When Hopf meets saddle: bifurcations in the diffusive Selkov model for glycolysis

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Abstract We study the linear instabilities and bifurcations in the Selkov model for glycolysis with diffusion. We show that this model has a zero wave-vector, finite frequency Hopf bifurcation, which is a forward or supercritical bifurcation, to a growing oscillatory but spatially homogeneous state and a saddle-node bifurcation, which is a backward or subcritical bifurcation, to a growing inhomogeneous state with a steady pattern characterised by a finite wavevector. We further demonstrate that by tuning the relative diffusivity of the two concentrations, it is possible to make both the instabilities to occur at the same point in the parameter space, leading to an unusual type of codimension-two bifurcation. We then show that in the vicinity of this codimension-two bifurcation, the initial conditions decide whether a spatially uniform oscillatory or a spatially periodic steady pattern emerges in the long time limit. It is also possible to form a co-existing patterned and time-periodic state by fine-tuning the diffusivity ratio for moderate values, in qualitative agreement with recent experimental studies.

Keywords Bifurcations · Pattern formation · Amplitude equations · Perturbation theory · Codimension-two point

1 Introduction

Pattern formation had primarily been the domain of fluid mechanics, where different kinds of patterns like convection rolls, Taylor columns, viscous fingering, droplet formation due to surface tension, etc., have been known for more than a century [1–12]. A somewhat different mechanism for pattern formation involving two antagonistic species, undergoing diffusive motion and interacting with each other, was introduced by Turing in 1952 [13]. The Turing pattern is triggered by a critical ratio of the two diffusivities. Turing’s original work has been followed by extensive works on reaction diffusion systems. Adding the diffusive terms to the dynamical system with two different diffusivities makes a reaction diffusion system. In principle, one now has a reaction diffusion system where the dynamical system instabilities can compete with the pattern forming part and produce a rich system. The system variables are now fields (functions of space and time) [14–29]. For the convective instability of a fluid layer on the other hand, the instability is driven by an external parameter like an adverse temperature gradient. It is known in the mathematical analysis of the fluid dynamics problem that a few mode truncation of the partial differential equations in the case of the convective instability can lead to a
reasonable description in a restricted domain. This sets up a dynamical systems description (a set of coupled ordinary differential equations) of a problem featuring instabilities.

The state of the physical system is characterised by the stable fixed point of the dynamical system and an instability of the fixed point corresponds to that physical state becoming unstable. The instability of a stable fixed point as a system parameter is varied is a bifurcation and generally leads to a new stable state of the system. The parameter involved is the control parameter. If there are more than one control parameters, there can be different kinds of bifurcations and for each bifurcation there will be a surface defined in the parameter space and these surfaces may intersect. For two control parameters, the surfaces will be curves which can terminate at a special value of the parameters giving what is called a codimension-two point. A simple dynamical system capable of showing a wide variety of fixed points is the Brusselator [30, 31]. The addition of the reaction diffusion term to the Brusselator has led to the generation of a large number of interesting possibilities over almost three decades [30–34].

Given the general wisdom that addition of diffusion in dynamical systems can lead to competitions, making those systems exhibit novel and unexpected behaviour, it is useful to revisit the instabilities in diffusive dynamical systems in models with specific structures. In this paper we propose a variation of the previous studies, which has a couple of extra features and leads to some new physical phenomena. For this purpose, we focus on the two-variable (corresponding to two chemicals) Selkov model [5, 17–19] of glycolysis which has a closed loop in parameter space separating the oscillatory response from a fixed point. All along the loop, small perturbations lead to temporal oscillations in the system, in contrast to time-independent states. We now add diffusion to the dynamics which makes the variables functions of space and time and thus fields. Our purpose in this work is to look at the role of the Turing terms in the vicinity of this closed loop.

