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Notas de Matemática
Serie: Pre-Print
No. 232

Mérida - Venezuela
2004

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The second author gratefully acknowledges support from CDCHT of Universidad de Los Andes. The comments and constructive criticisms of the anonymous referee were very helpful for improving the manuscript

Abstract

In the present paper we study the effect of the diffusion on the stability of the endemic equilibrium in a SIS epidemiological model with disease-induced mortality and nonlinear incidence rate, and see under which parameter values Turing instability can occur giving rise to non-uniform stationary solutions.

1 Introduction

The role of spatial dispersal on epidemic systems and the study of the spatio-temporal dynamics of a population during an epidemic have been the subject of research for many scientists, see for instance [?, ?, ?, ?, ?, ?].

As stated by Mollison [?], one of the key questions in the study of mathematical models for animal and plant diseases concerns endemic patterns. Motivated by this question, the focus of this work is to find out if spatial pattern formation can be a dynamical feature of an epidemiological model.

In this paper, we examine the geotemporal evolution of a population in a SIS epidemiological model, in which the population is assumed to be divided in two interacting classes of individuals, namely susceptibles S and infectives I. To introduce the spatial dispersal of the population in the model, we assume that the susceptible and infective individuals are diffusing randomly through space with diffusion coefficients d_1 and d_2, respectively. The validity and the importance of investigating the spatial effect in epidemic systems modelled with a diffusion or random walk mechanism has been asserted by Murray [?], Capasso [?, ?], and Metz and van den Bosch [?]. The approach of modelling the spatial spread of a population with the diffusion equation was introduced by Skellam [?], and has been found to be a useful tool in population dynamics and epidemics [?, ?, ?, ?, ?, ?, ?, ?, ?]. In this paper, we focus on the study of the effect of spatial diffusion on the stability of the endemic equilibrium of the population, and answer the question of whether or not the model exhibits pattern formation. The mechanism by which diffusion can have a destabilizing effect that might result in heterogeneous space-dependent structures is usually called Turing instability or diffusion-driven instability [?, ?], and the idea dates back to Turing's work, [?], in the 1950's.

The epidemiological model to be considered assumes that infectives can die from the disease with a disease-induced mortality rate αI, where $1/\alpha$ is the life expectancy of an infective. The effect of the disease-induced mortality in the dynamics of epidemiological models was studied by Anderson and May [?], and the consideration of this rate causes the total population of the epidemic system not to be constant, but rather a dynamical variable [?, ?, ?].

The standard incidence rate considered in epidemic models is bilinear, and is given by βSI, where β is the transmission rate. In this paper, we consider a more general nonlinear incidence rate of the disease, namely $\beta S^q I^p$, where q and p are constant parameters describing the incidence rate. This type of incidence rate was first considered by Severo [?]. Capasso and Serio [?] suggested that the bilinear case should be regarded as a special case of an infection rate of the form $g(I)S$, where the force of infection $g(I)$ is constrained such that $g'(0)$ is positive and finite, but this excludes the form βSI^p if $p \neq 1$. It was Liu et al. [?, ?] who provided a thorough analysis of the dynamical behaviour of epidemiological models with nonlinear incidence rate $\beta S^q I^p$, and explained the possible mechanisms leading to such incidence rates. After their work, many scientists have considered this type of incidence rate in the study of the dynamics of epidemiological models, for example, [?, ?, ?, ?].

With the assumptions explained above in mind, we propose the following system of reaction-diffusion equations subject to Neumann boundary conditions as a model for the spatial spread of the disease

$$\begin{aligned} \frac{\partial S(t,x)}{\partial t} &= d_1 \Delta S - \beta S^q I^p - bS + \gamma I + a(S+I)\,, \\ \frac{\partial I(t,x)}{\partial t} &= d_2 \Delta I + \beta S^q I^p - (\alpha + b + \gamma) I\,, \\ \frac{\partial S}{\partial \eta} &= \frac{\partial I}{\partial \eta} = 0 \quad \text{on } \partial\Omega\,, \end{aligned} \tag{1.1}$$

where $p \geq 1$ and $q \geq 1$ are constants describing the incidence rate of the disease; a is the birth rate of the population and the model is assuming that new individuals are born in the susceptible class; b is the mortality rate of the population affecting both the susceptibles and infected; γ is the recovery rate and α represents the mortality caused by the disease. Here Δ is the Laplacian operator, $\Omega \subset \mathbb{R}^n$ is a bounded region with a smooth boundary $\partial\Omega$, η is the outer normal vector to $\partial\Omega$, and $(t,x) \in \mathbb{R}^+ \times \Omega$. The Neumann boundary condition indicates that there is no population flux on the boundary.

The goal of this paper is to describe a possible mechanism for the existence of endemic geographical foci during the disease. In particular, we study the conditions under which the intrinsic epidemiological parameters and the diffusion of the population destabilize the homogeneous endemic equilibrium, giving rise to nonhomogeneous steady-state solutions (pattern formation).

The main results of this paper are stated in Theorem 4.1, where we prove the destabilizing effect of the diffusion on the homogeneous endemic equilibrium, and in Theorems 5.1 and 6.1, where we prove the existence of heterogeneous steady-state solutions via Turing bifurcation, and analize their stability.

2 Preliminaries

In this section we show that the reaction-diffusion system (1.1) generates a dynamical system and is biologically well posed on a suitable Banach space.

Let

$$F_1(S,I) = -\beta S^q I^p - bS + \gamma I + a(S+I)\,, \quad F_2(S,I) = \beta S^q I^p - (\alpha+b+\gamma)I\,, \tag{2.1}$$

$U = (S,I)\,,\ F = (F_1,F_2)\,,$ and $D =$ diag$[d_1,d_2]$. System (1.1) can be rewritten as

$$\begin{aligned} &\frac{\partial U(t,x)}{\partial t} = D\Delta U(t,x) + F(U), \quad t>0\ ,\ x\in\Omega\ ,\\ &\frac{\partial U}{\partial \eta} = 0, \quad t>0\ ,\ x\in\partial\Omega\ ,\\ &U(0,x) = \varphi(x), \quad x\in\Omega\ , \end{aligned} \tag{2.2}$$

where we have included the initial condition $U(0,x) = \varphi(x)$. We let X be the Banach space $X_1 \times X_2$, where $X_i = C(\bar{\Omega}), i = 1,2$. The norm on X is defined by $|\varphi| = |\varphi_1| + |\varphi_2|$. Let A_S^0 and A_I^0 be the differential operators $A_S^0 S = d_1\Delta S$ and $A_I^0 I = d_2\Delta I$ defined on the domains $D(A_S^0)$ and $D(A_I^0)$, respectively, where

$$\begin{aligned} D(A_S^0) &= \{S\in C^2(\Omega)\cap C^1(\bar{\Omega}) : A_S^0 S\in C(\bar{\Omega}), \frac{\partial S}{\partial\eta}(x) = 0, x\in\partial\Omega\}\ ,\\ D(A_I^0) &= \{I\in C^2(\Omega)\cap C^1(\bar{\Omega}) : A_I^0 I\in C(\bar{\Omega}), \frac{\partial I}{\partial\eta}(x) = 0, x\in\partial\Omega\}\ . \end{aligned}$$

The closures A_S of A_S^0, and A_I of A_I^0 in X_i generate analytic semigroups of bounded linear operators $T_S(t)$ and $T_I(t)$ for $t\geq 0$.

