Formation of spatial patterns in an epidemic model with constant removal rate of the infectives

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Abstract. This paper addresses the question of how population diffusion affects the formation of the spatial patterns in the spatial epidemic model by Turing mechanisms. In particular, we present a theoretical analysis of results of the numerical simulations in two dimensions. Moreover, there is a critical value for the system within the linear regime. Below the critical value the spatial patterns are impermanent, whereas above it stationary spot and stripe patterns can coexist over time. We have observed the striking formation of spatial patterns during the evolution, but the isolated ordered spot patterns do not emerge in the space.

Keywords: pattern formation (theory), pattern formation (experiment), population dynamics (theory), population dynamics (experiment)

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1. Introduction

The dynamics of spontaneous spatial pattern formation, first introduced to biology by Turing [1] five decades ago, has recently been attracting attention in many subfields of biology to describe various phenomena. Non-equilibrium labyrinthine patterns are observed in chemical reaction–diffusion systems with a Turing instability [2] and in bistable reaction–diffusion systems [3, 4]. Such dynamic patterns in a two-dimensional space have recently been introduced into ecology [5–9]. In the past few years, geophysical patterns over a wide range of scales for vegetation have been presented and studied in [10–14] using the Turing mechanisms.

In epidemiology, one of the central goals of mathematical epidemiology is to predict in populations how diseases transmit in space. For instance, the SARS epidemic spread through 12 countries within a few weeks. The classical epidemic SIR model describes the infection and recovery process in terms of three ordinary differential equations for susceptibles (S), infected (I) and recovered (R), which has been studied by many researchers [15–18] and the reference cited therein. These systems depend mainly on two parameters, the infection rate and the recovery rate.

A growing body of work reports on the role of spatial patterns on evolutionary processes in the host population structure [19–25]. Recent studies have shown large-scale spatiotemporal patterns in measles [26] and dengue fever (DF) [27, 28]. More dramatically the wave is often caused by the diffusion (or invasion) of a virus within the population in a given spatial region, thus generating periodic infection, which has been observed in the occurrence of dengue hemorrhagic fever (DHF) in Thailand [29]. Existing theoretical work on pathogen evolution and spatial pattern formation has focused on a model in which local invasion to the susceptible hosts plays a central role [20, 21, 25]. Projections of the spatial spread of an epidemic and the interactions of human movement at multiple levels with a response protocol will facilitate the assessment of policy alternatives. Spatially
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explicit models are necessary to evaluate the efficacy of movement controls [30, 31]. A wide variety of methods have been used for the study of spatially structured epidemics, such as cellular automata [32–34], networks [35, 36], metapopulations [37, 38], diffusion equations [39–41] and integro-differential equations, which are useful tools in the study of geographic epidemic spread. In particular, spatial models can be used to estimate the formation of spatial patterns in large scale and the transmission velocity of diseases, and in turn guide policy decisions.

This paper addresses how diffusive contacts and diffusive movement affect the formation of spatial patterns in two dimensions. The diffusion term is from the earlier work that can be traced back to Fisher and Kolmogorov. Noble applied diffusion theory to the spread of bubonic plague in Europe [42]. Noble’s model relies on the assumptions that disease transmits through interactions between dispersing individuals and infected individuals move in uncorrelated random walks. In light of the Turing theoretical model and study of recent spatial models, we investigate the formation of spatial patterns in the spatial SIR model based on the study of a non-spatial SIR model with constant removal rate of the infectives [15].

2. Model

2.1. Basic model

We consider, as the basic model, the following susceptible–infected–recovery (SIR) model

\[
\frac{dS}{dt} = A - dS - \lambda SI, \tag{1a}
\]

\[
\frac{dI}{dt} = \lambda SI - (d + \gamma)I - h(I), \tag{1b}
\]

\[
\frac{dR}{dt} = \gamma I + h(I) - dR, \tag{1c}
\]

where \(S(t)\), \(I(t)\) and \(R(t)\) denote the numbers of susceptible, infective and recovered individuals at time \(t\), respectively. \(A\) is the recruitment rate of the population (such as growth rate of average population size, a recover becomes an susceptible, immigrant and so on), \(d\) is the natural death rate of the population, \(\gamma\) is the natural recovery rate of the infective individuals and \(\lambda\) is a measure of the transmission efficiency of the disease from susceptibles to infectives. In equation (1), \(h(I)\) is the removal rate of infective individuals due to the treatment. We suppose that the treated infectives become recovered when they are treated in treatment sites. We also suppose that

\[
h(I) = \begin{cases}
  r, & \text{for } I > 0, \\
  0, & \text{for } I = 0,
\end{cases} \tag{2}
\]

where \(r > 0\) is constant and represents the capacity of treatment for infectives. The detail about model (1) can be found in [15].