In this work it is found that the Turing instability occurs along a curve in the parameter space and has to intersect the loop at a point different from the origin for a whole range of parameters. The intersection is a codimension-two point whose properties are well known. However, this point is slightly unusual. Along a particular direction from this point the solution is purely oscillatory in time with no spatial dependence and in another direction it is spatially oscillatory with no temporal variation. Further, of the two bifurcations which meet at this co-dimension two point, one (Hopf bifurcation) is forward (“super-critical”) and the other (Turing instability) is backward (“sub-critical”) and we expect the pattern dynamics to be somewhat unusual. This is the motivation behind the choice of the Selkov model for this analysis. Further analysis leads to

- Finding a very strong initial condition dependence of the eventual pattern because of the simultaneous occurrence of a forward and a backward bifurcation at the codimension-two point.
- Establishing nonlinear amplitude equations near the codimension-two point.
- Exploring the interplay of the two instabilities from the amplitude equations.
- Studying the possibility of diffusivity controlled coexisting patterned and time-periodic states.

We have obtained these results very close to the codimension-two point analytically by using a low-order perturbation theory, where the amplitudes of the basic growing modes, or equivalently, the “distance” between the codimension-two point and the point of observation serve as the small parameters.

These results should be testable in experiments on appropriate systems and numerical simulations of the model equations. A similar study on the codimension-two point in the Brusselator model is available in Refs. [30, 31], where the generic structures of the amplitude equations are discussed and their numerical solutions have been obtained. Pure states as well as mixed states that are born out of the interacting Hopf and steady state pattern modes are predicted. Such codimension-two points have been studied in the context of the diffusive Gray-Scott model [32] and delayed Schnakenberg systems [33, 34]. The rest of this article is organised in the following manner. In Sec. 2, we introduce the Selkov model for glycolysis with diffusion. Then, in Sec. 3 we analyse the linear instabilities in the model and discuss the ensuing phase diagram in the parameter space. Next, in Sec. 4.1 we set up the amplitude equations. Finally, in Sec. 5 we summarise and conclude.

2 Selkov model for glycolysis

The Selkov model for glycolysis was introduced to model glycolytic oscillations and has two species. The
When Hopf meets saddle: bifurcations in the diffusive

model equations read

\[
\begin{align*}
\frac{\partial \rho_1}{\partial t} &= -\rho_1 + a\rho_2 + \rho_1^2\rho_2 + \nabla^2\rho_1, \\
\frac{\partial \rho_2}{\partial t} &= b - \rho_2 - \rho_1^2\rho_2 + D\nabla^2\rho_2,
\end{align*}
\]

where \(\rho_1, \rho_2\) are the dimensionless concentrations of ADP (adenosine diphosphate) and F6P (fructose-6-phosphate), respectively [5]; see Ref. [35] for the model equations in the original form. We have added diffusion terms \(\nabla^2\rho_1\) and \(D\nabla^2\rho_2\) in (1) and (2), respectively, that represent diffusion of the two species in space; the conventional Selkov model does not consider diffusion [35]. All the parameters \(a, b, D\) are positive. Notice that without diffusion, (1) and (2) are just two coupled ordinary differential equations (ODEs) that define a dynamical system, whereas with diffusion they become partial differential equations (PDEs). In what follows below, we study Eqs. (1) and (2) in general \(d\)-dimensions with periodic boundary conditions.

3 Linear instabilities

At the fixed points of the model equations (1) and (2) \(\rho_1\) and \(\rho_2\) are constants given by

\[
\rho_1^* = b, \quad \rho_2^* = \frac{b}{a + b^2}.
\]

Equations (1) and (2) may be linearised around the fixed points (3) to give

\[
\begin{align*}
\frac{\partial u}{\partial t} &= \frac{b^2 - a}{b^2 + a} u + av + b^2v + \nabla^2 u, \\
\frac{\partial v}{\partial t} &= -(b^2 + a)v - \frac{2ab}{b^2 + a} + D\nabla^2 v,
\end{align*}
\]

where \(u = \rho_1 - \rho_1^*, v = \rho_2 - \rho_2^*\). Since (4) and (5) are PDEs, they actually correspond to an infinite number of modes. In treating the partial differential equations (4) and (5), we use the standard techniques for describing the instability of a uniform state to a patterned state or a spatially uniform but oscillatory state. Since the emergence of the instability is obtained from a linearised system, the general condition for separating the different wavenumber modes is simply the condition for the existence of the Fourier transforms of the functions \(u(x, t)\) and \(v(x, t)\). Further, assuming periodic boundary conditions, these modes may be conveniently labelled by the Fourier wavevector \(k\). The stability matrix \(J\) for the pair of equations (4) and (5) take the form in the Fourier space

\[
J(k^2) = \begin{pmatrix}
\frac{b^2 - a}{b^2 + a} - k^2 & a + b^2 \\
-\frac{2ab}{a + b^2} & -a - b^2 - Dk^2
\end{pmatrix}.
\]