Moreover, if $\mathcal{T}(t) = T_S(t)\times T_I(t) : X\to X$, then $\mathcal{T}(t)$ is a semigroup of operators on X generated by the operator $\mathcal{A} = A_S\times A_I$ defined on $D(\mathcal{A}) = D(A_S)\times D(A_I)$ and $U(t,x) = [\mathcal{T}(t)\varphi](x)$ is a classical solution of the initial boundary value problem (2.2) with $F_1 = F_2 = 0$.

The nonlinear term F is twice continuously differentiable in U since $p,q\geq 1$. Therefore, we can define the map $[F^*(\varphi)](x) = F(\varphi(x))$ which maps X into itself and equation (2.2) can be viewed as the abstract O.D.E. in X given by

$$u'(t) = \mathcal{A}u(t) + F^*(u(t))\ , \quad u(0) = \varphi\ . \tag{2.3}$$

While a solution $u(t)$ of (2.3) can be obtained under the restriction that $\varphi\in D(\mathcal{A})$, a mild solution can be obtained for every $\varphi\in X$ by requiring only that $u(t)$ is a continuous solution of the integral equation

$$u(t) = \mathcal{T}(t)\varphi + \int_0^t \mathcal{T}(t-s)F^*(u(s))ds\ . \tag{2.4}$$

Restricting our attention to functions φ in the set

$$X_\Lambda = \{\varphi\in X : \varphi(x)\in\Lambda\ ,\ x\in\bar{\Omega}\}\ ,$$

where $\Lambda = \{U = (S, I) \in \mathbb{R}^2 : S \geq 0 \ , \ I \geq 0\}$, and taking into account the definition of the functions F_i, we obtain that $F_1(0, I) \geq 0$ and $F_2(S, 0) = 0$ for $U \in \Lambda$. Thus, corollary 3.2, p.129 in [?] implies that the Nagumo condition for the positive invariance of Λ is satisfied, i.e.,

$$\lim_{h \to 0^+} h^{-1} \text{dist}(\Lambda, v + hF(v)) = 0 \ , \quad v \in \Lambda \ , \tag{2.5}$$

and that the linear semigroup $\mathcal{T}(t)$ leaves X_Λ positively invariant, i.e.,

$$\mathcal{T}(t) X_\Lambda \subset X_\Lambda \quad , \quad t \geq 0 \ . \tag{2.6}$$

Finally, Nagumo condition (2.5) together with (2.6) allow us to apply theorem 3.1, p.127 in [?], to obtain

THEOREM 2.1

For each $\varphi \in X_\Lambda$, (2.2) *has a unique mild solution* $u(t) = u(t, \varphi) \in X_\Lambda$ *and a classical solution* $U(t, x) = [u(t)](x)$. *Moreover, the set* X_Λ *is positively invariant under the flow* $\Psi_t(\varphi) = u(t, \varphi)$ *induced by* (2.2).

Thus, the model (1.1) is biologically well posed and its relevant dynamic is concentrated in X_Λ .

3 Endemic equilibrium

In this section we will study system (1.1) without diffusion, i.e.,

$$S'(t) = F_1(S, I) \ , \quad I'(t) = F_2(S, I) \ , \tag{3.1}$$

where $F_1(S, I)$ and $F_2(S, I)$ are as in (2.1), and focus our attention on the existence of *endemic equilibria* (nontrivial equilibria with positive I), and their local stability.

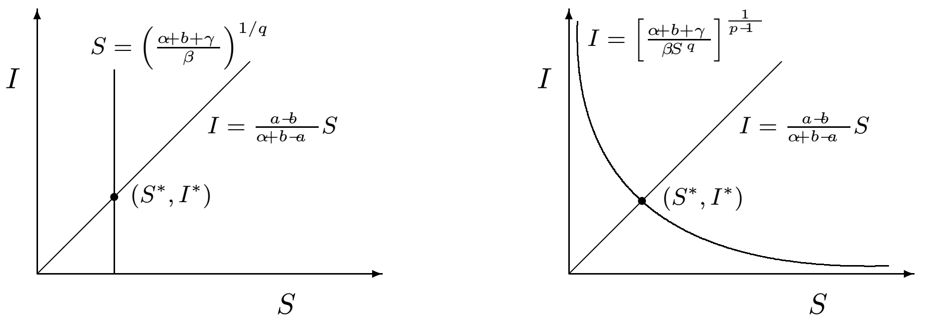
Summing the two equations in (3.1) provides the equation for the total population

$$N'(t) = (a - b)N - \alpha I \ . \tag{3.2}$$

Thus, the total population is not a constant, as traditionally assumed. Epidemiological models with population of varying size have been studied, for example, by Busenberg and van den Driessche [?], and by Derrick and van den Driessche [?]. Also, it is worthwhile to mention that system (3.1) with a bilinear incidence rate βSI was proposed by Anderson and May [?], and is presented by Capasso [?] as a basic example for epidemic models with nonconstant total population.

In the absence of a mortality rate caused by the disease, and assuming a greater birth rate than a mortality rate, i.e., $\alpha = 0$ and $a > b$, the population will grow indefinitely. Therefore, we could think of the disease as regulating the growth of the population. For this reason, we will assume from here on that $\alpha > a - b > 0$.

By equating the right hand side of both equations in (3.1) to zero, it becomes clear that there is a trivial equilibrium $(S_0, I_0) = (0, 0)$, and a direct computation shows that this equilibrium is a saddle point. Also, we note that the nullclines of (3.1) change depending on the parameter p.



