Chapter 11
Turing Instabilities in Reaction–Diffusion Systems with Temporally or Spatially Varying Parameters

In Chap. 10 we considered the Turing instability in systems where the kinetic parameters and the transport coefficients are constant in space and time. While the vast majority of theoretical work on Turing patterns deals with such systems, there are good reasons from applications in biology and ecology to account for the effect of spatial or temporal variations on the threshold of the Turing instability. Chemical or biological systems are rarely completely uniform. Pattern formation in the *Drosophila* egg, for example, occurs in the presence of maternally imposed gradients of gene products [106]. Experimental studies of Turing patterns in the CIMA and CDIMA reactions use continuously fed unstirred reactors (CFURs), see Chap. 12, which unavoidably exhibit gradients in the concentrations of the feed reactants. The problem of determining diffusion-driven instabilities in reacting systems with spatially or temporally varying parameters is in general a rather difficult one. The tools of the linear stability analysis employed in Chap. 10 cannot be extended to such systems, since they do not posses a uniform steady state in most cases. Reaction–diffusion systems with weak heterogeneities can be studied with perturbation techniques [19, 50, 92, 40, 341, 342]. Lengyel and coworkers [249] used an approximation of the reaction–diffusion equation to study the effect of the gradients in CFURs on the position and the possible three-dimensional character of the Turing structures. In general, numerical studies are required to address the problem of Turing patterns in heterogeneous systems, see for example [192, 433, 365, 394, 395, 55]. Voroney and coworkers carried out numerical simulations of the Sel'kov model with a complexing reaction [462]. They considered the case where the immobile complexing species is confined to disks or stripes. If the spatial distribution of the complexing agent varies on a scale small compared to the intrinsic length scales of the reaction–diffusion system, normal Turing pattern formation occurs. If the spatial scales are comparable, interactions between oscillatory behavior and Turing patterns generate spatiotemporal dynamics not observed in a homogeneous medium.

While in general the problem of pattern formation in heterogeneous media is a difficult one, the analysis is more manageable in situations where the spatial or temporal variations in parameters of the reaction–diffusion system do not compromise the existence of a uniform steady state. Such is the case for a varying diffusion

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coefficient. In that situation, a uniform steady state exists, but the standard tools of bifurcation theory cannot be applied.

11.1 Turing Instability with Time-Varying Diffusivities

Ecological systems can display temporal oscillations in parameter values due to seasonal variations. The effects of time-varying diffusivities on the Turing instability were first considered by Timm and Okubo [436] in a predator–prey model describing the interaction between zooplankton and phytoplankton. Temporal variations in the horizontal diffusion coefficients arise from the interaction of vertical current shear with vertical mixing processes.

Consider the two-variable system

$$\frac{\partial \rho_u}{\partial t} = D_u \frac{\partial^2 \rho_u}{\partial x^2} + F_1(\rho_u, \rho_v), \tag{11.1a}$$

$$\frac{\partial \rho_v}{\partial t} = D_v(t) \frac{\partial^2 \rho_v}{\partial x^2} + F_2(\rho_u, \rho_v), \tag{11.1b}$$

with no-flow boundary conditions (10.20) on the interval $[0, L]$. For simplicity, we assume that only one of the diffusion coefficients is time-dependent, namely the diffusivity of the inhibitor,

$$D_v(t) = D_u[\theta + \epsilon \sin(\omega t)], \tag{11.2}$$

with

$$\theta > 1, \quad \theta > |\epsilon|\,. \tag{11.3}$$

We impose the first inequality in (11.3), since a Turing instability can occur in a two-variable reaction–diffusion system with constant parameters only if $\theta_{RD} > 1$. The second inequality ensures the positivity of $D_v(t)$. We assume that the system (11.1) possesses a uniform steady state, $(\overline{\rho}_u(x), \overline{\rho}_v(x)) = (\overline{\rho}_u, \overline{\rho}_v)$, with $F_1(\overline{\rho}_u, \overline{\rho}_v) = F_2(\overline{\rho}_u, \overline{\rho}_v) = 0$, which fulfills the stability conditions (10.23), and U is an activator and V an inhibitor.

