Models in population dynamics: from discrete to continuous and back

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The SIS model

$$\begin{aligned} S + I &\xrightarrow{\alpha} 2I; \\ I &\xrightarrow{\beta} S. \end{aligned} \tag{1}$$

Classical SIS-ODE:

$$\begin{array}{rcl} \dot{S} &=& -\bar{\alpha} SI + \bar{\beta} I \\ \dot{I} &=& \bar{\alpha} SI - \bar{\beta} I \end{array} .$$

Without loss of generality, that $S(0) + I(0) = 1$:

$$I' = \bar{\alpha} I \left(1 - \frac{\bar{\beta}}{\bar{\alpha}} - I \right). \tag{2}$$

Let $\bar{R}_0 := \bar{\alpha}/\bar{\beta}$.

$$\lim_{t \to \infty} I(t) = \begin{cases} 0, & \bar{R}_0 <= 1; \\ I_* = 1 - \frac{1}{\bar{R}_0}, & \bar{R}_0 > 1. \end{cases}$$

SIS-DTMC

- If he or she is of type **I**, then it becomes **S** with probability β;
- If he or she is of type **S**, then it becomes **I** with probability proportional to the number of infected in the population: αx.

$$
\begin{aligned}
T^{+}(x) &= \alpha x(1-x)\ , \\
T^{0}(x) &= 1 - T^{+}(x) - T^{-}(x)\ , \\
T^{-}(x) &= x\beta\ .
\end{aligned}
$$

Let $P_{(N,\Delta t)}(x,t)$ be the probability to find a fraction x of **I** individuals at time t in a population of size N, evolving in time steps of size Δt.
The master equation is:

$$
\begin{aligned}
P_{(N,\Delta t)}(x,t+\Delta t) = {} & T^{+}(x-z)P_{(N,\Delta t)}(x-z,t) \\
& + T^{0}(x)P_{(N,\Delta t)}(x,t) \\
& + T^{-}(x+z)P_{(N,\Delta t)}(x+z,t).
\end{aligned}
$$

Let $p_{(N,\Delta t)}(x,t) = NP_{(N,\Delta t)}(x,t)$, and $\epsilon = 1/N$.
If $p_{(N,\Delta t)}$ is a smooth function then it need to satisfy

$$\partial_t p = -\partial_x \{x[R_0(1-x)-1]p\} + \frac{\epsilon}{2}\partial_x^2 \{x(R_0(1-x)+1)p\} + \mathcal{O}(\epsilon^2),$$
$$\frac{\epsilon}{2}((1-R_0)p(1,t) + \partial_x p(1,t)) + p(1,t) = 0$$

Theorem

For smooth initial conditions, Lax-Richtmyer equivalence theorem implies that $p_{(N,\Delta t)} \to p$ pointwise, as $\epsilon \to 0$, where p satisfies

$$\partial_t p + \partial_x \{x[R_0(1-x)-1]p\} = 0 \quad \textit{PDE form of SIS-ODE}$$
$$p(1,t) = 0.$$

Write

$$u(x,t) = x\,[R_0(1-x)-1]\,p(x,t)$$

Then u satisfies

$$\partial_t u = x\,[R_0(1-x)-1]\,\partial_x u.$$

Hence

$$p(x,t) = \frac{\phi_{-t}(x)\,[R_0(1-\phi_{-t}(x))-1]}{x\,[R_0(1-x)-1]} p_0(\phi_{-t}(x))$$

where ϕ_t is the flowmap for the SIS-ODE.

Want to keep finite population effects — do not send $\epsilon \to 0$
Look for solution to

$$\partial_t p = -\partial_x \left\{ x \left[R_0(1-x) - 1 \right] p \right\} + \frac{\epsilon}{2} \partial_x^2 \left\{ x(R_0(1-x)+1)p \right\} + \mathcal{O}(\epsilon^2),$$

$$\frac{\epsilon}{2} \left((1-R_0)p(1,t) + \partial_x p(1,t) \right) + p(1,t) = 0$$

$$p(x,0) = p^0(x);$$

$$\frac{\mathrm{d}}{\mathrm{d}t} \int_0^1 p(x,t) \, \mathrm{d}x = 0;$$

$$\lim_{t\to\infty} p(\cdot,t) = \delta_0.$$

$$
\begin{aligned}
&\int_0^\infty \int_0^1 p(x,t)\partial_t g(x,t)\mathrm{d}x\mathrm{d}t + \\
&+ \frac{\epsilon}{2}\int_0^\infty \int_0^1 p(x,t)x\left(R_0(1-x)+1\right)\partial_x^2 g(x,t)\mathrm{d}x\mathrm{d}t \\
&\int_0^\infty \int_0^1 p(x,t)x\left(R_0(1-x)-1\right)\partial_x g(x,t)\mathrm{d}x\mathrm{d}t + \\
&\int_0^1 p(x,0)g(x,0)\mathrm{d}x = 0,
\end{aligned} \tag{3}
$$