A: Endemic equilibrium for $p = 1$ **B:** Endemic equilibrium for $p > 1$

Figure 1: Endemic Equilibrium.

For $p = 1$ the system has a unique endemic equilibrium (S^*, I^*), determined by the intersection of the curves

$$S = \left(\frac{\alpha + b + \gamma}{\beta}\right)^{1/q}, \qquad I = S\frac{a-b}{\alpha + b - a},$$

in the (S, I) plane (Figure 1 A), whereas for $p > 1$, the unique endemic equilibrium (S^*, I^*) is determined by the intersection of the following curves (Figure 1 B):

$$I = \left[\frac{\alpha + b + \gamma}{\beta S^q}\right]^{\frac{1}{p-1}}, \qquad I = S\frac{a-b}{\alpha + b - a},$$

where $\frac{a-b}{\alpha+b-a}$ is the ratio of two positive numbers.

To study the local stability of the endemic equilibrium, we denote $A(p) = (A_{ij}(p))_{i,j=1,2} = F'(S^*, I^*)$, where $F'(S^*, I^*)$ is the Jacobian matrix of F evaluated at (S^*, I^*), i.e.,

$$A(p) = \begin{pmatrix} -q\dfrac{a-b}{\alpha+b-a}(\alpha+b+\gamma) + a - b & -p(\alpha+b+\gamma) + a + \gamma \\ \\ q\dfrac{a-b}{\alpha+b-a}(\alpha+b+\gamma) & (p-1)(\alpha+b+\gamma) \end{pmatrix}. \tag{3.3}$$

The equilibrium (S^*, I^*) is locally asymptotically stable if the zeroes of the characteristic polynomial

$$\lambda^2 - \text{trace}A(p)\lambda + \det A(p) = 0 \tag{3.4}$$

have negative real part.

Case $p = 1$

For this case,

$$\text{trace}A(1) = A_{11}(1) = -q\frac{a-b}{\alpha+b-a}(\alpha+b+\gamma) + a - b < 0,$$

and

$$\det A(1) = -A_{12}(1)A_{21}(1) = -q\frac{a-b}{\alpha+b-a}(\alpha+b+\gamma)(a-b-\alpha) > 0.$$

Therefore, the zeroes of the characteristic polynomial (3.4) have negative real part, and the unique endemic equilibrium (S^*, I^*) is asymptotically stable.

This result can be strengthened to global stability in the region $G = \{(S, I) \, : S \geq 0, I > 0\}$. To prove this, we will

(i) rule out the existence of periodic orbits in G, and

(ii) show that any positive orbit Γ^+ in G is bounded.

To prove (i), let us assume that (3.1) with $p = 1$ admits a ω periodic solution $(S(t), I(t))$. It is known that one multiplier is 1 and the other is given by $\rho = \exp(\int_0^\omega \text{div}F(S(t), I(t))dt)$, where

$$\text{div}F(S(t), I(t)) = -\beta q S^{q-1} I + (a - b) + \beta S^q - (\alpha + b + \gamma) \ .$$

From (3.1), we obtain

$$I'/I = \beta S^q - (\alpha + b + \gamma) \ .$$

Integrating from 0 to ω the previous equation and taking into account that $\int_0^\omega dI/I = 0$, it follows that

$$\int_0^\omega \beta S^q dt = (\alpha + b + \gamma)\omega \ .$$

Thus,

$$\int_0^\omega \text{div}F(S(t), I(t))dt = -\beta q \int_0^\omega S^{q-1} I + (a - b)\omega \ .$$

Also, from (3.1),

$$S'/S = -\beta S^{q-1} I + (a - b) + (a + \gamma) I/S \ .$$

Denoting $M = \min\{I(t)/S(t), t \in [0, \omega]\} > 0$, and using $q \geq 1$, we obtain that

$$S'/S \geq -\beta q S^{q-1} I + (a - b) + (a + \gamma)M.$$

Integrating the last inequality from 0 to ω, and taking into account that $\int_0^\omega S'/S = 0$, it follows that

$$-\beta q \int_0^\omega S^{q-1} I dt + (a - b)\omega \leq -(a + \gamma)\Delta\omega.$$

This implies that $\int_0^\omega \text{div}F(S(t), I(t))dt < 0$, and $\rho < 1$.

Therefore, if the system (3.1) with $p = 1$ admits a periodic solution, it will be orbitally asymptotically stable. Assuming that such periodic solution exists, the endemic equilibrium (proved to be asymptotically stable) must lie in the region bounded by the periodic orbit. This forces the existence of an unstable periodic solution in that region, which is a contradiction. Therefore, the system (3.1) with $p = 1$ does not admit periodic solutions.

We now provide a geometrical dynamical argument, illustrated in Figure 2, to prove (ii). Throughout the argument, the nonexistence of periodic orbits is assumed. Let

$$C_1 : \, S = S^* \ , \quad C_2 : \, I = f(S) \ , \quad C_3 : \, I = g(S) \ ,$$

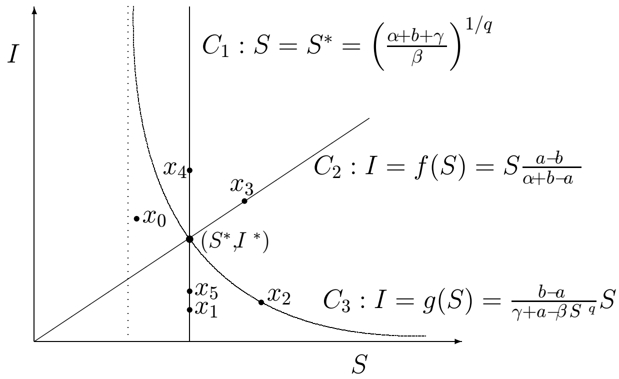


Figure 2: If the positive orbit $\Gamma^+(x_0)$ attempted to become unbounded, the worst-case scenario would be described by a bounded trajectory that passes through x_1, x_2, x_3, x_4 and x_5. See text for details.