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2.2. Spatial model

Next we intend to add the spatial parts. Up to the first approximation, the dispersal of individuals can be taken random, so that Fick’s law holds. This gives the flux terms as

$$\frac{\partial S}{\partial t} = D_s \nabla^2 S, \quad \frac{\partial I}{\partial t} = D_i \nabla^2 I, \quad \frac{\partial R}{\partial t} = D_r \nabla^2 R,$$

(3)

where $\nabla^2$ ($\nabla^2 = \partial^2 / \partial x^2 + \partial^2 / \partial y^2$) is the Laplacian operator in Cartesian coordinates. $D_s$, $D_i$ and $D_r$ are the diffusion coefficients of the susceptible, infective and recovered, respectively. Incorporating spatial terms into equation (1), it becomes

$$\frac{\partial S}{\partial t} = A - dS - \lambda SI + D_s \nabla^2 S,$$

(4a)

$$\frac{\partial I}{\partial t} = \lambda SI - (d + \gamma)I - h(I) + D_i \nabla^2 I,$$

(4b)

$$\frac{\partial R}{\partial t} = \gamma I + h(I) - dR + D_r \nabla^2 R.$$

(4c)

Generally, we are concerned with the susceptible and infective individuals. Moreover equations (4a) and (4b) are independent of equation (4c) whose dynamic behaviour is trivial when $I(t_0) = 0$ for some $t_0 > 0$. So it suffices to consider equations (5a) and (5b) with $I > 0$. Thus, we restrict our attention to the following reduced spatial model

$$\frac{\partial S}{\partial t} = A - dS - \lambda SI + D_s \nabla^2 S,$$

(5a)

$$\frac{\partial I}{\partial t} = \lambda SI - (d + \gamma)I - r + D_i \nabla^2 I.$$

(5b)

It is assumed that all the parameters are positive constants from the biological point of view.

3. Theoretical analysis of spatial patterns and results

To study the mechanism of the formation of spatial patterns, firstly, we analyse the stability criterion of the local system. This can be obtained from [15]. The system (5) has two positive equilibrium points if $R_0 > 1$ and $0 < H < (\sqrt{R_0} - 1)^2$, where $R_0 = \lambda A / d(d + \gamma)$ and $H = \lambda r / d(d + \gamma)$. The two positive equilibrium points are $E_1 = (S_1, I_1)$ and $E_2 = (S_2, I_2)$, where

$$I_1 = \frac{d}{2\lambda} (R_0 - 1 - H - \sqrt{(R_0 - 1 - H)^2 - 4H}),$$

$$S_1 = A / (d + \lambda I_1),$$

$$I_2 = \frac{d}{2\lambda} (R_0 - 1 - H + \sqrt{(R_0 - 1 - H)^2 - 4H}),$$

$$S_2 = A / (d + \lambda I_2).$$

Diffusion is often considered a stabilizing process, yet it is the diffusion-induced instability in a homogeneous steady state that results in the formation of spatial patterns in a reaction–diffusion system [1]. The stability of any system is expressed by the
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eigenvalues of the system’s Jacobian matrix. The stability of the homogeneous steady state requires that the eigenvalues have negative real parts. To ensure this negative sign, the trace of the Jacobian matrix must be less than zero at steady state if the determinant is greater than zero.

The Jacobian matrix of system (1) at \((S_2, I_2)\) is

\[
J_2 = \begin{pmatrix}
-d - \lambda I_2 & -\lambda S_2 \\
\lambda I_2 & \lambda S_2 - d - \gamma
\end{pmatrix}.
\]

From [43], we easily know that there is the Turing space in the system (5) at point \(E_2\), but at point \(E_1\) there is no Turing space.

3.1. Stability of the positive equilibrium point in the spatial model

In contrast to the local model, we employ the spatial model in a two-dimensional (2D) domain, so that the steady-state solutions are 2D functions. Let us now discuss the stability of the positive equilibrium point with respect to perturbations. Turing proves that it is possible for a homogeneous attracting equilibrium to lose stability due to the interaction of diffusion processes. To check under what conditions these Turing instabilities occur in the model (5), we test how perturbation of a homogeneous steady-state solution behaves in the long-term limit. Here we choose perturbation functions consisting of the following 2D Fourier modes

\[
\hat{s} = \exp((k_x x + k_y y)i + \delta_k t),
\]

(7a)

\[
\hat{i} = \exp((k_x x + k_y y)i + \delta_k t).
\]

(7b)

Since we will work with the linearized form of equation (5) and the Fourier modes are orthogonal, it is sufficient to analyse the long-term behaviour of an arbitrary Fourier mode.

