Epidemic Spread in Populations at Demographic Equilibrium

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Timeline

The role of dispersal in the evolution of communities has been a central topic in population biology.

Pioneer mathematical work includes:

- Fisher and Kolmogoroff (1937) Genetics, Travelling Waves
- Skellam (1951) Muskrats Dispersal
- Kendall (1965) Epidemic Models
- Mollison (1977) Epidemic Spread

- Okubo (1980) Monumental Biological Work
- Aronson (1977, 1975) Mathematical Contributions
- Weinberger (1978,1984) Mathematical Contributions
- Levin (1986) Significant Impact in Ecology and Evolutionary Biology
- Kot (1992, 1996) Major contributions to Ecology
- and others.

Motivation I:
Discrete-time travelling waves

Modeling with integrodifference equations (IDE).

Asymptotic Behavior of a model of populations genetics (Weinberger (1978)).

- Study IDE using recursion formula $N_{t+1} = g(N_t)$.
- Show minimum asymptotic speed of propagation for the IDE, c^*, exist.
- Proved that there are travelling waves with speed c precisely when $|c| \geq c^*$.

Main motivation is the work of Kot (1992,1996) and Weinberger (1978,1984) on one-dimensional habitat dispersal in invading populations with non-overlapping generations.

$$N_{t+1}(x) = \int_{-\infty}^{\infty} g(N_t(y))k(x-y)dy \tag{1}$$

where $N_{t+1} = g(N_t)$ models the local population dynamics and $k(x-y)\Delta y$ denotes the probability that an individual will disperse from location y to location x.

Travelling Waves

Weinberger (1978) showed that travelling wave solutions exist for all speeds c greater than a minimum wave speed c^* if

(i) $g(N)$ is continuously differentiable on the interval $[0, N^*]$;

(ii) $g(0) = 0$ and $g(N^*) = N^*$;

(iii) $g'(N) \geq 0$, $N < g(N) \leq g'(0)N$ in $(0, N^*)$;

(iv) $k(x)$ is exponentially bounded.

He further showed, for such exponentially bounded kernels, initial conditions with compact support, that is,

$$N_0(x) > 0,\ \ x \in [-\delta, \delta] \text{ and } N_0(x) = 0,\ \ x \notin [-\delta, \delta],$$

converge to travelling waves with minimum speed of propagation given by

$$c^* = \min_{\mu>0} \left\{ \frac{1}{\mu}\, ln\ \ [g'(0)M(\mu)] \right\} \tag{2}$$

where $M(\mu) = \int_{-\infty}^{\infty} e^{\mu x} k(x) dx$, the moment generating function of $k(x)$.

Discrete-time travelling waves: Ecological examples (Kot (1992)).

- Use of models for organisms with discrete non-overlapping generations ($N_{t+1} = g(N_t)$) and well defined growth and dispersal functions.

- Analyze the varied travelling waves that arise in some simple ecological-interesting IDE, i.e. Beverton-Holt equation.

- Derived the speed and approximate the shape of the observed waveforms using different redistribution kernels.

Goal

- Our main goal is to apply these results to the case of epidemics that can be reduced to the single non-linear map $I_{t+1} = g(I_t)$.
- To expand the work of ecological research in IDE to the case of discrete time epidemics in populations with overlapping and non-overlapping epidemiological generations.
- Study speed of travelling waves solutions for the epidemics modeled via integrodifference equations (IDE).

Motivation II:
Discrete Epidemics

Dispersal, disease and life-history evolution (Castillo-Chavez $\&$ Yakubu, 2001).

- Local disease dynamic model via $S-I-S$ epidemic process, does not include disease induced mortality.
- Dynamic of total population size at generation t,

$$P_{t+1} = f(P_t) + \gamma P_t \tag{3}$$

where P_t total population at generation t, $f(P_t)$ density dependent birth rate or recruitment and $\gamma \in [0, 1)$ is the probability of survival from generation t to $t+1$.

- Here $P_t = S_t + I_t$ and $P_\infty \equiv \lim_{t\to\infty} P_t$ is the demographic steady state of total population.

- Discrete time $S - I - S$ model

$$\begin{aligned} S_{t+1} &= f(P_t) + \gamma Q(z_t)S_t + \gamma(1-\sigma)I_t, && (4) \\ I_{t+1} &= \gamma(1 - Q(z_t))S_t + \gamma\sigma I_t, && (5) \end{aligned}$$

where $0 < \gamma, \sigma < 1$.

- σ gives the fraction of infected individuals that remain infected from one time step to the next.

- The function $Q(z_t)$ denotes the proportion of susceptible individuals that do not become infected at time t given that the disease prevalence is $z_t = \frac{I_t}{P_t}$.