denote the nullcline $I' = 0$, the curve determined by $N' = 0$, and the nullcline $S' = 0$, respectively, where $S^* = \left(\frac{\alpha+b+\gamma}{\beta}\right)^{1/q}$, $f(S) = S\frac{a-b}{\alpha+b-a}$ and $g(S) = \frac{b-a}{\gamma+a-\beta S^q}S$ (Figure 2). Consider, without loss of generality, an initial condition $x_0 = (S_0, I_0)$ such that $S_0 < S^*$, and $I_0 < g(S)$. Since $I' < 0$ whenever $S < S^*$, either the positive orbit $\Gamma^+(x_0) = \{(S(t;x_0), I(t;x_0)) : t \geq 0\}$ stays to the left of C_1 and $\lim_{t\to\infty}(S(t;x_0), I(t;x_0)) = (S^*, I^*)$, in which case (ii) is proved, or the orbit crosses C_1 at a point x_1 (Figure 2). If the latter happens, we note that because $I' > 0$ whenever $S > S^*$ and $\lim_{S\to\infty} \frac{b-a}{\gamma+a-\beta S^q}S = 0$, either the positive orbit stays below C_3 and $\lim_{t\to\infty}(S(t;x_0), I(t;x_0)) = (S^*, I^*)$ (and (ii) will be proved), or the orbit crosses C_3 at a point x_2

(Figure 2). If this last case happens, note that because $S' < 0$ whenever $I > g(S)$, either $\lim_{t\to\infty}(S(t;x_0), I(t;x_0)) = (S^*, I^*)$, in which case (ii) is proved, or the positive orbit $\Gamma^+(x_0)$ crosses the straight line C_2 at a point x_3 (Figure 2). If the latter is the case, we denote the value of the total population $N = S + I$ at x_3 by K, and use the fact that for (S, I) above C_2, $N' = (S + I)' < 0$, to show that the positive orbit $\Gamma^+(x_0)$ lies below $I = K - S$ and therefore has to cross again C_1 at a point x_4 (Figure 2). Now, using again the fact that $I' < 0$ whenever $S < S^*$, the orbit either goes from x_4 to the endemic equilibrium without crossing C_1 (and (ii) will be proved), or it crosses again at a point x_5. If x_5 is above x_1 then the positive orbit will be bound, and that would end our proof of (ii) (Figure 2). To see that this is, indeed, the case, we assume that x_5 is below x_1, and consider the α-limit set $\alpha(\Lambda)$ of an orbit Λ of any point lying in the segment of line joining x_5 and x_1, and conclude that $\alpha(\Lambda) = \{(S^*, I^*)\}$, which is a contradiction because the endemic equilibrium is locally asymptotically stable.

Thus, by using the Poincaré-Bendixon theorem [?], we conclude that since there are no periodic orbits and any positive orbit Γ^+ in $G = \{(S, I) : S \geq 0, I > 0\}$ of (3.1) with $p = 1$ is bounded, the ω-limit set $\omega(\Gamma^+) = \{(S^*, I^*)\}$, i.e., the endemic equilibrium is globally asymptotically stable.

Case $p > 1$

For this case,

$$\det A(p) = q\frac{b-a}{a-b-\alpha}(\alpha+b+\gamma)(\alpha+b-a)+(a-b)(p-1)(\alpha+b+\gamma) > 0 ,$$

Therefore, the endemic equilibrium (S^*, I^*) will be locally asymptotically stable if trace$A(p) < 0$, which is the case iff

$$q > q^* = (p-1)\frac{\alpha+b-a}{a-b} + \frac{\alpha+b-a}{\alpha+b+\gamma} ,$$

and trace$A(p) = 0$ at $q = q^*$, where the system undergoes a Hopf bifurcation. We can summarize these results as follows

THEOREM 3.1

Let us assume $\alpha > a - b > 0$.

i) If $p = 1$, *the system* (3.1) *has a unique endemic equilibrium* (S^*, I^*) *and it is globally asymptotically stable in the region* $G = \{(S, I) : S \geq 0, I > 0\}$.

ii) If $p > 1$, *the system* (3.1) *has a unique endemic equilibrium* (S^*, I^*) *and it is asymptotically stable if* $q > q^*$ *and unstable if* $q < q^*$, *where*

$$q^* = (p-1)\frac{\alpha+b-a}{a-b} + \frac{\alpha+b-a}{\alpha+b+\gamma} .$$

4 Turing instability

Hereafter, we will assume that $x \in \mathbb{R}$. Hence, the system (2.2) becomes

$$\begin{aligned} U_t &= DU_{xx} + F(U) , \\ U_x(t,0) &= U_x(t,L) = 0 . \end{aligned} \tag{4.1}$$

This section will be devoted to analyzing the stability of the family of nontrivial equilibria $U^* = (S^*, I^*)$ of system (3.1), understood as homogeneous steady-state solutions of (4.1). The following definition of Turing instability or diffusion-driven intability [?], will be used throughout this paper.

DEFINITION 4.1 *The equilibrium* U^* *of* (4.1) *is said to be diffusionally (Turing) unstable if it is an asymptotically stable equilibrium of* (3.1) *but it is unstable with respect to* (4.1) .

The stability of a homogeneous stationary solution U^* of (3.1) will be studied via linearized stability analysis. According to Casten & Holland [?], the steady-state solution U^* is an asymptotically stable solution of (4.1) if for each integer $n \geq 0$ the eigenvalues of

$$B_n(p) = A(p) - \lambda_n D \tag{4.2}$$

have negative real parts, where $A(p)$ is as defined in (3.3), and $\lambda_n = \left(\frac{n\pi}{L}\right)^2$ are the eigenvalues of the scalar equation

$$\Phi'' = -\lambda\Phi , \quad \Phi'(0) = \Phi'(L) = 0 , \tag{4.3}$$

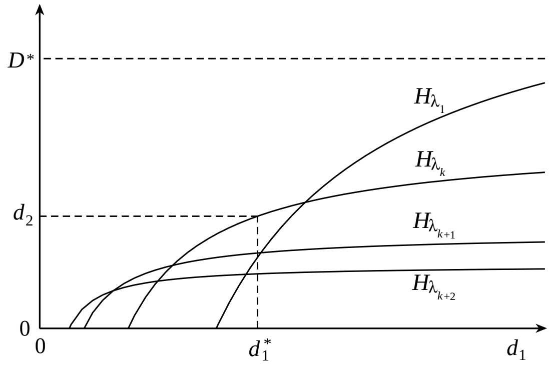


Figure 3: Turing instabity. If a pair (d_1, d_2) lies below a hyperbola H_{λ_n}, the homogeneous steady-state $U^* = (S^*, I^*)$ is unstable. When $d_2 < D^*$, the uniform steady-state solution U^* of (4.1) undergoes a Turing bifurcation at $d_1 = d_1^*$.

where prime denotes differentiation with respect to x. Following the idea in [?] of keeping all the parameters constant except the diffusion coefficients, we will study the stability in the (d_1, d_2) plane. The following theorem gives detailed information on the stability of the homogeneous stationary solution U^*.