After substituting \(S = S_2 + \hat{s}\) and \(I = I_2 + \hat{i}\) in equation (5), we linearize the diffusion terms of the equations via a Taylor expansion about the positive equilibrium point \(E_2(S_2, I_2)\) and obtain the characteristic equation

\[
(J_{sp} - \delta_k I) \cdot \begin{pmatrix}
\hat{s} \\
\hat{i}
\end{pmatrix} = 0,
\]

(8)

with

\[
J_{sp} = \begin{pmatrix}
j_{11} & j_{12} \\
j_{21} & j_{22}
\end{pmatrix} = \begin{pmatrix}
-d - \lambda I_2 & -\lambda S_2 \\
\lambda I_2 & \lambda S_2 - d - \gamma
\end{pmatrix},
\]

(9)

here \(j_{11} = -d - \lambda I_2, j_{12} = -\lambda S_2, j_{21} = \lambda I_2\) and \(j_{22} = \lambda S_2 - d - \gamma\). \(k^2 = k_x^2 + k_y^2\) and \(k\) represents the wavenumbers.

To find Turing instabilities we must focus on the stability properties of the attracting positive equilibrium point \(E_2(S_2, I_2)\). The loss of stability occurs if at least one of the eigenvalues of the matrix \(J_{sp} - \delta_k I\) crosses the imaginary axis. From equations (8) and (9), we can obtain the characteristic equation

\[
\det(J_{sp} - \delta_k I) = \delta_k^2 - \text{tr}(J_{sp}) \delta_k + \det(J_{sp}) = 0,
\]

(10)
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Figure 1. These graphs illustrate the eigenvalues of the spatial model (5) at positive equilibrium point $E_2(S_2, I_2)$, and the loss of stability occurs in relation to the limit range wavenumbers. (a) For diffusion-driven instability to arise both $\text{tr}(J_{sp})$ and $\text{det}(J_{sp})$ must be negative for some range of $k^2$. (b) The real parts of the eigenvalues of matrix (9) at positive equilibrium $(S_2, I_2)$. Model parameters used here are: $A = 3$, $d = 0.3$, $\lambda = 0.35$, $r = 0.5$, $\gamma = 0.8$, $D_s = 0.02$ and $D_i = 0.0005$.

where $\text{tr}(J_{sp}) = \text{tr}(J_2) - (D_s + D_i)k^2$ and $\text{det}(J_{sp}) = \text{det}(J_2) - k^2(j_{11}D_i + j_{22}D_s) + k^4D_sD_i$.

Taking $\text{tr}(J_2) > \text{tr}(J_{sp})$ into account, we can obtain that, for saddles and attractors (both with respect to the non-spatial model), a change of stability coincides with a change of the sign of $\text{det}(J_{sp})$.

Doing some calculations we find that a change of the sign of $\text{det}(J_{sp})$ occurs when $k^2$ takes the critical values

$$k_-^2 = \frac{j_{11}D_i + j_{22}D_s - \sqrt{(j_{11}D_i + j_{22}D_s)^2 - 4D_sD_i\text{det}(J_2)}}{2D_sD_i}, \quad (11a)$$

$$k_+^2 = \frac{j_{11}D_i + j_{22}D_s + \sqrt{(j_{11}D_i + j_{22}D_s)^2 - 4D_sD_i\text{det}(J_2)}}{2D_sD_i}. \quad (11b)$$

In particular, we have

$$\text{det}(J_{sp}) < 0 \iff k_-^2 < k^2 < k_+^2. \quad (12)$$

If both $k_-^2$ and $k_+^2$ exist and have positive values, they limit the range of instability for a local stable equilibrium. We refer to this range as the Turing space (or Turing region, see figure 1).