To assess the stability of the uniform steady state, we carry out a linear stability analysis. We set

$$\rho_u(x, t) = \overline{\rho}_u + \delta_u(t) \cos(kx), \tag{11.4a}$$

$$\rho_v(x, t) = \overline{\rho}_v + \delta_v(t) \cos(kx), \tag{11.4b}$$

and obtain the linearized evolution equations

$$\frac{d\delta_u(t)}{dt} = [J_{11} - k^2 D_u]\delta_u(t) + J_{12}\delta_v(t), \tag{11.5a}$$

$$\frac{d\delta_v(t)}{dt} = J_{21}\delta_u(t) + [J_{22} - k^2 D_v(t)]\delta_v(t). \tag{11.5b}$$

We rescale time, $\tau \equiv \omega t$, and find

$$\frac{d\delta_u(\tau)}{d\tau} = \hat{J}_{11}\delta_u(\tau) + \hat{J}_{12}\delta_v(\tau), \tag{11.6a}$$

$$\frac{d\delta_v(\tau)}{d\tau} = \hat{J}_{21}\delta_u(\tau) + \hat{J}_{22}(\tau)\delta_v(\tau), \tag{11.6b}$$

with

$$\hat{J}_{11} = [J_{11} - k^2 D_u]\omega^{-1}, \tag{11.7a}$$

$$\hat{J}_{12} = J_{12}\omega^{-1}, \tag{11.7b}$$

$$\hat{J}_{21} = J_{21}\omega^{-1}, \tag{11.7c}$$

$$\hat{J}_{22}(\tau) = [J_{22} - k^2 D_u\theta]\omega^{-1} - (k^2 D_u \epsilon \omega^{-1}) \sin(\tau). \tag{11.7d}$$

From (11.6a) we obtain

$$\delta_v(\tau) = [d\delta_u(\tau)/d\tau - \hat{J}_{11}\delta_u(\tau)]/\hat{J}_{12}, \tag{11.8}$$

and substitution of this result into (11.6b) yields

$$\frac{d^2\delta_u(\tau)}{d\tau^2} - [\hat{J}_{11} + \hat{J}_{22}(\tau)]\frac{d\delta_u(\tau)}{d\tau} + [\hat{J}_{11}\hat{J}_{22}(\tau) - \hat{J}_{12}\hat{J}_{21}]\delta_u(\tau) = 0. \tag{11.9}$$

With the transformation

$$\delta_u(\tau) = \exp\left\{\frac{1}{2}\int^{\tau}\left[\hat{J}_{11} + \hat{J}_{22}(\tau')\right]d\tau'\right\}\hat{\delta}_u, \tag{11.10}$$

(11.9) turns into Hill's equation [259]

$$\frac{d^2\hat{\delta}_u}{d\tau^2} + Q(\tau)\hat{\delta}_u = 0, \tag{11.11}$$

where

$$Q(\tau) = \frac{1}{2}\frac{d\hat{J}_{22}(\tau)}{d\tau} - \frac{1}{4}[\hat{J}_{11} + \hat{J}_{22}(\tau)]^2 + [\hat{J}_{11}\hat{J}_{22}(\tau) - \hat{J}_{12}\hat{J}_{21}]. \tag{11.12}$$

If the corresponding system with constant parameters, i.e., $\epsilon = 0$, is at the Turing threshold, i.e., $\theta = \theta_{\mathrm{RD},c} = \left[J_{11}^{-1}\left(\sqrt{\Delta} + \sqrt{-J_{12}J_{21}}\right)\right]^2$, see (10.41), and if $k^2 = k_{\mathrm{T,RD}}^2 = \sqrt{\Delta/(D_{\mathrm{u}}D_{\mathrm{v}})}$, then a perturbation analysis of Hill's equation (11.11) shows that the uniform steady state of (11.1) with a temporally varying diffusion coefficient of the inhibitor is stable for sufficiently small oscillations, $\epsilon \ll 1$ [436]. In other words, small oscillations in the diffusion coefficient have a stabilizing effect; they delay the onset of the Turing instability.

Gourley and coworkers [168] have generalized Timm and Okubo's result and have applied perturbation theory to the system (11.1) with $D_i = D_i^{(0)} + \epsilon D_i^{(1)}(t)$ positive ($i = \mathrm{u, v}$), where ϵ small and the $D_i^{(1)}$ are periodic with period $\mathcal{T}$ and average zero. Choosing the system parameters again such that the corresponding system with constant parameters, i.e., $\epsilon = 0$, is at the Turing threshold, i.e., $\theta = \theta_{\mathrm{RD},c}$, and $k^2 = k_{\mathrm{T,RD}}^2$, they find that the uniform steady state is stable. In other words, all small-amplitude periodic perturbations with average zero in the diffusion coefficients delay the onset of the Turing instability. Further, if the periodic variations are $O(\epsilon)$, then the stabilizing effect is $O(\epsilon^2)$.