Theorem 4.1

Let us assume that $\alpha > a - b > 0$.

i) If $p = 1$ and $q \geq 1$, then the unique homogeneous stationary solution U^* of (4.1) is asymptotically stable for both systems (3.1) and (4.1).

ii) If

(a) $p > 1$,

(b) $q > q^* = (p-1)\dfrac{\alpha + b - a}{a - b} + \dfrac{\alpha + b - a}{\alpha + b + \gamma}$, and

(c) $0 < d_2 < D^*$, where $D^* = (p-1)(\alpha + b + \gamma)\frac{L^2}{\pi^2}$,

then $d_1 > d_2$ can be chosen such that the homogeneous steady-state solution U^* of (4.1) is diffusionally unstable. Moreover, there exists a $k \in \mathbb{N}$ such that the homogeneous stationary solution U^* becomes unstable for perturbations in the k^{th} eigenmode, i.e. with wavenumber $\sqrt{\lambda_k} = k\pi/L$, as d_1 passes through

$$d_1^* = \frac{A_{12}(p)A_{21}(p) + A_{11}(p)(\lambda_k d_2 - A_{22}(p))}{\lambda_k^2 d_2 - A_{22}(p)\lambda_k}. \tag{4.4}$$

iii) If $p > 1$ and $1 \leq q < q^*$, then the homogeneous steady-state solution U^* is unstable for both systems (3.1) and (4.1).

Proof.-
Case $p = 1$

From (3.3), we know that $A_{22}(1) = 0$, $\text{trace}A(1) = A_{11}(1) < 0$ and $\det A(1) = -A_{12}(1)A_{21}(1) > 0$. Taking this into account, we obtain that $\text{trace}B_n(1) = A_{11}(1) - \lambda_n(d_1 + d_2) < 0$ and $\det B_n(1) = (A_{11}(1) - \lambda_n d_1)(-\lambda_n d_2) - A_{21}(1)A_{12}(1) > 0$ for any $n \geq 0$. Therefore, U^* is asymptotically stable for both systems (3.1) and (4.1), no matter what the values of the diffusion coefficients are.

Case $p > 1$
From Theorem 3.1, we know that the $\text{trace}A(p) > 0$, for $q < q^*$. Hence, $\text{trace}B_0(p) = \text{trace}A(p) > 0$, which implies that the homogeneous steady-state solution U^* is unstable for both systems (3.1) and (4.1), for $q < q^*$.

Also from Theorem 3.1, $\det A(p) > 0$, $\text{trace}A(p) < 0$ and $A_{11}(p) < 0$, for $q > q^*$. Therefore,

$$\text{trace}B_n(p) = \text{trace}A(p) - \lambda_n(d_1 + d_2) < 0 \,, \tag{4.5}$$

and Turing instability may occur only if

$$\det B_n(p) = (\lambda_n d_1 - A_{11}(p))(\lambda_n d_2 - A_{22}(p)) - A_{21}(p)A_{12}(p) \leq 0 \,, \tag{4.6}$$

for some $n \geq 1$. Let

$$H_{\lambda_n} \,:\, (\lambda_n d_1 - A_{11}(p))(\lambda_n d_2 - A_{22}(p)) - A_{21}(p)A_{12}(p) = 0 \tag{4.7}$$

denote the family of hyperbolas in the (d_1, d_2) plane (Figure 3). Isolating d_2 in (4.7), we obtain

$$d_2 = \frac{A_{12}(p)A_{21}(p) + (\lambda_n d_1 - A_{11}(p))A_{22}(p)}{\lambda_n(\lambda_n d_1 - A_{11}(p))} \,. \tag{4.8}$$

Now, if $d_1 \to \infty$ the right hand side of (4.8) will increase and tend to $\frac{A_{22}(p)}{\lambda_n} = \frac{(p-1)(\alpha+b+\gamma)L^2}{(n\pi)^2}$. Thus, for $n = 1$, $\frac{A_{22}(p)}{\lambda_1} = D^*$ (see Figure 3). It is clear that the set of $(d_1, d_2) \in \mathbb{R}^2_+$ satisfying (4.6) for some $n \in \mathbb{N}$ consists of all points which are below the graph of the hyperbola H_{λ_n} (Figure 3). Since $0 < d_2 < D^*$, there exists a $k \in \mathbb{N}$ such that (d_1^*, d_2) belongs to the hyperbola H_{λ_k}, where d_1^* is as in Eq. (4.4). Moreover, if $d_1 > d_1^*$ then (d_1, d_2) will lie below of the graph of H_{λ_k} and the homogeneous steady-state solution $U^* = (S^*, I^*)$ will be diffusionally unstable. □

For the purpose of performing numerical simulations and showing that the results of Theorem 4.1 are relevant for diseases, we choose realistic parameter values. In particular, we choose the estimations obtained by Anderson and May [?], who fitted real data obtained by Greenwood et al. [?, ?] in their experiments on the maintenance of pasteurellosis, *Pasteurella muris*, in mouse populations. The parameter values are as follows:

$$\alpha = 0.06 \,,\; \beta = 0.0056 \,,\; \gamma = 0.04 \,,\; a = 0.05 \,,\; b = 0.006 \text{ days}^{-1} \,.$$

We choose the values $p = 2$ and $q = 1$ for the incidence rate $\beta S^q I^p$. These are the standard values for p and q that are used by Liu et al. [?, ?], and Derrick and van den Driessche [?, ?] for their numerical simulations of epidemic models with nonlinear incidence rate. The possible mechanisms leading to this type of incidence rate are discussed in Liu et al. [?, ?]. With this choice of parameter values, we obtain that $q^* = 0.515$ and $D^* = 4.3$, where q^* and D^* are as in Theorem 4.1. To ensure that diffusion driven instability is possible, conditions (a), (b) and

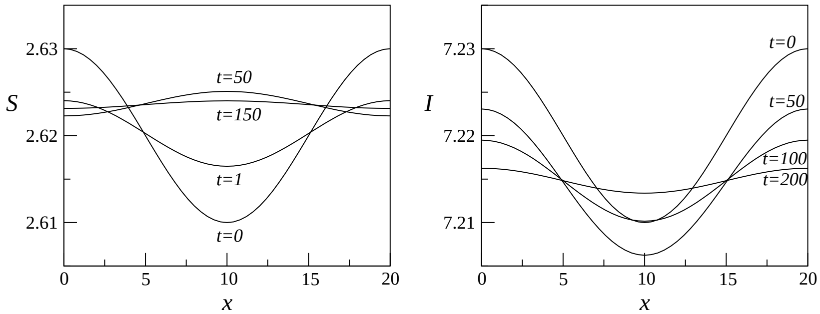


Figure 4: Evolution of (S, I) after perturbating the stable steady-state $(S^*, I^*) = (2.624, 7.215)$. Initial condition $(S_0, I_0) = (S^* + 0.01\,\cos(2\pi x/20), I^* + 0.01\,\cos(2\pi x/20))$; $d_1 = 5$, $d_2 = 0.7$.