- In general, $Q : [0, \infty) \to [0, 1)$ is a monotone concave function with $Q(0) = 1$; $Q'(u) < 0$ and $Q''(u) \geq 0$ for all $u \in [0, \infty)$.

- As is common, we model the "probability" of not becoming infected as

$$Q(z_t) = e^{-\alpha z_t}. \tag{6}$$

  That is encounters that lead to infection are modeled via a Poisson process.

- The parameter α is the transmission constant, it models the impact of prevalence $\left(z_t = \frac{I_t}{P_t}\right)$ on Q.

- If it is assumed that $f(P_t) = \Lambda$ a constant then the total population reach a stable positive steady state P_∞. Rescaling by P_∞ one gets

$$y_{t+1} = \gamma(1 - Q(z_t))(1 - y_t) + \gamma\sigma y_t. \tag{7}$$

where y_t is the proportion of infected at generation t.

- The disease basic reproductive number, R_0, is

$$R_0 = \frac{-\gamma\alpha Q'(0)}{1-\gamma\sigma}. \tag{8}$$

- (a) If $R_0 < 1$, then $y_t \to 0$ as $t \to \infty$, hence the number of infectives will decrease to zero.

- (b) If $R_0 > 1$, then $y_t \to \bar{y} > 0$ as $t \to \infty$, hence the number of infectives will grows.

Constant Recruitment

Local population dynamic governed by $P_{t+1} = f(P_t) + \gamma P_t$.

With $f(P_t) = \Lambda$, we have

$$\Lambda^* \equiv \lim_{t \to \infty} P_t = \frac{\Lambda}{1-\gamma} \tag{9}$$

which is the demographic steady state of the total population.

SIS Epidemic Model with Overlapping Generations

(General Model)

Discrete SIS model with overlapping generations:

$$\begin{aligned} S_{t+1} &= \varphi(S_t, I_t) = Q(z_t)f(P_t) + \gamma Q(z_t)S_t + \gamma(1-\sigma)I_t, && (10) \\ I_{t+1} &= \psi(S_t, I_t) = (1-Q(z_t))f(P_t) + \gamma(1-Q(z_t))S_t + \gamma\sigma I_t && (11) \end{aligned}$$

where $P_{t+1} = S_{t+1} + I_{t+1}$ and $Q(z_t) = e^{-\alpha z_t}$ is the probability of not becoming infected in t to $t+1$ when the disease prevalence is $z_t = \frac{I_t}{f(P_t)+P_t}$.

Basic Reproductive Number, R_0

The basic reproductive number, R_0, at a demographic equilibrium is given by

$$R_0 = \frac{\alpha}{1-\gamma\sigma}\frac{1}{(2-\gamma)} \tag{12}$$

Locally,

$R_0 > 1 \implies$ epidemic growth
$R_0 < 1 \implies$ local extinction of the diseases

System has two equilibria $I_0 = 0$ and $I_1 = I^*$ as long as $R_0 > 1$.

Adding Dispersal

Assuming that dispersal occurs after mortality, and that the disease does not affect the dispersal process, we can add dispersal to model (10) to give

$$S_{t+1}(x) = \int_{-\infty}^{\infty} \varphi(S_t(y), I_t(y))\, k(x-y)\, dy, \tag{13}$$

$$I_{t+1}(x) = \int_{-\infty}^{\infty} \psi(S_t(y), I_t(y))\, k(x-y)\, dy. \tag{14}$$

Travelling Waves for Model Reduction

In this case since we are working with an epidemic spreading through populations at demographic equilibrium, we can eliminate $S_t(x)$ from system (13) to obtain the single IDE

$$I_{t+1}(x) = \int_{-\infty}^{\infty} g(I_t(y))k(x-y)dy \qquad (15)$$

where $g(I_t(y)) = [1 - Q(\tilde{z}_t)][\Lambda^* - \gamma I_t] + \gamma\sigma I_t$, and $z_t = \frac{I_t}{\Lambda^* + \Lambda}$.

The task before us now is to determine the conditions under which the function g satisfy Weinberger's conditions, specifically Conditions (ii) and (iii).

An Example with Non-overlapping Generations (SI)

If $\gamma = 0$ (discrete model with non-overlapping generations), the general model becomes SI:

$$\begin{aligned} S_{t+1} &= \varphi(S_t, I_t) = Q(z_t)\, f(P_t), & (16) \\ I_{t+1} &= \phi(S_t, I_t) = (1 - Q(z_t))\, f(P_t), & (17) \end{aligned}$$

with basic reproductive number $g'(0) = R_0 = \frac{\alpha}{2}$.