More general analytical results can be obtained if the periodic oscillations of the inhibitor diffusion coefficient are dichotomous or of "square-tooth" form [400]:

$$D_{\mathrm{v}}(t) = \begin{cases} D^+ & \text{on } n\mathcal{T} \leq t < (n+1/2)\mathcal{T}, \\ D^- & \text{on } (n+1/2)\mathcal{T} \leq t < (n+1)\mathcal{T}, \end{cases} \tag{11.13}$$

where $n \in \mathbb{Z}$. We assume $D^+ > D^- \geq 0$ and define $\overline{D} \equiv (D^+ + D^-)/2$ and $d \equiv (D^+ - D^-)/2$. For simplicity, we rescale x such that $D_{\mathrm{u}} = 1$:

$$\frac{\partial \rho_{\mathrm{u}}}{\partial t} = \frac{\partial^2 \rho_{\mathrm{u}}}{\partial x^2} + F_1(\rho_{\mathrm{u}}, \rho_{\mathrm{v}}), \tag{11.14a}$$

$$\frac{\partial \rho_{\mathrm{v}}}{\partial t} = D_{\mathrm{v}}(t)\frac{\partial^2 \rho_{\mathrm{v}}}{\partial x^2} + F_2(\rho_{\mathrm{u}}, \rho_{\mathrm{v}}). \tag{11.14b}$$

We assume again that (11.14) possesses a uniform steady state, $(\overline{\rho}_{\mathrm{u}}(x), \overline{\rho}_{\mathrm{v}}(x)) = (\overline{\rho}_{\mathrm{u}}, \overline{\rho}_{\mathrm{v}})$, with $F_1(\overline{\rho}_{\mathrm{u}}, \overline{\rho}_{\mathrm{v}}) = F_2(\overline{\rho}_{\mathrm{u}}, \overline{\rho}_{\mathrm{v}}) = 0$, which fulfills the stability condition (10.23), and that U is an activator and V an inhibitor.

With (11.4), the linearized evolution equations read

$$\frac{\mathrm{d}\delta_{\mathrm{u}}(t)}{\mathrm{d}t} = [J_{11} - k^2]\delta_{\mathrm{u}}(t) + J_{12}\delta_{\mathrm{v}}(t), \tag{11.15a}$$

$$\frac{\mathrm{d}\delta_{\mathrm{v}}(t)}{\mathrm{d}t} = J_{21}\delta_{\mathrm{u}}(t) + [J_{22} - k^2 D_{\mathrm{v}}(t)]\delta_{\mathrm{v}}(t). \tag{11.15b}$$

As is well known, any nth order homogeneous system of nonautonomous linear ordinary differential equations

$$\frac{d\mathbf{u}}{dt} = \mathsf{A}(t)\mathbf{u} \tag{11.16}$$

has n linearly independent solutions [458, 435]. We compose these n linearly independent solutions $\mathbf{u}_1(t), \ldots, \mathbf{u}_n(t)$ to a matrix $\Phi(t)$ with these solutions as columns, $\Phi(t) = (\mathbf{u}_1(t)\mathbf{u}_2(t)\ldots\mathbf{u}_n(t))$. Such a matrix is called a fundamental matrix of (11.16). The solution of (11.16) with the initial condition $\mathbf{u}(t_0) = \mathbf{u}_0$ is then given by

$$\mathbf{u}(t) = \Phi(t)\Phi(t_0)^{-1}\mathbf{u}_0. \tag{11.17}$$

If the linear equation (11.16) has periodically varying coefficients with period $\mathcal{T}$, $\mathsf{A}(t+\mathcal{T}) = \mathsf{A}(t)$, the Floquet theorem provides the fundamental result that the fundamental matrix of (11.16) can be written as the product of a $\mathcal{T}$-periodic matrix and a (generally) nonperiodic matrix [458, p. 80].

Theorem 11.1 *Suppose* $\mathsf{A}(t)$ *is periodic with period* $\mathcal{T}$*. Each fundamental matrix* $\Phi(t)$ *of* (11.16) *can be written as the product of two* $n \times n$ *matrices*

$$\Phi(t) = \mathsf{P}(t)\exp(\mathsf{B}t), \tag{11.18}$$

where $\mathsf{P}(t)$ *is* $\mathcal{T}$*-periodic and* B *is a constant matrix.*

Equation (11.18) implies that

$$\Phi(t+\mathcal{T}) = \Phi(t)\exp(\mathsf{B}\mathcal{T}) = \Phi(t)\mathsf{M}. \tag{11.19}$$

Remark 11.1 The matrix $\mathsf{M} = \exp(\mathsf{B}\mathcal{T})$ is called the monodromy matrix of $\dot{\mathbf{u}} = \mathsf{A}(t)\mathbf{u}$ [458].