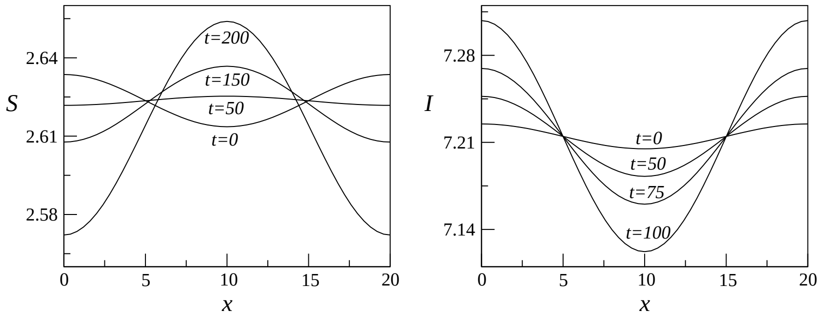


Figure 5: Evolution of (S, I) after perturbating the unstable steady-state $(S^*, I^*) = (2.624, 7.215)$. Initial condition $(S_0, I_0) = (S^* + 0.01\,\cos(2\pi x/20), I^* + 0.01\,\cos(2\pi x/20))$; $d_1 = 20$, $d_2 = 0.7$.

(c) in Theorem 4.1 ii) must be satisfied. Since $p = 2$ and $q = 1$, conditions (a) and (b) are satisfied. To guarantee that condition (c) is satisfied, we will assume that infective individuals move randomly with a diffusion coefficient less than D^*. This is a reasonable assumption because one can think of the disease as weakening the mobility of infective individuals. Moreover, since the objective of this paper is not to obtain a measurement for the spatial dispersal of the specific disease studied by Anderson and May [?], or any other particular disease, but rather to present a possible dynamical mechanism for the existence of epidemic spatial patterns, we assume, without loss of generality, a diffusion coefficient $d_2 = 0.7 < D^*$ for the infectives and a space of 20 units of longitude. To illustrate the destabilizing effect of the diffusion in model (1.1), we perturb the homogeneous steady-state found for our choice of parameter values, $(S^*, I^*) = (2.624, 7.215)$, with a cosine mode of wave number $\sqrt{\lambda_k} = \frac{k\pi}{L}$, where $k = 2$. For this particular mode, $d_1^* = 7.25$ (Eq. (4.4)). Thus, by choosing $d_1 = 5 < d_1^*$, we see from Figure 4, that the homogeneous steady-state (S^*, I^*) is stable, while a choice of $d_1 = 20 > d_1^*$ (Figure 5) causes the stationary solution to become unstable. Note that if a need of a realistic interpretation of the numerical simulations is felt, it suffices to assign units to the space and diffusion coefficients.

5 Pattern Formation

In this section we study the mechanism by which the diffusion-driven instability phenomenon gives rise to nonhomogeneous steady-state solutions of (4.1) that bifurcate from the uniform stationary solution. Consider the following reaction diffusion system

$$\begin{aligned} U_t &= D(\mu)\, U_{xx} + F^*(U,\mu)\ , \\ U_x(t,0) &= U_x(t,L) = 0\ , \end{aligned} \tag{5.1}$$

where $U \in \mathbb{R}^2$, D is a 2×2 nonnegative diagonal matrix depending smoothly on the real parameter $\mu \in [0,\infty)$ and $F^* : \mathbb{R}^2 \times [0,\infty) \to \mathbb{R}^2$ is a smooth function. Assume that U^* is a uniform stationary solution of (5.1), i.e. $F^*(U^*,\mu) = 0$ for all $\mu \in [0,\infty)$.

Definition 5.1 *We say that U^* undergoes a Turing bifurcation at $\mu_0 \in (0,\infty)$ if the solution U^* changes its stability at μ_0 and in some neighborhood of μ_0 there exists a one-parameter family of nonconstant stationary solutions of system* (5.1)*.*

Having shown in Theorem 4.1 that U^* becomes unstable as d_1 passes through d_1^*, we will prove in Theorem 5.1 that the bifurcation is a Turing bifurcation. To obtain the nonhomogeneous stationary solutions of (4.1) we will apply the results regarding the bifurcation from a simple eigenvalue found in [?, ?] and summarized in theorems 13.4 and 13.5 in [?].

Following the notation in system (5.1) we take d_1 as the bifurcation parameter and set $F^* = F$. The following result holds:

Theorem 5.1

Let $B_n(p)$ be as in (4.2)*. Let us denote their eigenvalues by λ_{1n} and λ_{2n}, and the corresponding eigenvectors by v_{1n} and v_{2n}. Assume that*

(a) $\alpha > a - b > 0$, $p > 1$ and $q > q^*$ (where q^* is as in Theorem 3.1), i.e., restrict parameters where diffusion-driven instability might occur, and

(b) $0 < d_2 < D^*$, where $D^* = (p-1)(\alpha + b + \gamma)\dfrac{L^2}{\pi^2}$.

Then there exists a $k \in \mathbb{N}$ such that if v_{2k} is not parallel to $(\xi_1, 0)^T$, where $v_{1k} = (\xi_1,\xi_2)^T$, the uniform steady-state solution U^* of (4.1) *undergoes a Turing bifurcation at (see Figure 3)*

$$d_1^* = \frac{A_{12}(p)A_{21}(p) + A_{11}(p)(\lambda_k d_2 - A_{22}(p))}{\lambda_k^2 d_2 - A_{22}(p)\lambda_k}\ . \tag{5.2}$$

Proof.-

By setting $W = U - U^*$, where U^* is a nontrivial homogeneous steady-state solution of (4.1), system (4.1) can be rewritten as

$$\begin{aligned} W_t &= D\, W_{xx} + A(p)W + G(W)\ , \\ W_x(t,0) &= W_x(t,L) = 0\ . \end{aligned} \tag{5.3}$$

where $A(p)$ is the Jacobian matrix of F at U^*, and $G(W) = F(U^* + W) - A(p)W$. With this notation, the nontrivial homogeneous steady-state has been translated to a trivial homogeneous steady-state, and the reaction term has been split into its linear and nonlinear components.