Since $P_{t+1} = f(P_t) + \gamma P_t = f(P_t) \implies \Lambda = \Lambda^*$ then,

$$g(I_t(y)) = \Lambda \left(1 - \exp\left[\frac{-\alpha I_t(y)}{2\Lambda} \right] \right). \tag{18}$$

- Computations show that Weinberger's conditions hold, i.e. $g(0) = 0$, there exist I^* such that $g(I^*) = I^*$, $g'(I) \geq 0$ and $I < g(I) \leq g'(0)I$ for $I \in (0, I^*)$.

- Thus a spreading epidemic will ensue, as long as $R_0 = \frac{\alpha}{2} > 1$.

- Consequently, when dispersal is added to the model travelling wave solutions and a minimal speed of propagation do exist.

Example with Overlapping Generations (SI)

If $\gamma > 0$ and $\sigma = 1$ (discrete model with overlapping generations), then the general model for the SI case reduces to:

$$S_{t+1} = \varphi(S_t, I_t) = Q(z_t)f(P_t) + \gamma Q(z_t)S_t, \quad (19)$$

$$I_{t+1} = \psi(S_t, I_t) = (1 - Q(z_t))f(P_t) + \gamma(1 - Q(z_t))S_t + \gamma I_t, \quad (20)$$

and its basic reproductive number is now given by

$$R_0 = \frac{\alpha}{1-\gamma}\frac{1}{(2-\gamma)}. \quad (21)$$

In this case,

$$g(I_t(y)) = \left(1 - \exp\left[\frac{-\alpha I_t(y)}{\Lambda + \Lambda^*}\right]\right)(\Lambda^* - \gamma I) + \gamma I, \tag{22}$$

- Naturally, since Equation (22) satisfy Conditions (i)-(iii) the work of Weinberger (1978) applies.
- Thus a spreading epidemic will occur, as long as $R_0 = \frac{\alpha}{(1-\gamma)(2-\gamma)} > 1$.
- The minimal speed c^* of disease propagation can be “identified” and computed for specific kernels.

Speed

- For all three examples, when dispersal is added to the epidemic models travelling wave solutions and a minimal speed of propagation will exist as long as $R_0 > 1$.

- We look for travelling wave solutions of

$$I_{t+1}(x) = \int_{-\infty}^{\infty} g(I_t(y))\, k(x-y)\, dy, \tag{23}$$

that is, solutions of the form $I_t(x) = i(\phi)$ where $\phi = x - ct$. Direct substitution into (23) yields

$$i(\phi - c) = \int_{-\infty}^{\infty} g(i(\eta))\, k(\phi - \eta)\, d\eta \qquad \text{where} \qquad \eta = y - ct. \tag{24}$$

- The minimal speed is given by $c^* = \min_{\mu > 0} \left\{ \frac{1}{\mu}\, ln\ [g'(0)M(\mu)] \right\}$.
- Focus on nonnegative integral curves that connect the two fixed points, $I_0 = 0$ and $I_1 = I^* > 0$.
- If $\mu > 0$ in c^* the model will supports a rightward moving wave

$$\lim_{z \to -\infty} I(z) = I^*, \qquad \lim_{z \to \infty} I(z) = 0. \tag{25}$$

Speed for Epidemic Examples

For the normal redistribution kernel (with zero mean) the m.g.f is $M(\mu) = e^{\frac{\sigma_n^2 \mu^2}{2}}$ and the corresponding minimum wave speed is:

$$c^* = \sigma_n \sqrt{2 \ln\, g'(0)}. \tag{26}$$

The minimum speed of disease propagation for general model (SIS)

$$c^* = \sigma_n \sqrt{2\ \ln \left[\frac{\alpha}{(2-\gamma)} + \gamma\sigma \right]}. \tag{27}$$

For SI with non-overlapping generations and SI with overlapping generations $g'(0) = \frac{\alpha}{2}$ and $g'(0) = \frac{\alpha}{(2-\gamma)} + \gamma\sigma$, respectively.

