- We select $k = 1, 3, 10, 25$, and $s_f = 0.3, s_h = 0.7, \delta = 0.5$.
- ▶ As the amplitude of the function $v_0(x)$, a represents the initial infection rate over the domain $[-L, L]$. In the figures below, we plot $Pr(Y_i = k)$.

Gaussian Kernel

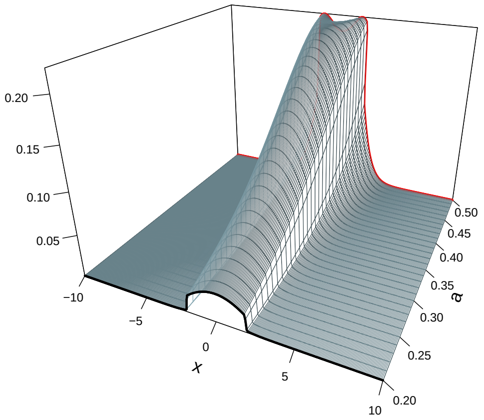


$k = 1$



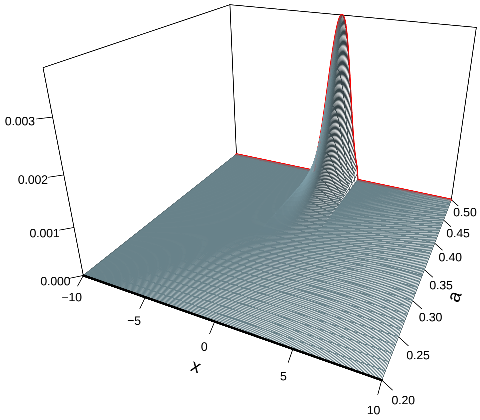
0.3
0.2
0.1
−10
−5
0
5
10
x
0.20
0.25
0.30
0.35
0.40
0.45
0.50
a

$k = 3$



0.20
0.15
0.10
0.05
−10
−5
0
5
10
x
0.20
0.25
0.30
0.35
0.40
0.45
0.50
a

$k = 10$


0.003
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5
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x
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0.25
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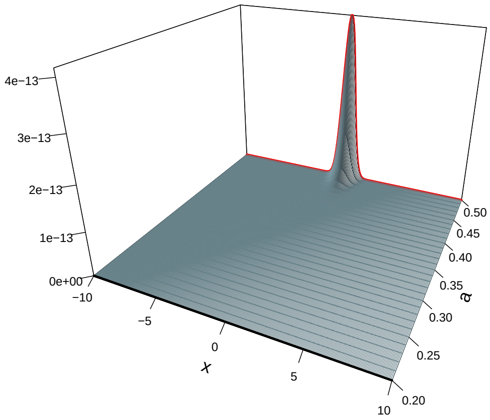
0.35
0.40
0.45
0.50
a

$k = 25$


4e−13
3e−13
2e−13
1e−13
0e+00
−10
−5
0
5
10
x
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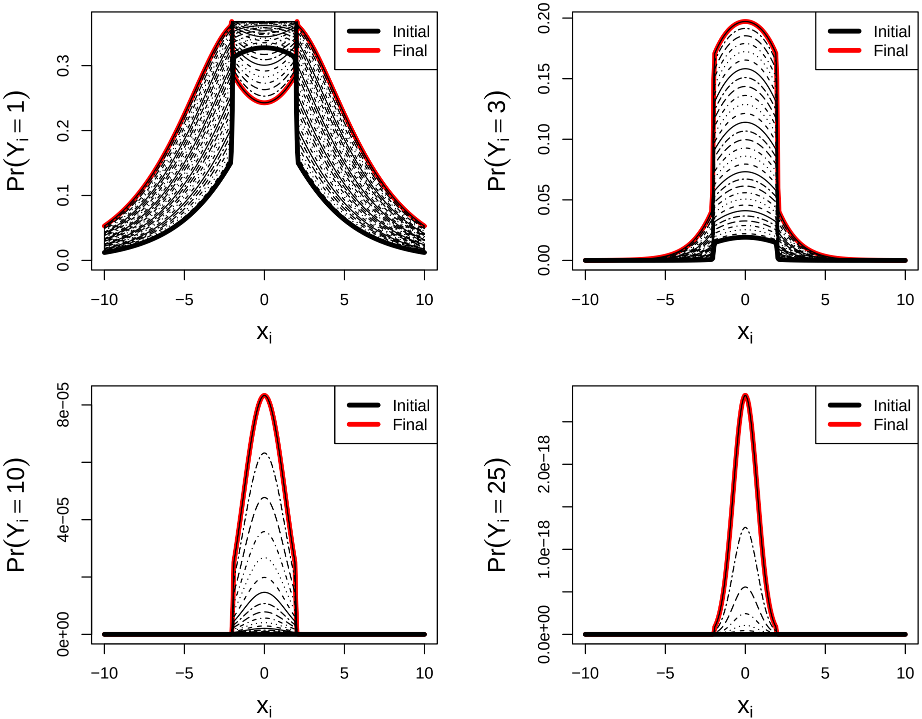
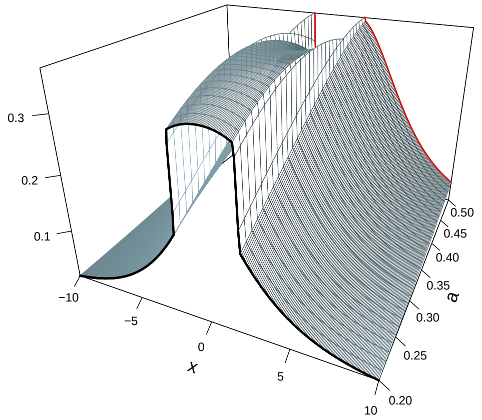
0.25
0.30
0.35
0.40
0.45
0.50
a