where

$$
g \in C_c^\infty([0,1]\times[0,\infty)), \quad \partial_x g(1,t) = 0.
$$

Proposition

If $p \in L^\infty\big([0,\infty);\mathcal{BM}^+([0,1])\big)$ *is a solution to* (3) *then*

$$\frac{d}{dt}\int_0^1 p(x,t)\,dx = 0.$$

Theorem

Let $p^0(x) \in \mathcal{BM}^+([0,1])$. *Then Equation* (3) *has a unique solution* $p \in L^\infty\left([0,\infty); \mathcal{BM}^+([0,1])\right)$, *that is given by*

$$p(x,t) = a(t)\delta_0 + r(x,t)$$

where r *satisfies*

$$\partial_t r = -\partial_x \left\{x\left[R_0(1-x)-1\right]r\right\} + \frac{\epsilon}{2}\partial_x^2\left\{x(R_0(1-x)+1)r\right\},$$
$$\frac{\epsilon}{2}\left((1-R_0)r(1,t)+\partial_x r(1,t)\right) + r(1,t) = 0$$
$$r(x,0) = r_0 + b_0\delta_1$$

and

$$a(t) = \frac{\epsilon(R_0+1)}{2}\int_0^t r(0,s)\,ds + a_0.$$

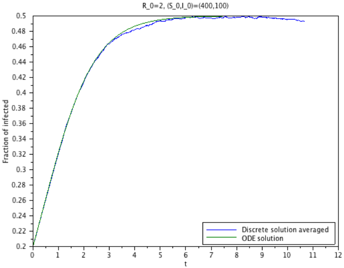
Proposition

Given the representation of p above, we also have

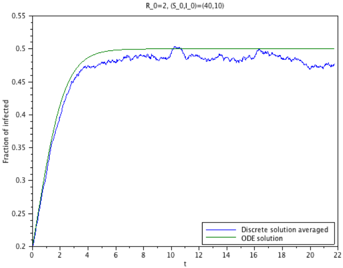
$$\lim_{t\to\infty} r(x,t) = 0 \quad \textit{and} \quad \lim_{t\to\infty} a(t) = 1.$$

In particular,

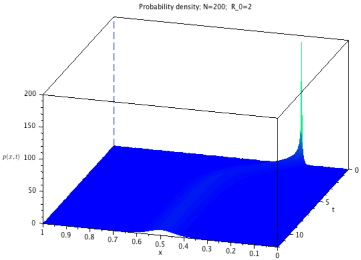
$$\lim_{t\to\infty} p(\cdot,t) = \delta_0$$

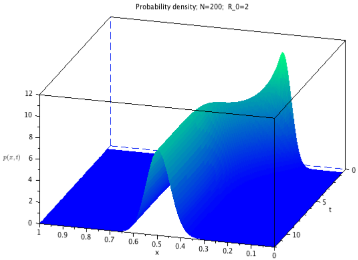


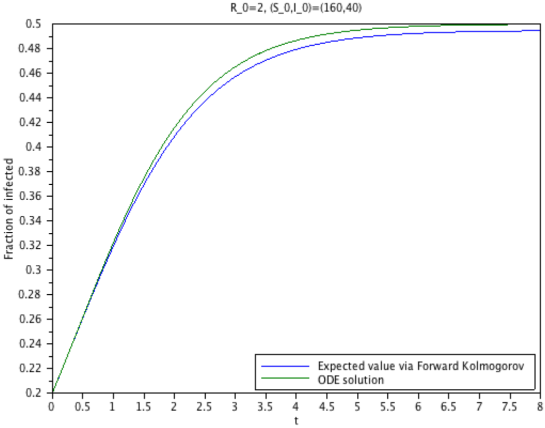
R_0=2, (S_0,I_0)=(400,100)
Fraction of infected
t
Discrete solution averaged
ODE solution



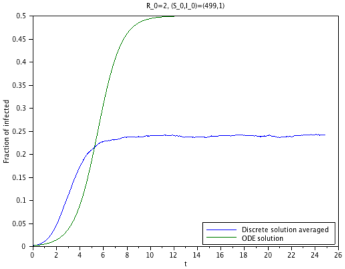
R_0=2, (S_0,I_0)=(40,10)
Fraction of infected
t
Discrete solution averaged
ODE solution

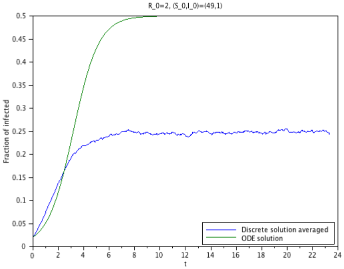

Probability density; N=200; R_0=2
$p(x,t)$
200
150
100
50
0
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
x
t
5
10

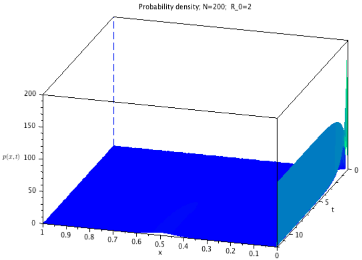

Probability density; N=200; R_0=2
$p(x,t)$
12
10
8
6
4
2
0
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
x
t
5
10