Remark 11.2 The eigenvalues μ_i of M are known as *Floquet multipliers* or *characteristic multipliers* and the eigenvalues ν_i of B are known as the *Floquet exponents* or *characteristic exponents*. They are related by $\mu_i = \exp(\nu_i\mathcal{T})$ [435].

Theorem 11.2 *A periodic linear system is stable if all Floquet multipliers satisfy* $|\mu_i| \le 1$ *(respectively all Floquet exponents satisfy* $\mathrm{Re}\,\nu_i \le 0$*) and for all Floquet multipliers with* $|\mu_i| = 1$ *(respectively all Floquet exponents with* $\mathrm{Re}\,\nu_i = 0$*) the algebraic and geometric multiplicities are equal.*

A periodic linear system is asymptotically stable if all Floquet multipliers satisfy $|\mu_i| < 1$ *(respectively all Floquet exponents satisfy* $\mathrm{Re}\,\nu_i < 0$*)* [435].

Equation (11.19) implies that the monodromy matrix is given by $\mathsf{M} = \Phi(t_0)^{-1}\Phi(t_0+\mathcal{T})$, independent of the choice of t_0. The main difficulty in applying Theorem 11.2 to a particular set of equations lies in obtaining a linearly independent set of solutions.

In the following we provide a summary of the stability analysis of (11.15) as carried out by Sherratt [400]. We write (11.15) in the form

$$\frac{\mathrm{d}\boldsymbol{\delta}}{\mathrm{d}t} = \widehat{\mathsf{J}}^{+}\boldsymbol{\delta} \quad \text{on } n\mathcal{T} \le t < (n+1/2)\mathcal{T}, \tag{11.20a}$$
$$\frac{\mathrm{d}\boldsymbol{\delta}}{\mathrm{d}t} = \widehat{\mathsf{J}}^{-}\boldsymbol{\delta} \quad \text{on } (n+1/2)\mathcal{T} \le t < (n+1)\mathcal{T}, \tag{11.20b}$$

where

$$\boldsymbol{\delta}(t) = \begin{pmatrix} \delta_{\mathrm{u}}(t) \\ \delta_{\mathrm{v}}(t) \end{pmatrix} \tag{11.21}$$

and

$$\widehat{\mathsf{J}}^{\pm} = \begin{pmatrix} J_{11} - k^2 & J_{12} \\ J_{21} & J_{22} - k^2 D^{\pm} \end{pmatrix}. \tag{11.22}$$

We denote the eigenvalues and corresponding eigenvectors of $\widehat{\mathsf{J}}^{\pm}$ by $\lambda_i^{\pm}$ and $\mathbf{z}_i^{\pm}$ with $i = 1, 2$ and write $\Lambda^{\pm}(t) = \mathrm{diag}(\exp(\lambda_1^{\pm} t), \exp(\lambda_2^{\pm} t))$. Let $\mathsf{Z}^{\pm}$ be the matrix whose first and second columns are $z_1^{\pm}$ and $z_2^{\pm}$. Then any fundamental matrices $\Phi(t)$ of (11.20a) and (11.20b) have the form $\mathsf{Z}^{+}\Lambda^{+}(t)\mathsf{C}^{+}$ and $\mathsf{Z}^{-}\Lambda^{-}(t)\mathsf{C}^{-}$, respectively, where $\mathsf{C}^{\pm}$ are matrices whose entries are constants of integration. Without loss of generality, we choose $\mathsf{C}^{+} = [\Lambda^{+}(\mathcal{T}/2)]^{-1}$. Continuity at $t = \mathcal{T}/2$ imposes that

$$\mathsf{C}^{-} = [\Lambda^{-}(\mathcal{T}/2)]^{-1}[\mathsf{Z}^{-}]^{-1}\mathsf{Z}^{+} \tag{11.23}$$

and

$$\mathsf{M} = [\Phi(0)]^{-1}\Phi(\mathcal{T}) = [\mathsf{Z}^{+}]^{-1}\mathsf{Z}^{-}\Lambda^{-}(\mathcal{T}/2)[\mathsf{Z}^{-}]^{-1}\mathsf{Z}^{+}\Lambda^{+}(\mathcal{T}/2). \tag{11.24}$$