For any non-homogeneous stationary solution U^* of (4.1), $W = U - U^*$ satisfies the elliptic equation

$$\begin{aligned} D\,W_{xx} + A(p)W + G(W) = 0 \,, \\ W_x(t,0) = W_x(t,L) = 0 \,. \end{aligned} \tag{5.4}$$

Taking into account this observation, we define the function $f : \mathbb{R} \times X \to Y$ as follows

$$f(d_1, W) = D\,W_{xx} + A(p)W + G(W) \,,$$

where $X = \{W \in C^2([0,L], \mathbb{R}^2)\,;\ W_x(0) = W_x(L) = 0\}$ is a Banach space with the usual supremum norm involving the first and second derivatives, $Y = C([0,L], \mathbb{R}^2)$ is a Banach space with the usual supremum norm, and d_1 is the diffusion coefficient of the susceptible class.

Note that since $0 < d_2 < D^*$, there exists a $k \in \mathbb{N}$ such that (d_1^*, d_2) belongs to the hyperbola H_{λ_k} and is above the hyperbolas H_{λ_n} for $n \neq k$ (see Figure 3), where d_1^* is given precisely by (5.2).

Now, we define the linear operators L_0 and L_1 as follows

$$L_0 = D_2 f(d_1^*, 0) = \frac{\partial f(d_1^*, 0)}{\partial W} \,, \quad L_1 = D_1 D_2 f(d_1^*, 0) = \frac{\partial}{\partial d_1}\left(\frac{\partial f}{\partial W}\right)(d_1^*, 0) \,.$$

In order to apply theorem 13.5 in [?], we need to prove that the following conditions hold:

(i) The null subspace $N(L_0)$ is one-dimensional, spanned by u_0.

(ii) The range $R(L_0)$ has codimension 1; i.e., $\dim[Y/R(L_0)] = 1$

(iii) $L_1 u_0 \notin R(L_0)$.

The spectrum of the linear operator L_0 is given by the eigenvalues λ_{in} of the matrices $B_n(p) = A(p) - \lambda_n D$ evaluated at $d_1 = d_1^*$, where $i = 1, 2$ and $n = 0, 1, 2, \ldots$. We know that (d_1^*, d_2) belongs to the hyperbola H_{λ_k} and is above the hyperbolas H_{λ_n} for $n \neq k$ (Figure 3). This implies, using that $H_{\lambda_n} : \det B_n(p) = 0$ (Eq. (4.7)), that $\det B_n(p) > 0$ for $n \neq k$ and $\det B_k(p) = 0$. Noticing that the eigenvalues λ_{1n} and λ_{2n} of $B_n(p)$ are given by the zeroes of the characteristic polynomial

$$\lambda^2 - \mathrm{trace} B_n(p)\lambda + \det B_n(p) = 0 \,, \tag{5.5}$$

and that $\mathrm{trace} B_n(p) < 0$ (Eq. (4.5)), we conclude that for $i = 1, 2$ and $n = 0, 1, 2, \ldots, k-1, k+1, \ldots$ all eigenvalues λ_{in} have negative real part, and for $n = k$, one eigenvalue, say λ_{1k}, is zero and the other one is negative, i.e., $\lambda_{2k} < 0$.

Recalling that v_{1k} is the eigenvector of $B_k(p)$ corresponding to the zero eigenvalue λ_{1k}, the eigenfunction of the linear operator L_0 corresponding to $\lambda_{1k} = 0$ is given by $\psi_k = v_{1k} \cos\left(\frac{k\pi x}{L}\right)$, which is a non-uniform stationary solution of the linearized system

$$\begin{aligned} W_t = DW_{xx} + A(p)W \,, \\ W_x(t,0) = W_x(t,L) = 0 \,. \end{aligned} \tag{5.6}$$

Therefore, the null subspace $N(L_0)$ of the operator $D_2f(d_1^*,0)$ is one-dimensional, spanned by ψ_k. Because of the orthogonality of the system,

$$\Phi_m = \cos\left(\frac{m\pi x}{L}\right) , \quad m = 0, 1, 2, \dots ,$$

obtained by solving the eigenvalue problem (4.3), the range $R(L_0)$ of this operator is given by

$$R(L_0) = \{U \in C([0,L],\mathbb{R}^2) \ : \text{ The Fourier expansion of } U \text{ does not contain}$$
$$\text{the term } \cos\left(\tfrac{k\pi x}{L}\right)\} \cup \{v_{2k}\cos\left(\tfrac{k\pi x}{L}\right)\} ,$$

and has codimension one. So conditions (i) and (ii) are satisfied.

Note that

$$L_1\psi_k = \begin{pmatrix} \dfrac{\partial^2}{\partial x^2} & 0 \\ 0 & 0 \end{pmatrix} v_{1k}\cos\left(\frac{k\pi x}{L}\right) = -\left(\frac{k\pi}{L}\right)^2 \begin{pmatrix} \xi_1 \\ 0 \end{pmatrix} \cos\left(\frac{k\pi x}{L}\right) ,$$

with $\xi_1 \neq 0$, and $\begin{pmatrix} \xi_1 \\ 0 \end{pmatrix}$ not being parallel to v_{2k}. Therefore, $L_1\psi_{1k} \notin R(L_0)$ and condition (iii) is also satisfied.

Now, by choosing $Z = R(L_0)$ we apply theorems 13.4 and 13.5 in [?] to conclude that there exists a $\delta > 0$ and a C^1 curve $(d,\phi) : (-\delta,\delta) \to \mathbb{R}\times Z$ with $d(0) = d_1^*$ and $\phi(0) = 0$ such that

$$W(s,x) = s v_{1k}\cos\left(\frac{k\pi x}{L}\right) + s\phi(s,x)$$

is a one-parameter family of solutions of the elliptic equation (5.4) with $d_1 = d(s)$, $s \in (-\delta,\delta)$. Finally, taking into account that $W = U - U^*$, we obtain that

$$U(s,x) = U^* + s v_{1k}\, cos\left(\frac{k\pi x}{L}\right) + \mathcal{O}(s^2) \tag{5.7}$$

is a family of non-uniform stationary solutions of (4.1) with $d_1 = d(s)$, and $s \in (-\delta,\delta)$. Therefore, at $d_1 = d_1^*$, the uniform steady-state solution U^* undergoes a Turing bifurcation.□

6 Stability of bifurcating solutions

In this section we will study the stability of the one-parameter family of non-uniform stationary solutions $U(s,x)$ given by (5.7) that bifurcate from the homogeneous steady-state U^*. For this purpose we shall apply the results on perturbation of simple eigenvalues due to Crandall and Rabinowitz [?] to our case.