The corresponding eigenvalues are given by

\[
\lambda_{\pm}(k^2) = \frac{1}{2}[\text{Tr} \pm \sqrt{\text{Tr}^2 - 4\det}],
\]

where \(\text{Tr}\) and \(\det\), respectively, are the trace and determinant of the matrix \(J(k^2)\), and both of these are functions of \(k^2 = ||k||^2\), implying the Euclidean norm. Here, periodic boundary condition implies \(k = 2\pi n/L, n = 0, \pm 1, \pm 2\ldots\). Unsurprisingly, each of these \(k\)-modes is independent of each other for the linear equations (4) and (34). This evidently allows us to examine the linear instability of the individual \(k\)-modes, and thereby identify the marginal mode(s) (i.e. the ones which neither grow nor decay) at the threshold of the linear instabilities. The remaining modes decay at the instability threshold. We have

\[
\text{Tr}(k^2) = \frac{b^2 - a}{b^2 + a} - (a + b^2) - k^2(D + 1),
\]

\[
\text{Det}(k^2) = a + b^2 + k^2(a + b) - Dk^2\left(\frac{b^2 - a}{b^2 + a} + Dk^2\right).
\]

Notice that in obtaining the stability matrix (6) from (4) and (5), we have assumed the existence of linearly independent (and considered small) amplitudes of the individual Fourier modes. This serves as the initial condition on the model. Furthermore, there are no restrictions on the relative amplitudes of the initial values of the different modes as the different modes are completely independent of one another due to the linearity of (4) and (5).

Linear instability occurs when the real part of one or both the eigenvalues pass through zero. This can happen when either (i) \(\text{Tr}(k^2)=0\), when both \(\lambda_{\pm}(k^2)\) become fully imaginary, or (ii) \(\text{Det}(k^2)=0\), when \(\lambda_{-}(k^2)\) entirely vanishes, for some \(k\)-values. The former is the condition for the onset of Hopf bifurcation, whereas the second one is for saddle-node bifurcation. The latter actually corresponds to the well-known Turing instability in nonlinear systems; see, for example, Refs. [36, 37].

Since \(\lambda_{\pm}(k^2)\) is the growth rate of the mode labelled by \(k\), we note from the form of \(\lambda_{\pm}(k^2)\) that at the onset of Hopf bifurcation for the \(k = 0\) mode, all other modes with \(k > 0\) are stable. At \(k = 0\), at the onset \(\lambda_{\pm}(k^2 = 0)\)
are fully imaginary corresponding to a Hopf frequency \( \omega_0 = \sqrt{a + b^2} \) [5]. This implies a steady oscillation permeating the entire system; the system remains spatially homogeneous everywhere. The phase boundary in the \( a - b \) plane that demarcates a steady homogeneous phase and a phase with oscillatory instability (i.e. with a growing amplitude) is given by [5]

\[
\text{Tr}(k^2 = 0) = 0 \implies b^2 = \frac{1}{2}(1 - 2a \pm \sqrt{1 - 8a}),
\]

(10)
as shown in Fig. 1. At the onset of Hopf bifurcation, i.e. on the line (10) in the \( a - b \) plane, only the mode \( \omega = \omega_0 \), \( k = 0 \) is marginal, all other modes decay. Different finite-\( k \) modes also undergo Hopf bifurcation, at the onset of which the \( k = 0 \) mode has the maximum growth rate. Thus, the \( k = 0 \) mode is the most relevant mode for Hopf bifurcation in the linear stability analysis. Notice that this Hopf bifurcation exists for all \( D \), simply because the \( k = 0 \) mode, the dominant mode at the onset of Hopf bifurcation, is unaffected by the diffusivity.