The eigenvalues μ of M, i.e., the Floquet multipliers are given by

$$\mu = \hat{\mu}\exp(-\Gamma\mathcal{T}/4), \tag{11.25}$$

where

$$\hat{\mu}^2 - a_1\hat{\mu} + 1 = 0 \tag{11.26}$$

and ($K = k^2$)

$$\Gamma = 2[(1+\overline{D})K - (J_{11}+J_{22})], \tag{11.27a}$$

$$a_1 = \frac{1}{2}\exp[(P^+ + P^-)\mathcal{T}/4]\Big\{\Big[1+\exp(-P^+\mathcal{T}/2)\Big]\Big[1+\exp(-P^-\mathcal{T}/2)\Big] + \frac{4J_{12}J_{21}+Q^+Q^-}{P^+ + P^-}\Big[1-\exp(-P^+\mathcal{T}/2)\Big]\Big[1-\exp(-P^-\mathcal{T}/2)\Big]\Big\}, \tag{11.27b}$$

$$Q^{\pm} = KD^{\pm} - K + J_{11} - J_{22}, \tag{11.27c}$$

$$P^{\pm} = \sqrt{4J_{12}J_{21} + (Q^{\pm})^2}. \tag{11.27d}$$

We focus on the case, most relevant in applications, that the period $\mathcal{T}$ of $D_v(t)$ is much longer than the characteristic time scale of the kinetics, which implies that $\left|P^{\pm}\mathcal{T}\right| \gg 1$. Analysis of (11.25), (11.26), and (11.27) leads to the conclusion that there exists a $\mu > 1$, i.e., the uniform steady state is unstable to nonuniform perturbations if either (i) $P^+ > \Gamma$ or (ii) $[\Gamma + (P^+)^2 - (P^-)^2]^2 < 4\Gamma^2(P^+)^2$. Somewhat lengthy further calculations show that, to leading order for large $\mathcal{T}$, the uniform steady state will be driven unstable by diffusion if and only if either

$$\text{(i)} \quad 3J_{11} + J_{22} > 0, \tag{11.28a}$$

$$\frac{D^+ - 1}{D^- + 3} > \chi_c, \tag{11.28b}$$

or

$$\text{(ii)} \quad \overline{D}J_{11} + J_{22} > 0, \tag{11.29a}$$

$$[\overline{D}J_{11} + J_{22}]^2 > 4\overline{D}\Delta, \tag{11.29b}$$

$$d < d_c. \tag{11.29c}$$

Here, $\Delta = \det \mathsf{J} = J_{11}J_{22} - J_{12}J_{21}$, and $\chi_c > 0$ is the larger root of

$$(3J_{11}+J_{22})^2\chi^2 + 2(3J_{11}^2 - 2J_{11}J_{22} - J_{22}^2 + 4J_{12}J_{21})\chi + J_{11}^2 - 2J_{11}J_{22} + 4J_{12}J_{21} + J_{22}^2 = 0. \tag{11.30}$$

Further, d_c is the unique value of d for which

$$F(K) = \overline{D}K^2 - (\overline{D}J_{11} + J_{22})K + \Delta + d^2\frac{K^2(J_{11}-K)(\overline{D}K - J_{22})}{[(1+\overline{D})K - (J_{11}+J_{22})]^2} \tag{11.31}$$

touches the K-axis on $(0, J_{11})$.

The instability conditions (ii), (11.29), are an extension of the Turing instability conditions (10.43) when $D^+ = D^- = \overline{D}$. (Recall we rescaled space to set $D_\mathrm{u} = 1$.) The first two inequalities, (11.29a) and (11.29b), are identical with the Turing instability condition (10.43) for the system (11.14) with a constant inhibitor diffusion coefficient $D_\mathrm{v}(t) = \overline{D}$. It is therefore a necessary condition that the system with constant diffusion coefficients be Turing unstable, in order for condition (11.29) to be fulfilled. In that sense, square-tooth temporal oscillations in the diffusion coefficient of the inhibitor have a stabilizing effect, since an additional condition, namely (11.29c), needs to be satisfied. Further, it turns out that condition (i), (11.28), defines a region of diffusion-driven instability in parameter space that is separate from the unstable region defined by condition (ii), (11.29), only if d is sufficiently large, i.e., D^+ and D^- are sufficiently different. Then, if the system possesses parameter values that fall inside the region defined by condition (i), temporal variations in D_v can have destabilizing effect.