Laplacian Kernel



$k = 1$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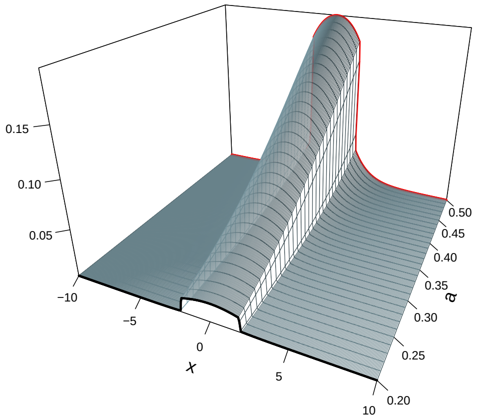
0.50
a

$k = 3$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x
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0.25
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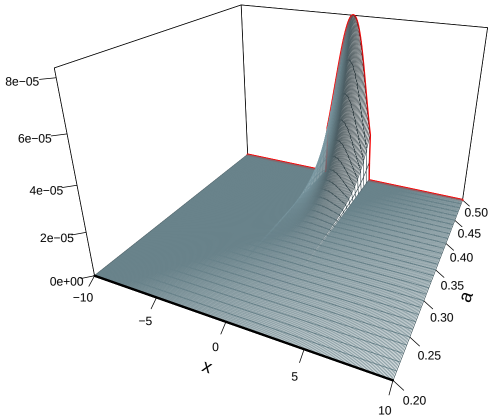
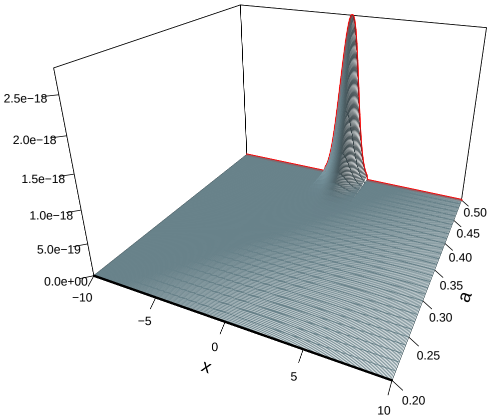
0.35
0.40
0.45
0.50
a

$k = 10$



8e−05
6e−05
4e−05
2e−05
0e+00
−10
−5
0
5
10
x
0.20
0.25
0.30
0.35
0.40
0.45
0.50
a

$k = 25$



2.5e−18
2.0e−18
1.5e−18
1.0e−18
5.0e−19
0.0e+00
−10
−5
0
5
10
x
0.20
0.25
0.30
0.35
0.40
0.45
0.50
a

▶ What the previous analysis reveals is that at low outbreak sizes (k small), the spatial distribution of outbreak sizes ($\mathbb{P}(Y_i = k)$)) has two regimes:

- a unimodal regime which corresponds to low values of the amplitude a
- a bimodal regime which corresponds to high values of a.