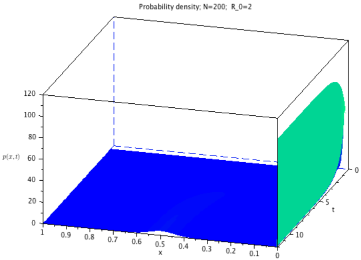


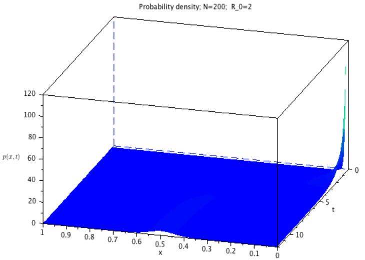
R_0=2, (S_0,I_0)=(160,40)
Fraction of infected
t
Expected value via Forward Kolmogorov
ODE solution
0.5
0.48
0.46
0.44
0.42
0.4
0.38
0.36
0.34
0.32
0.3
0.28
0.26
0.24
0.22
0.2
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
6.5
7
7.5
8

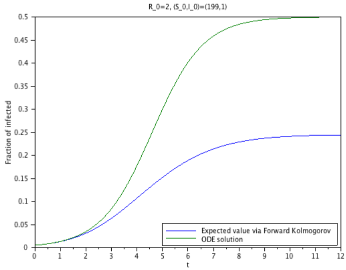

R_0=2, (S_0,I_0)=(499,1)
Fraction of infected
t
Discrete solution averaged
ODE solution

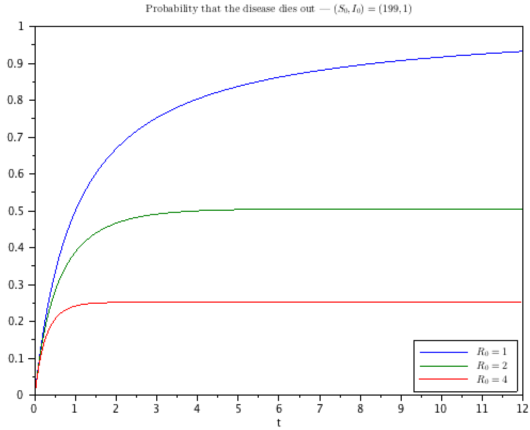

R_0=2, (S_0,I_0)=(49,1)
Fraction of infected
t
Discrete solution averaged
ODE solution


Probability density; N=200; R_0=2
200
150
100
50
0
$p(x,t)$
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
x
0
5
10
t


Probability density; N=200; R_0=2
120
100
80
60
40
20
0
$p(x,t)$
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
x
0
5
10
t


Probability density; N=200; R_0=2
p(x,t)
x
t


R_0=2, (S_0,I_0)=(199,1)
Fraction of infected
t
Expected value via Forward Kolmogorov
ODE solution



Probability that the disease dies out — $(S_0, I_0) = (199, 1)$
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0 1 2 3 4 5 6 7 8 9 10 11 12
t
$R_0 = 1$
$R_0 = 2$
$R_0 = 4$

- For the Moran process an inverse numerical analysis argument yields

$$
\begin{aligned}
& -\int_0^\infty \int_0^1 p(x,t)\partial_t g(x,t)\,\mathrm{d}x\,\mathrm{d}t - \int_0^1 p(x,t_0)g(x,t_0)\,\mathrm{d}x \\
& = \frac{\kappa}{2}\int_0^\infty \int_0^1 p(x,t)\left(x(1-x)\partial^2 g(x,t)\right)\,\mathrm{d}x\,\mathrm{d}t \qquad (4) \\
& \quad + \int_0^\infty \int_0^1 p(x,t)\left[x\left(\psi(x)-\bar{\psi}(x)\right)\partial g(x,t)\right]\mathrm{d}x\,\mathrm{d}t.
\end{aligned}
$$

- $p(x,t) = a(t)\delta_0 + q(x,t) + b(t)\delta_1$, with q being the unique L^2 classical solution to (4).

- Also
$$\lim_{t\to\infty} q(x,t) = 0.$$

Additionally, we have the following conservation laws:

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_0^1 p(x,t)\,\mathrm{d}x = 0 \quad \text{and} \quad \frac{\mathrm{d}}{\mathrm{d}t}\int_0^1 \phi(x)p(x,t)\,\mathrm{d}x = 0,$$

$$\phi'' + x\left(\psi(x) - \bar{\psi}(x)\right)\phi' = 0, \quad \phi(0) = 0, \quad \phi(1) = 1.$$

- Results extended to multidimensional Wright-Fisher process via measure solutions.
- Similar derivation for infinite population limit of SIR model
- Derivation of three Holling functional responses for Lotka type predator-prey models.
- Approximation of slow manifold via center-manifold theory in other scalings.
- Multiscale reduction for Wolbachia models recovering invasion thresholds by Turelli et al.

References

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Thank You!