In figure 1, the real parts of the eigenvalues of the spatial model (5) at positive equilibrium point $E_2(S_2, I_2)$ are plotted. From equations (7a) and (7b), we know that the parameter $\delta_k$ can either be a real number or a complex number. If it is a real number, the spatial patterns will emerge and be stable over time and otherwise the spatial patterns will die away quickly. In both case, the sign of the real parts of $\delta_k$ (written as $\text{Re}(\delta_k)$) is crucially important to determine whether the patterns will grow or not. In particular if $\text{Re}(\delta_k) > 0$, spatial patterns will grow in the linearized system because $|e^{\delta_k t}| > 1$, but if $\text{Re}(\delta_k) < 0$ the perturbation decays because $|e^{\delta_k t}| < 1$ and the system returns to the homogeneous steady state. Further details concerning linear stability analysis can be

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Figure 2. The graphs illustrate Turing space versus the parameter $\lambda$ and $r$, respectively. In the Turing space $k_-$ and $k_+$ curves are shown, respectively. Left: the bifurcation diagrams show the formation of the two stationary solutions of equation (5) with fixed $r$ and varying $\lambda$, and values of the parameters are $A = 3$, $d = 0.3$, $r = 0.5$, $\gamma = 0.8$, $D_s = 0.02$, and $D_l = 0.0005$; in the lower diagram, the green dashed line represents the loss of stability for the positive equilibrium. The red line represents the stable equilibrium. Right: the values of the parameters are $A = 3$, $d = 0.3$, $\lambda = 0.35$, $\gamma = 0.8$, $D_s = 0.02$ and $D_l = 0.0005$.

found in [44]. Figure 1 presents the typical situation of Turing instability. With respect to homogeneous perturbations, $E_2(S_2, I_2)$ is stable at first, but when $k^2$ increases, one eigenvalue changes its sign (when $k^2$ arrives at $k^2_-$), the instability occurs. The instability exist until $k^2$ reaches $k^2_+$. When $k^2$ is over $k^2_+$, $(S_2, I_2)$ returns stability again. Thus the Turing space is bounded between $k^2_-$ and $k^2_+$. The change of the bounds $k_-$ and $k_+$ with respect to the variation of the $\lambda$ and $r$ are illustrated in figure 2, respectively. The typical feature of Turing space in the model (5) can be observed in figure 2. The Turing space is limited by two different bounds. From figure 2 (left-top) we can see that $k_-$ and $k_+$ converge in one point A which corresponds to the critical value, $\lambda_c$. Beyond the right bound (line $a$), the $E_2(S_2, I_2)$ exists and is stable. The left bound (line $b$) of the Turing space shows an ‘open end’, which corresponds to the saddle-node in the bifurcation plot (see figure 2 (left-bottom)) for the model (1) and the equilibrium point $E_2(S_2, I_2)$ does not exist under this bound. This figure shows the solutions of equilibrium points $I_1$ and $I_2$, where the solid curves represent attractors, the dashed curve represents the repellers and saddles, while the dotted line $a$ represents the periodic points. This diagram explains the $E_2(S_2, I_2)$ changes from repeller to attractor, and an unstable orbit of periodical points emerges. From figure 2 (right), the curves indicates that $k_-$ and $k_+$ converge in one point (A). Below that bound, the $E_2(S_2, I_2)$ exists and is stable. The right bound of the Turing space also shows an ‘open end’.

Comparing to the two graphs in figure 2, one can obtain that the parameters $\lambda$ and $r$ have a similar dynamical behaviour in the system for the Turing bifurcation, but their effects are opposite. We use the parameter $\lambda$ as the Turing bifurcation parameter in the present paper. Figure 3 shows growth rate curves of the spatial patterns, where at bifurcation (curve b), $\lambda = \lambda_c \approx 0.547$ (the threshold $\lambda_c$ can be derived analytically, see the appendix. The analytical and numerical values of $\lambda_c$ are approximately equal),

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Figure 3. Basic dispersion relation giving the growth rate \( \text{Re}(\delta_k) \) as a function of the wavenumber \( k^2 \). The mode become marginal at the point \((H, \lambda = \lambda_c)\), a finite-\(k^2\) (Turing) mode. The parameter values are \( A = 3, d = 0.3, r = 0.5, \gamma = 0.8, D_h = 0.02 \) and \( D_t = 0.0005 \).

from spatially uniform to spatially heterogeneous the critical wavenumber (point \( H \)) is \( k_c = \sqrt{k_{xc}^2 + k_{yc}^2} \). The curves \( a \) and \( c \) correspond to the parameter \( \lambda = 0.35 \) below the \( \lambda_c \), and \( \lambda = 0.8 \) above the \( \lambda_c \), respectively. The spatial patterns are generated when \( \lambda \) passes through the critical Turing bifurcation point \( \lambda_c \). And for \( \lambda < \lambda_c \) there is a finite range of unstable wavenumbers which grow exponentially with time, \( O(\exp(\delta_k t)) \), where \( \delta_k > 0 \) for a finite range of \( k \).