▶ For low values of a, regions around the initial release point $x = 0$ inside the release interval $[-L, L]$ are very likely to be infected whereas regions outside this interval are unlikely to be infected overtime.

▶ Given an initial release frequency $v_0(x)$ with amplitude a and interval $[-L, L]$, its costs is defined as

$$\boxed{Cost(a, L) = \int v_0(x)dx.}$$

▶ It **the total biological or logistical effort required to initiate an infection invasion by releasing infected individuals (e.g., mosquitoes) into a population**.

Release Profile function	Expression	Cost
Pulse	$v_0(x) = a \cdot 1_{\|x\| \le L}(x)$	$2aL$
Triangular	$v_0(x) = a\left(1 - \frac{\|x\|}{L}\right) \cdot 1_{\|x\| \le L}(x)$	aL
Quadratic	$v_0(x) = a\left(1 - \frac{x^2}{L^2}\right) \cdot 1_{\|x\| \le L}(x)$	$\frac{4aL}{3}$

- Minimizing the cost of release is therefore of interest.

- Classically, the **Asymptotic Constraints Minimization** (ACM) is used:

$$(a^*, L^*) = \text{Argmin}\left\{ Cost(a, L) \quad s.t.\ \ v(0, x) = v_0(a, L) \quad \text{and}\ \lim_{t\to\infty} v(t, x) = 1 \right\}.$$

- ▶ It's computationally expensive to check $\lim_{t\to\infty} v(t, x) = 1$.

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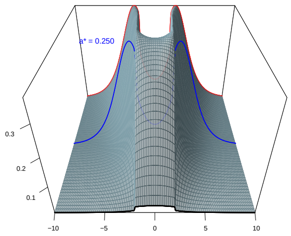
- - It's computationally expensive to check $\lim_{t\to\infty} v(t, x) = 1$.

- We propose the **Modality Constraint Minimization** (MCM)

$$(a^*, L^*) = \text{Argmin}\left\{Cost(a, L) \quad s.t. \;\; \text{Mode}(a, L) = 2\right\} \; .$$

Pulse



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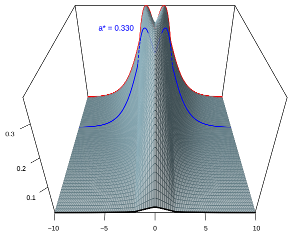
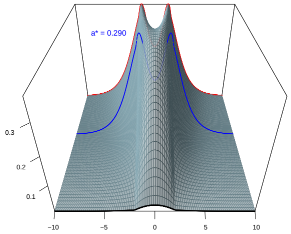


Quadratic



Kernel	Profile	Outbreak Size	MCM a^*	ACM a^*	MCM Cost	ACM Cost
	Pulse	$k=1$	0.200	0.395	0.200	0.395
		$k=2$	0.290		0.290	
		$k=3$	0.340		0.340	
		$k=4$	0.360		0.360	
Laplacian	Quadratic	$k=1$	0.220	0.518	0.147	0.345
		$k=2$	0.320		0.213	
		$k=3$	0.380		0.253	
		$k=4$	0.420		0.280	
	Triangular	$k=1$	0.260	0.720	0.130	0.360
		$k=2$	0.380		0.190	
		$k=3$	0.450		0.225	
		$k=4$	0.490		0.245	

Bi-modality as a Cost minimization Criterion

Kernel	Profile	Outbreak Size	MCM a^*	ACM a^*	MCM Cost	ACM Cost
	Pulse	$k=1$	0.200	0.390	0.200	0.390
		$k=2$	0.290		0.290	
		$k=3$	0.330		0.330	
		$k=4$	0.360		0.360	
Gaussian	Quadratic	$k=1$	0.220	0.493	0.147	0.329
		$k=2$	0.330		0.220	
		$k=3$	0.380		0.253	
		$k=4$	0.420		0.280	
	Triangular	$k=1$	0.260	0.640	0.130	0.320
		$k=2$	0.380		0.190	
		$k=3$	0.450		0.225	
		$k=4$	0.490		0.245	

- We proposed a **discrete-space framework** for invasion dynamics using Lattice Difference Equations (LDEs), offering a tractable alternative to classical PDE and IDE models.
- The LDE's discrete structure allows easy **integration of spatial heterogeneity**, seasonal variation, and environmental factors affecting *Wolbachia* dynamics.
- Extending the model to **stochastic or random environments** enables estimation of invasion probabilities beyond deterministic outcomes.

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Thank you for listening!
Any questions?