Linear instability also arises when \( \text{Det}(k^2) = 0 \), at which point one of the eigenvalues \( \lambda_\text{min}(k^2) \) vanishes entirely for some \( k \)-value. This is the saddle-node bifurcation. In our model, the threshold for this instability is given by the condition \( \text{Det}(k^2) = 0 \), where \( k_c \) is a preferred wavevector, such that for all other \( k \neq k_c \), \( \text{Det}(k^2) > 0 \), ruling out instabilities at all these \( k \)-values different from \( k_c \). Thus, \( k = k_c \) minimises \( \text{Det}(k^2) \). This condition of minimisation allows us to obtain \( k_c \) from the condition

\[
\frac{\partial \text{Det}}{\partial k^2} |_{k^2=k_c^2} = 0.
\]

(11)

We have

\[
\frac{\partial \text{Det}}{\partial k^2} |_{k^2=k_c^2} = 2Dk_c^2 + \Gamma_1 = 0 \implies k_c^2 = -\frac{\Gamma_1}{2D} > 0 \implies \Gamma_1 < 0,
\]

(12)

where \( \Gamma_1 = a + b^2 - D(b^2 - a)/(a + b^2) < 0 \) for \( k_c^2 > 0 \). On the other hand, at the threshold of the saddle-node instability,

\[
\text{Det}(k_c^2) = 0 \implies [a + b^2 + D \frac{a - b^2}{a + b^2}] = 4D(a + b^2).
\]

(13)

Together with the requirement of \( k_c^2 > 0 \) (see Eq. (12)) in a steady pattern, we find

\[
a + b^2 + D \frac{a - b^2}{a + b^2} = -2\sqrt{D} \sqrt{a + b^2}
\]

(14)
as the phase boundary in the \( a - b \) plane for a given \( D \), separating a homogeneous phase and a steady pattern with \( k_c \) as the preferred wavevector. This curve intersects the \( b \)-axis \( (a = 0) \) at \( b = \sqrt{D}(-1 + \sqrt{2}) \). Furthermore, as \( a \to 0 \), \( b \to 0 \) on this curve, i.e. the curve passes arbitrarily close to the origin. In order to ascertain its behaviour near the origin, we assume

\[
b^2 = a + \Gamma a^\gamma, \quad \gamma \neq 1,
\]

(15)
as \( a \to 0 \). Substituting (15) in (14), we find in the limit \( a \to 0 \)

\[
-\frac{D\Gamma a^{\gamma - 1}}{2a + \Gamma a^{\gamma}} = -2\sqrt{D}[2a + \Gamma a^{\gamma}]^{1/2}.
\]

(16)

This has no solution for \( \gamma < 1 \). For \( \gamma > 1 \), we find

\[
D\Gamma a^{\gamma - 1} = 4\sqrt{2}\sqrt{D}\sqrt{a} \implies \Gamma = \frac{4\sqrt{2}}{D}, \quad \gamma = \frac{3}{2}.
\]

(17)

On the other hand, the phase boundary (10) between the stable homogeneous phase and oscillatory instability phase very close to the origin takes the form

\[
b^2 = a + O(a^2), \quad a \to 0.
\]

(18)

Thus, the phase boundary (14) lies above the boundary (10) very close to the origin.

The upper part of the Hopf line (10) meets the \( b \)-axis \( (a = 0) \) at \( b = 1 \). Intersection of the pattern boundary (14) with the \( b \)-axis depends upon \( D \). The threshold value of \( D \) for which (14) intersects the \( b \)-axis as well as (10) at \( (0, 1) \) is given by

\[
D_{\min} = \frac{1}{(\sqrt{2} - 1)^2} \approx 5.83.
\]

(19)

For \( D < D_{\min} \), (14) never intersects (10); for \( D < D_{\min} \) (14) intersects (10) at \( a > 0 \), \( b < 1 \). For instance, the two branches of the Hopf boundary meet at \( a = 1/8 \), \( b = \sqrt{3}/8 \). The pattern boundary passes through this point for \( D = (\sqrt{2} + \sqrt{3})^2 = D_c \approx 9.9 > D_{\min} \). In general, the point of intersection \( (a_c, b_c) \) between the two lines (10) and (14) is given by

\[
a_c = \frac{2D}{(D - 1)^2} - \frac{8D^2}{(D - 1)^2}, \quad b_c^2 = \frac{2D}{(D - 1)^2} + \frac{8D^2}{(D - 1)^4}.
\]