The stable characteristics of \( E_2(S_2, I_2) \) can be changed by the variation of parameter \( \lambda \); a sufficiently high increase of \( \lambda \) will turn \( E_2(S_2, I_2) \) into an attractor. When changing its characteristics, \( E_2(S_2, I_2) \) traverses a subcritical Hopf bifurcation and an unstable periodic orbit emerges (the dotted line \( a \) in figure 2 (left)). Surprisingly, the latter is not necessarily true, if the effect of diffusion comes into play.

3.2. Spatial patterns of the spatial model

The numerical simulations are performed in this section for the spatial model (5) in two dimensions. During the simulation, the periodic boundary conditions are used and part of the parameter values can be determined following [15] (see figures 1 and 2). We assume that the homogeneous \( E_2(S_2, I_2) \) distributions are in uniform states for each start of the simulation. To induce the dynamics that may lead to the formation of spatial patterns, we perturb the \( I \) distribution by small random values.

We study the spatial model (5) by performing stable analysis of the uniform solutions and by integrating equations (5a) and (5b) numerically at different values of \( \lambda \) on a grid of 100 \times 100 sites by a simple Euler method with a time step of \( \Delta t = 0.01 \). The results for the infected are summarized below in two dimensions. The model has a uniform free-disease state (no infected) for all constant values of \( \lambda \), represented by the solution \( S = A/d, I = 0 \). The free-disease state is stable when \( \lambda < \lambda_c \). Here \( \lambda_c \) is a critical value (or threshold) corresponding to the dotted line \( b \) in figure 2 (left). Above \( \lambda_c \) two new states appear, shown in figure 2 (left) as lines \( I_1 \) and \( I_2 \). The state \( I_2 \) represents a uniformly distributed population with infected density monotonically increasing with \( \lambda \). It is unstable only for relative values of \( \lambda \), \( \lambda_c < \lambda < \lambda_c \) and regains stability when \( \lambda > \lambda_c \), where the infected
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Figure 4. Snapshots of contour pictures of the time evolution of $I(x,y,t)$ at different instants. (a)–(c) Numerical results in $100 \times 100$ sites. The parameter values are $A = 3$, $d = 0.3$, $r = 0.5$, $\gamma = 0.8$, $\lambda = 0.65$, $D_s = 0.02$, $D_l = 0.0005$ and $\Delta x = \Delta y = 0.05$. (A) 0 iteration; (B) 5000 iterations; (C) 30000 iterations; (D) 40000 iterations. (See also movie.)

density is high. The types of spatial patterns are dependent on the range of parameter $\lambda$ as in figures 4–6. Movies of figures 4–6 are also available.

We test several different initial states within the linear regime and the nonlinear regime respectively. Figures 4 and 5 show that stationary stripe and spot patterns emerge mixed in the distribution of the infected population density, where the $\lambda$ is above $\lambda_c$ in the linear regime. The initial state of figure 4 is the random perturbation of the stable uniform infected state. The initial state of figure 5 consists of a few spots (100 scattered spots). Values of the parameters are the same in both figures. In the linear regime, the result shows that the stripes and spots which describe asymptotic patterns for the spatial model (5) converge at long times. Different initial states may lead to the same type of asymptotic patterns, but the transient behaviours are obviously different (compare figure 4(b) with 5(b)). Unfortunately, the linear predictions are not accurate in the nonlinear regime.

Figure 6 shows the snapshots of spatial patterns when the $\lambda$ is between $\lambda_{c'}$ and $\lambda_c$. One can see that the spatial patterns resemble figures 4 and 6 at the beginning phase, but differ in the middle and last phases. In figure 6, the spatial patterns appear spotted, holed and labyrinthine states in the middle phases, and the spatial patterns appear uniform spatial states in the last phase.