Definition 6.1 *Let X and Y be Banach spaces and let L_0 and $K \in B(X,Y)$, the set of bounded linear operators. We say that $\mu \in$ is a K-simple eigenvalue of L_0 with eigenfunction ψ if (i) $dim N(L_0 - \mu K) = codim R(L_0 - \mu K) = 1$, (ii) ψ spans $N(L_0 - \mu K)$, and (iii) $K\psi \notin R(L_0 - \mu K)$, where N and R stand for the nullspace and range of an operator (see Crandall and Rabinowitz [?]).*

The importance of this definition stems from the fact that one can determine the sign of K-simple eigenvalues that persist along the bifurcating branches. More concretely, in the proof of Theorem 5.1, we showed that $\lambda_{1k} = 0$ is a L_1-simple eigenvalue of L_0, where $L_1 = D_1 D_2 f(d_1^*, 0)$ and $L_0 = D_2 f(d_1^*, 0)$. Thus, for $|\epsilon|$ and $|s|$ small enough, the operators $D_2 f(d_1^* + \epsilon, 0)$ and $D_2 f(d(s), s\psi_k + s\phi(s,x))$ are close to L_0, and we can apply lemma 1.3 in [?] (or lemma 13.7 in [?]) to conclude that there exist smooth functions

$$d \to (\lambda(d), \psi_c(d)) \ , \quad s \to (\eta(s), \psi_b(s))$$

defined on neighborhoods of d_1^* and 0, respectively, such that

$$D_2 f(d, 0)\psi_c(d) = \lambda(d)\psi_c(d) \ ,$$

$$D_2 f(d(s), s\psi_k + s\phi(s,x))\psi_b(s) = \eta(s)\psi_b(s) \ ,$$

and $(\lambda(d_1^*), \psi_c(d_1^*)) = (0, \psi_k) = (\eta(0), \psi_b(0))$.

To study the stability of the bifurcating solutions we look for the sign of the family of eigenvalues $\eta(s)$. We start by applying theorem 1.16 in [?] (or theorem 13.8 in [?]) to conclude that $\lambda'(d_1^*) \neq 0$, and

$$\lim_{\substack{s \to 0 \\ \eta(s) \neq 0}} \frac{s d'(s) \lambda'(d_1^*)}{\eta(s)} = -1 \ . \tag{6.1}$$

Now, we are ready to state the stability result.

THEOREM 6.1

Let $(d(s), U(s,x))$ be the one-parameter family of bifurcating solutions given by (5.7). Assume that the conditions of Theorem 5.1 are satisfied, $d'(0) \neq 0$, and that the eigenvalues $\eta(s)$ of the nonhomogeneous steady-state bifurcating from the critical value $\lambda_{1k} = 0$ are nonzero for small $|s| \neq 0$. Then if $d(s) < d_1^*$, the corresponding solution $U(s,x)$ is unstable and if $d(s) > d_1^*$, the corresponding solution $U(s,x)$ is stable.

Proof.- We first determine the sign of $\lambda'(d_1^*)$. It is known that $\lambda(d_1)$ satisfies the equation

$$\lambda^2(d_1) - \text{trace} B_k(p)\lambda(d_1) + \det B_k(p) = 0 \ .$$

Differentiating implicitly the former equation with respect to d_1 and evaluating at d_1^*, we obtain

$$\lambda'(d_1^*) = \frac{\lambda_k A_{22}(p) - \lambda_k^2 d_2}{(d_1^* + d_2)\lambda_k - \text{trace} A(p)} \ ,$$

where $\text{trace}A(p) < 0$, and $0 < d_2 < (p-1)(\alpha + b + \gamma)\frac{L^2}{(k\pi)^2}$. Since $\lambda_k A_{22}(p) = \left(\frac{k\pi}{L}\right)^2 (p-1)(\alpha + b + \gamma) > 0$ and $\lambda_k^2 d_2 < \left(\frac{k\pi}{L}\right)^2 (p-1)(\alpha + b + \gamma)$, we obtain that $\lambda'(d_1^*) > 0$.

Let us determine the sign of $\eta(s)$. Since $d'(0) \neq 0$, we may assume that $d'(0) > 0$. Then by continuity we have that $d'(s) > 0$ for $|s|$ small enough. Therefore, using (6.1), it follows that $\eta(s) > 0$ for $s < 0$ small enough, which in turn implies that the bifurcating solution is unstable. For small $s > 0$, $\eta(s) < 0$, and the bifurcating nonhomogeneous stationary solution is asymptotically stable. If $d'(0) < 0$ the same result holds. This completes the proof of our claim.□

7 Discussion

In this paper, we discussed the main mathematical features exhibited by the reaction-diffusion system (1.1). We showed that when the host population is taken to be a dynamic variable and the spatial dispersal of the population is modelled as a diffusion process, nontrivial geotemporal dynamics of the population of infectious can be obtained. In the case when the disease-induced mortality rate α is greater than the difference between the birth rate a and the mortality rate b, we showed that for a wide range of parameter values and diffusion coefficients d_1 and d_2, the nonlinear system (1.1) can exhibit stable spatially heterogeneous solutions which arise from Turing bifurcations. More specifically, if a disease has a simple bilinear incidence rate (βSI), and is described with the SIS model (1.1), then it is not possible to obtain pattern formation, via Turing instability, as a feature of the geotemporal dynamics. On the other hand, if a disease has a strong nonlinear incidence rate ($\beta S^p I^q$, with $p > 1$ and $q \geq 1$), then the system (1.1) may admit spatially heterogeneous steady-state solutions (pattern formation). Also, we showed that if the mobility of the infective population is sufficiently weakened by the disease, the conditions for the system to exhibit spatial patterns will be favored.

In conclusion, the mathematical analysis of model (1.1) shows how an infectious disease, characterized by a nonlinear incidence rate, can stably regulate its host population around either spatially homogeneous or heterogeneous solutions through a Turing instability mechanism.

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