11.2 Turing Instability with Spatially Inhomogeneous Diffusivities

As discussed at the beginning of this chapter, biological and ecological systems are often spatially inhomogeneous, and consequently diffusion coefficients display spatial variations. In analogy to the case of temporally varying diffusivities, dealt with in Sect. 11.1, we study the simplest possible situation. Only the diffusion coefficient of the inhibitor varies spatially, and it is piece-wise constant, a step function in space with a single point of discontinuity. We consider the following two-variable system on the interval $[0, L]$ with no-flow boundary conditions:

$$\frac{\partial \rho_\mathrm{u}}{\partial t} = \frac{\partial^2 \rho_\mathrm{u}}{\partial x^2} + F_1(\rho_\mathrm{u}, \rho_\mathrm{v}), \tag{11.32a}$$

$$\frac{\partial \rho_\mathrm{v}}{\partial t} = \frac{\partial}{\partial x}\left[D_\mathrm{v}(x)\frac{\partial \rho_\mathrm{v}}{\partial x}\right] + F_2(\rho_\mathrm{u}, \rho_\mathrm{v}), \tag{11.32b}$$

with

$$D_\mathrm{v}(x) = \begin{cases} D^- & \text{on } 0 \le x < \xi L, \\ D^+ & \text{on } \xi L < x \le L, \end{cases} \tag{11.33}$$

$D^- > 0$, $D^+ > 0$, $D^- \neq D^+$, and $\xi \in (0, 1)$. We assume again that (11.32) possesses a uniform steady state, $(\overline{\rho}_\mathrm{u}(x), \overline{\rho}_\mathrm{v}(x)) = (\overline{\rho}_\mathrm{u}, \overline{\rho}_\mathrm{v})$, with $F_1(\overline{\rho}_\mathrm{u}, \overline{\rho}_\mathrm{v}) = F_2(\overline{\rho}_\mathrm{u}, \overline{\rho}_\mathrm{v}) = 0$, which fulfills the stability condition (10.23), and that U is an activator and V an inhibitor.

The linear stability analysis of (11.32) was carried out by Maini and coworkers [263, 41], and we provide a summary of their work in the following. With

$$\rho_{\rm u}(x,t) = \overline{\rho}_{\rm u} + \delta_{\rm u}(x)\exp(\lambda t), \tag{11.34a}$$

$$\rho_{\rm v}(x,t) = \overline{\rho}_{\rm v} + \delta_{\rm v}(x)\exp(\lambda t), \tag{11.34b}$$

the linearized evolution equations read

$$\delta_{\rm u}''(x) + [J_{11} - \lambda]\delta_{\rm u}(x) + J_{12}\delta_{\rm v}(x) = 0, \tag{11.35a}$$

$$[D_{\rm v}(x)\delta_{\rm v}'(x)]' + J_{21}\delta_{\rm u}(x) + [J_{22} - \lambda]\delta_{\rm v}(x) = 0, \tag{11.35b}$$

where the prime denotes $\mathrm{d}/\mathrm{d}x$. Since the system decomposes into parts, for each of which the diffusion coefficient of the inhibitor is a constant, we consider (11.35) separately on $[0, \xi L)$ and $(\xi L, L]$. For the first part, we multiply (11.35b) by s^-/D^- and add it to (11.35a) to obtain

$$[\delta_{\rm u}(x) + s^-\delta_{\rm v}(x)]'' + \left[J_{11} - \lambda + \frac{J_{21}s^-}{D^-}\right] \times \left[\delta_{\rm u}(x) + \frac{J_{12} + (J_{22} - \lambda)s^-/D^-}{J_{11} - \lambda + J_{21}s^-/D^-}\delta_{\rm v}(x)\right] = 0. \tag{11.36}$$

We choose s^- such that

$$\frac{J_{12} + (J_{22} - \lambda)s^-/D^-}{J_{11} - \lambda + J_{21}s^-/D^-} = s^-, \tag{11.37}$$

which is a quadratic equation:

$$J_{21}(s^-)^2 + [D^-(J_{11} - \lambda) - (J_{22} - \lambda)]s^- - J_{12}D^- = 0. \tag{11.38}$$

Let s_1^- and s_2^- be the roots of (11.38). Then (11.36) turns into two equations for the quantity $\delta_j(x) \equiv \delta_{\rm u}(x) + s_j^-\delta_{\rm v}(x)$ for $j = 1, 2$:

$$\delta_1(x)'' + \left[J_{11} - \lambda + \frac{J_{21}s_1^-}{D^-}\right]\delta_1(x) = 0, \tag{11.39a}$$

$$\delta_2(x)'' + \left[J_{11} - \lambda + \frac{J_{21}s_2^-}{D^-}\right]\delta_2(x) = 0. \tag{11.39b}$$