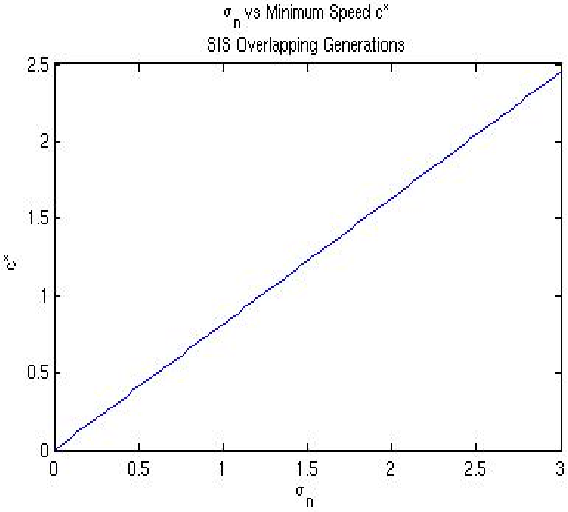
Illustrative Simulations

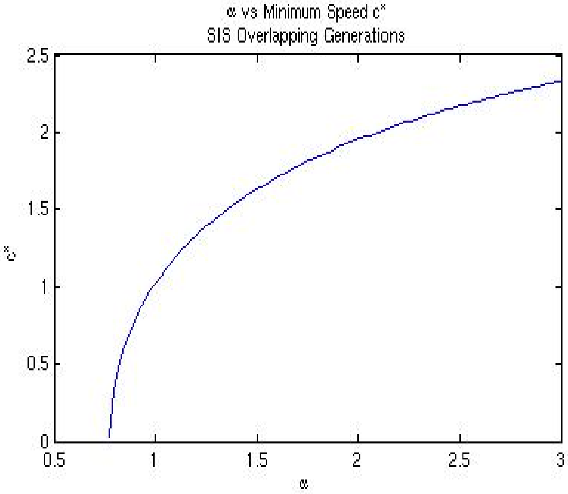
- For the general model we fix the probability of survival for each generation γ and the probability of not recovering σ, 0.98 and 0.25 respectively, however we use different values for α, in this case $\alpha = 1.5$.

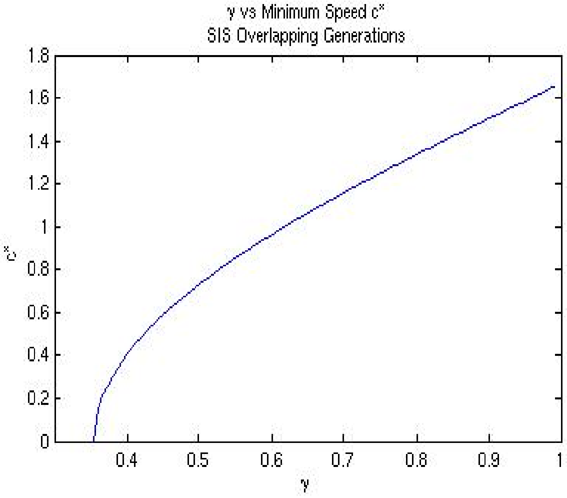
- The normal distribution used with standard deviation $\sigma_n = 0.5$.

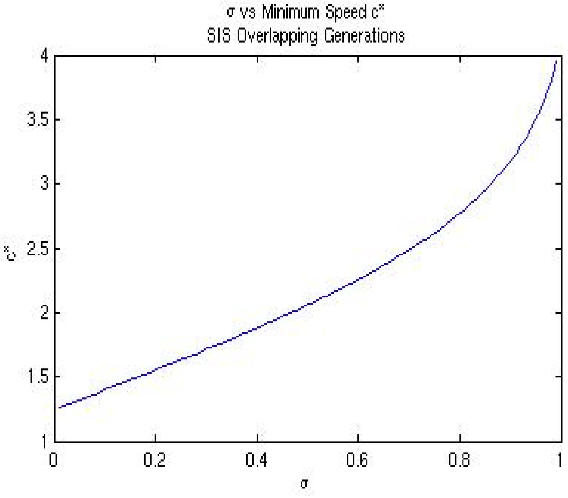
- Travelling wave solutions and minimum speed of propagation c^* provided as long as $R_0 > 1$.

- Plot of c^* versus parameters. Simulations shows that c^* increase as the parameters increase.


σ_n vs Minimum Speed c*
SIS Overlapping Generations


α vs Minimum Speed c*
SIS Overlapping Generations


γ vs Minimum Speed c*
SIS Overlapping Generations


σ vs Minimum Speed c*
SIS Overlapping Generations

Discussion

IDE are used to study, epidemic invasions derived from first principles using models with non-overlapping and overlapping epidemiological generations. For all three examples we were able to show that Weinberger's Conditions (i)-(iii) holds.

When dispersal is added to discrete time epidemic models at demographic equilibrium:

- Travelling waves solutions will exist.
- Minimal speed of disease propagation c^* can be "identified" and computed.
- A spreading epidemic will ensue as long as $R_0 > 1$.

Future Directions

- Apply this work to two and three spatial dimensions, mainly numerical work.
- Higher dimensions of epidemiological systems.
- Lots to be done... what happen when the function g is not monotonic increasing?