To explain spatial patterns arising from the spatial model, here we present some observations of the spatial and temporal dynamics of dengue hemorrhagic fever epidemics.
Dengue fever (DF) is an old disease that became distributed worldwide in the tropics during the 18th and 19th centuries. Figure 7 shows spotted and labyrinth-like spatial patterns of DHF from the field observations [45]. By comparing figures 4 and 5 with figure 7, our results simply capture some key features of the complex variation and explain the observation in spatial structure to most vertebrate species, including humans. In figures 4 and 5, the steady spatial patterns indicate the persistence of the epidemic in the space. This result agrees well with the field observation. More examples of the spatial patterns of epidemic, such as HIV and poliovirus, one can find in [46,47]. In the light of recent work of emphasizing the existence of ‘small world’ networks in human population, our results are also consistent with Boots and Sasaki’s conclusion that if the world is getting ‘small’—as populations become more connected—disease may evolve a higher virulence [20].

4. Discussion

In our paper, the labyrinthine patterns are found in the spatial epidemic model driven by the diffusion. The spatial epidemic model comes from the classical non-spatial SIR model which assumes that the epidemic timescale is so tiny related to the demographic timescale that demographic effects may be ignored. But here in the spatial model we take the births and deaths into account. The spatial diffusive epidemic model is more realistic than the classical model. For instance, the history of bubonic plague describes the movement of the disease from place to place carried by rats. The course of an infection usually cannot
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Figure 6. Snapshots of contour pictures of the time evolution of $I(x, y, t)$ at different instants. The parameters values are the same as figure 4 but $\lambda = 0.5$. (A) 0 iteration; (B) 1500 iterations; (C) 8500 iterations; (D) 9400 iterations. (See also movie.)

Figure 7. Field observations of DHF spatial patterns. Reprinted from Trends In Microbiology, [45], Copyright (2002), with permission from Elsevier. Aedes aegypti distribution in the Americas: 1930s, 1970 and 2001.

be modelled accurately without some attention to its spatial spread. To model this would require partial differential equations (PDE), possibly leading to descriptions of population waves analogous to disease waves which have often been observed. Here our spatial model is established from a basic dynamical ‘landscape’ rather than other perturbations, including environmental stochastic variations. From the analysis of the Turing space and numerical simulations one can see that the attracting positive equilibrium will produce

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instability driven by the diffusion and the instability leads to the labyrinthine patterns within the Turing space. This may explain the prevalence of disease in large-scale geophysics. The positive equilibrium is stable in the non-spatial models, but it may lose its stability with respect to perturbations of certain wavenumbers and converge to heterogeneous distributions of populations. It is interesting that we have not observed the isolated spots patterns in the spatial epidemic model (5).

The model (5) is introduced in a general form so that it has broad applications to a range of interacting populations. For example, it can be applied to diseases such as measles, AIDS, flu, etc. Our paper focuses on the deterministic reaction–diffusion equations. However, recent study shows noise plays an important role on the epidemic model [48, 49], which indicates that the noise induces sustained oscillations and coherence resonance in the SIR model.

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Appendix

Considering the dispersive relation associated with equations (7a) and (7b), the functions of \( \delta_k \) for the spatial model are defined by the characteristic equation (10). Now \( \text{Re}(\delta_k) \) predicts the unstable wave modes from equation (10). One can estimate the most unstable wavenumber and the critical value of the bifurcation parameter by noticing that at the onset of the instability \( \delta_k(k_c) = 0 \). Thus the constant term in equation (10) must be zero at \( k_c \). In the case of the spatial model this condition is a second-order equation on \( k_c^2 \), i.e.

\[
D_s D_i k_c^4 - k_c^2 ( -d - \lambda I_2) D_i + (\lambda S_2 - d - \gamma) D_s \\
+ ( -d - \lambda I_2)(\lambda S_2 - d - \gamma) + \lambda^2 S_2 I_2 = 0.
\]

(A.1)

And as a result the most unstable wavenumber is given by \( \frac{(-d-\lambda I_2)D_s+(\lambda S_2-d-\gamma)D_i}{2D_s D_i} \). The critical Turing bifurcation parameter value, which corresponds to the onset of the instability, is defined by equation (A.1). In the spatial model \( \lambda \) is the bifurcation parameter adjusting the distance to the onset of the instability. The discriminant of equation (A.1) equals zero for \( \lambda_c \) and an instability takes place for \( \lambda < \lambda_c \). Then, we have

\[
\lambda_c = \frac{(D_s S_2 + D_i I_2 + 2\sqrt{D_s D_i S_2 I_2}) (D_s \gamma + D_s d - D_i d)}{(D_i I_2 - D_s S_2)^2},
\]

(A.2)

where \( S_2 = S_2(\lambda_c) \) and \( I_2 = I_2(\lambda_c) \). We can calculate \( \lambda_c \) from equation (A.2) by computer.

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