The general solutions of (11.39) are given by

$$\delta_j(x) = C_j\cos(\alpha_j^- x) + \tilde{C}_j\sin(\alpha_j^- x), \tag{11.40}$$

where C_j and $\tilde{C}_j$ are constants of integration, and

$$\alpha_j^- = \sqrt{\frac{J_{11} - \lambda + J_{21} s_j^-}{D^-}}. \tag{11.41}$$

The no-flow boundary condition at $x = 0$ implies that the constants $\tilde{C}_j$ vanish. We express the constants C_j in terms of the values of $\delta_j(x)$ at $x = \xi L$ and solve for $\delta_{\mathrm{u}}(x)$ and $\delta_{\mathrm{v}}(x)$ on $[0, \xi L)$:

$$\delta_{\mathrm{u}}(x) = \frac{1}{s_2^- - s_1^-} \left[\frac{\left(\Gamma_{\mathrm{u}} + s_1^- \Gamma_{\mathrm{v}}\right) s_2^-}{\cos(\alpha_1^- \xi L)} \cos(\alpha_1^- x) - \frac{\left(\Gamma_{\mathrm{u}} + s_2^- \Gamma_{\mathrm{v}}\right) s_1^-}{\cos(\alpha_2^- \xi L)} \cos(\alpha_2^- x) \right], \tag{11.42a}$$

$$\delta_{\mathrm{v}}(x) = \frac{1}{s_2^- - s_1^-} \left[\frac{\left(\Gamma_{\mathrm{u}} + s_2^- \Gamma_{\mathrm{v}}\right)}{\cos(\alpha_2^- \xi L)} \cos(\alpha_2^- x) - \frac{\left(\Gamma_{\mathrm{u}} + s_1^- \Gamma_{\mathrm{v}}\right)}{\cos(\alpha_1^- \xi L)} \cos(\alpha_1^- x) \right], \tag{11.42b}$$

where $\Gamma_{\mathrm{u}} = \delta_{\mathrm{u}}(\xi L)$ and $\Gamma_{\mathrm{v}} = \delta_{\mathrm{v}}(\xi L)$. Proceeding similarly for the second part of the system, we obtain $\delta_{\mathrm{u}}(x)$ and $\delta_{\mathrm{v}}(x)$ on $(\xi L, L]$:

$$\begin{aligned} \delta_{\mathrm{u}}(x) = \frac{1}{s_2^+ - s_1^+} \Bigg[& \frac{\left(\Gamma_{\mathrm{u}} + s_1^+ \Gamma_{\mathrm{v}}\right) s_2^+}{\cos(\alpha_1^+ (1-\xi) L)} \cos(\alpha_1^+ (L - x)) \\ & - \frac{\left(\Gamma_{\mathrm{u}} + s_2^+ \Gamma_{\mathrm{v}}\right) s_1^+}{\cos(\alpha_2^+ (1-\xi) L)} \cos(\alpha_2^+ (L - x)) \Bigg], \end{aligned} \tag{11.43a}$$

$$\begin{aligned} \delta_{\mathrm{v}}(x) = \frac{1}{s_2^+ - s_1^+} \Bigg[& \frac{\left(\Gamma_{\mathrm{u}} + s_2^+ \Gamma_{\mathrm{v}}\right)}{\cos(\alpha_2^+ (1-\xi) L)} \cos(\alpha_2^+ (L - x)) \\ & - \frac{\left(\Gamma_{\mathrm{u}} + s_1^+ \Gamma_{\mathrm{v}}\right)}{\cos(\alpha_1^+ (1-\xi) L)} \cos(\alpha_1^+ (L - x)) \Bigg]. \end{aligned} \tag{11.43b}$$

By construction, the solutions $\delta_{\mathrm{u}}(x)$ and $\delta_{\mathrm{v}}(x)$ of (11.35) given by (11.42) and (11.43) are continuous at $x = \xi L$. However, the solution must also satisfy continuity of flux at $x = \xi L$:

$$\lim_{x \to (\xi L)^-} \delta_{\mathrm{u}}'(x) = \lim_{x \to (\xi L)^+} \delta_{\mathrm{u}}'(x), \tag{11.44a}$$

$$\lim_{x \to (\xi L)^-} D^- \delta_{\mathrm{v}}'(x) = \lim_{x \to (\xi L)^+} D^+ \delta_{\mathrm{v}}'(x). \tag{11.44b}$$