(20)
which are parametrised by $D$, and is a codimension-two point. This codimension-two point is a Turing-Hopf point, and has been studied in the context of other models; see, for example, Ref. [38], where it has been studied in the FitzHugh-Nagumo model. See Ref. [39] for a more recent reference on this topic. At this codimension-two point, clearly one has a zero eigenvalue and a pair of purely imaginary eigenvalues, a telltale signature of zero-Hopf or fold-Hopf bifurcation [5,40]. Thus, by varying $D > D_{\text{min}}$ the point of the intersection of (14) with (10) can be continuously shifted. In the limit of $D \to \infty$ (20) gives

$$a_c = \frac{2}{D}, \quad b_c^2 = \frac{2}{D}.$$  

Hence, for very large $D$, $(a_c, b_c) \to (0, 0)$. Further, by using (20) we obtain

$$k_c^2 = \frac{1}{\sqrt{D}} \sqrt{a_c + b_c^2} = \frac{2}{D - 1}, \quad \omega_0 = \sqrt{a_c + b_c^2}$$

at the point of intersection $(a_c, b_c)$. Furthermore, $u, v \sim \exp(\pm i \omega_0 t)$ and $u, v \sim \exp(\pm i k_c \cdot x)$ are the solutions of (4) and (5), and are the dominant modes at $(a_c, b_c)$; all other modes decay in time. Thus, the general solutions of $u, v$ at $(a_c, b_c)$ must be linear combinations of $\exp(\pm i \omega_0 t)$ and $\exp(\pm i k_c \cdot x)$ (see below for explicit forms) which are neither traveling nor standing waves, rather an oscillation superposed on a steady pattern.

Equations (8) and (9) further suggest that in the diffusive Selkov model the threshold of a finite wavevector Hopf bifurcation can coincide with the threshold of a saddle-node (pattern) instability having a periodicity corresponding to the finite wavevector of the Hopf bifurcation. This is known as the Takens-Bogdanov bifurcation [41–43]. We do not discuss it here further.

4 Amplitude equations

In this Section, we set up and study the amplitude equations for the growing modes. These will allow us to infer the general nature of the steady states in the long time limit. We first study the linear amplitude equations and discard the nonlinear effects. Next, we systematically set up and analyse the nonlinear amplitude equations by using perturbative expansions lowest order in the nonlinearities.

4.1 Linear amplitude equations

As mentioned in the previous Section, at $(a_c, b_c)$, the codimension-two point, the amplitudes of the two modes are constants. Slightly away from $(a_c, b_c)$ and on the unstable side, these amplitudes grow exponentially in time, and have the biggest growth rates, growing exponentially faster than all other modes. Thus sufficiently close to the codimension-two point and on the unstable side it suffices to retain only these two modes, dropping all others. Let us set $a = a_c(1 - \epsilon_1), b = b_c(1 - \epsilon_2)$, where $\epsilon_1, \epsilon_2$ are the distances from the threshold $(a_c, b_c)$, and are assumed to be small. At the threshold ($\epsilon_1 = 0, \epsilon_2 = 0$), only the modes with $\omega = \omega_0, k = 0$ and $\omega = 0, k = k_c$ survive and are marginal; all other modes decay and hence are ignored below. Thus at $\epsilon_1 = 0, \epsilon_2 = 0$, we can write

$$u = u_0 = A_1 \exp(i \omega_0 t) + A_2 \exp(i k_c \cdot x) + cc,$$  

$$v = v_0 = B_1 \exp(i \omega_0 t) + B_2 \exp(i k_c \cdot x) + cc,$$
where the direction of $k_c$ is arbitrary; $cc$ implies complex conjugates. Functions $u_0$ and $v_0$ satisfy the linearised equations of motion. We expect for appropriately chosen $\epsilon_1$ and $\epsilon_2$, the modes should be linearly unstable. In this Section below, we consider only the modes given by (23) and (24) and labelled by $(\omega = \omega_0, k = 0$ and $\omega = 0, k = k_c)$, instead of infinite number of modes, labelled by $k = 2\pi n/L$ and any frequency $\omega$.