Substituting (11.42) and (11.43) into (11.44), we obtain

$$\begin{pmatrix} P(\lambda) & Q(\lambda) \\ R(\lambda) & S(\lambda) \end{pmatrix} \begin{pmatrix} \Gamma_u \\ \Gamma_v \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \tag{11.45}$$

where

$$P(\lambda) = \frac{s_1^- T_2^- - s_2^- T_1^-}{s_2^- - s_1^-} + \frac{s_1^+ T_2^+ - s_2^+ T_1^+}{s_2^+ - s_1^+}, \tag{11.46a}$$

$$Q(\lambda) = \frac{s_1^- s_2^- (T_2^- - T_1^-)}{s_2^- - s_1^-} + \frac{s_1^+ s_2^+ (T_2^+ - T_1^+)}{s_2^+ - s_1^+}, \tag{11.46b}$$

$$R(\lambda) = \frac{D^-(T_1^- - T_2^-)}{s_2^- - s_1^-} + \frac{D^+(T_1^+ - T_2^+)}{s_2^+ - s_1^+}, \tag{11.46c}$$

$$S(\lambda) = \frac{D^-(s_1^- T_1^- - s_2^- T_2^-)}{s_2^- - s_1^-} + \frac{D^+(s_1^+ T_1^+ - s_2^+ T_2^+)}{s_2^+ - s_1^+}, \tag{11.46d}$$

with $T_j^- = \alpha_j^- \tan(\xi L \alpha_j^-)$ and $T_j^+ = \alpha_j^+ \tan((1-\xi)L\alpha_j^+)$ for $j = 1, 2$. Here we assume that $s_1^\pm \neq s_2^\pm$, $\cos(\alpha_j^- \xi L) \neq 0$, and $\cos(\alpha_j^+(1-\xi)L) \neq 0$ for $j = 1, 2$. From the solutions (11.42) and (11.43), $\Gamma_u = \Gamma_v = 0$ implies that $\delta_u(x) \equiv \delta_v(x) \equiv 0$. In order to obtain nontrivial solutions $\delta_u(x)$ and $\delta_v(x)$, the determinant of the matrix in (11.45) must vanish:

$$F(\lambda) \equiv P(\lambda)S(\lambda) - Q(\lambda)R(\lambda) = 0. \tag{11.47}$$

This is the dispersion relation for a two-variable reaction–diffusion system with a step-function diffusivity for V. It is the analog of (10.26) for homogeneous reaction–diffusion systems and relates the growth rates λ of spatial perturbations to the parameter values of the system. In contrast to the homogeneous case, the dispersion relation (11.47) is a complicated expression that cannot be solved analytically if $D^- \neq D^+$. A diffusion-driven instability of the uniform steady state of the system occurs if the stability condition (10.23) is satisfied and (11.47) has solutions with a positive real part.

Note that in deriving (11.47) we have assumed that $s_2^\pm - s_1^\pm$, $\cos(\alpha_j^- \xi L)$, and $\cos(\alpha_j^+(1-\xi)L)$ are all nonzero. The analysis can be carried out for those cases where one or more of these expressions are zero, but typically the solutions $\delta_u(x)$ and $\delta_v(x)$ cannot satisfy (11.44).

In general, the roots of the dispersion relation (11.47) will be complex valued. For homogeneous, two-variable reaction–diffusion systems, all complex solutions of the dispersion relation (10.26) have a negative real part. Extensive numerical simulations of the full nonlinear inhomogeneous system (11.32) by Maini and coworkers [263, 41] show that, if an instability occurs, the uniform steady state always evolves to a steady pattern and not a temporally oscillating solution. These observations suggest that the diffusion-driven instability is a Turing bifurcation, i.e., a real eigenvalue passes through zero. If λ is real, then $F(\lambda)$ is also real, and the dispersion relation is amenable to simple numerical solution. The Turing condition that $F(\lambda) = 0$ has positive real solutions is far less enlightening than the Turing condition (10.43) for homogeneous systems. In particular, it is not immediately clear that the system must be either a pure activator–inhibitor scheme or a cross activator–inhibitor scheme. Numerical solutions of (11.47) suggest, however, as expected, that these requirements are still necessary for a diffusion-driven instability to occur in the system (11.32). Studies of chemical and biological models [263, 41], such as the Schnakenberg model, see Sect. 1.4.5, show that as expected the uniform steady state of (11.32) undergoes a Turing instability if $D^+ > D^- > \theta_{\mathrm{RD},c}$, where the latter is given by (10.41). A Turing bifurcation can occur for $D^- < \theta_{\mathrm{RD},c}$, if D^+ exceeds some critical value D_c^+, which depends on the system parameters, with $D_\mathrm{c}^+ > \theta_{\mathrm{RD},c}$.

Exercise

11.1 Explore the dispersion relation (11.47) for the Brusselator.