In the linear theory, we find by using (24) and collecting all the linear terms with $\exp(i\omega_0 t)$

$$A_1 = \frac{a_c}{a_c + b^2} \frac{b^2 - a_c}{a_c + b^2} A_1 + (a_c + b^2) B_1$$

$$+ (a_c \epsilon_1 + 2b_c^2 \epsilon_2) B_1 + \nabla^2 A_1. \quad (25)$$

At the threshold of the instability ($\epsilon_1 = 0 = \epsilon_2$), amplitudes $A_1$ and $B_1$ are related by

$$A_1 \left[ i\omega_0 - \frac{b^2 - a_c}{a_c + b^2} \right] = (a_c + b^2) B_1. \quad (26)$$

Eliminating $B_1$, we obtain

$$\frac{\partial A_1}{\partial t} = \left[ \left( \frac{2a_c b_c^2}{\omega_0^4} + a_c \right) \epsilon_1 - \left( \frac{4a_c b_c^2}{\omega_0^4} - 2b_c^2 \right) \epsilon_2 \right]$$

$$A_1 - (a_c \epsilon_1 + 2b_c^2 \epsilon_2) \frac{i\omega_0}{\omega_0^2} A_1 + \nabla^2 A_1. \quad (27)$$

Notice that Eq. (27) is fully $O(\epsilon_1, \epsilon_2)$. This provides a post facto justification of using (26) to eliminate $B_1$. Clearly, $A_1$ is linearly unstable if

$$\Delta_1 = \left( \frac{2a_c b_c^2}{\omega_0^4} + a_c \right) \epsilon_1 - \left( \frac{4a_c b_c^2}{\omega_0^4} - 2b_c^2 \right) \epsilon_2 > 0, \quad (28)$$

which of course imposes restrictions on the amplitudes and signs of $\epsilon_1$ and $\epsilon_2$; the diffusion term in (27) is stabilising for all finite $k$. We note from the shape of the unstable region and the line (10) in the phase diagram in Fig. (1) that if $\epsilon_2 = 0, \epsilon_1 > 0$ is necessary in order to be inside the unstable region. Fixing the sign of $\epsilon_2$ for linear instability with $\epsilon_1 = 0$ is trickier. Again from the shape of the unstable region and the curve (10), we note that at the point $(a_c, b_c) = (1/8, \sqrt{3/8})$, the instability must disappear if $\epsilon_1 = 0$, independent of $\epsilon_2$. Furthermore, at any point on the lower half of the Hopf line (10), if $\epsilon_1 < 0$, we must have $\epsilon_2 < 0$ for instability, whereas on the upper half of the Hopf line, $\epsilon_2 > 0$. We now show that these conditions are indeed satisfied. First of all, if we set $a_c = 1/8, b_c = \sqrt{3/8}$ and correspondingly $D = D_c = (\sqrt{2} + \sqrt{3})^2$, we note that $4a_c b_c^2 + 2b_c^2 = 0$. Thus, (27) is independent of $\epsilon_2$ at $a_c = 1/8, b_c = \sqrt{3/8}$. Secondly, on the lower branch, $4a_c b_c^2 + 2b_c^2 > 0$, and hence, if $\epsilon_1 = 0$ then $\epsilon_2 < 0$ for linear instability. Similarly, on the upper branch $4a_c b_c^2 + 2b_c^2 < 0$, implying $\epsilon_2 > 0$ if $\epsilon_1 = 0$ for linear instability. If both $\epsilon_1$ and $\epsilon_2$ are non-zero, then they must satisfy Eq. (28) for $A_1$ to be linearly unstable.

Similarly, for the pattern mode we get by using (24) and collecting all the linear terms with $\exp(i k_c \cdot x)$

$$\frac{\partial A_2}{\partial t} = \frac{b^2 - a_c}{a_c + b^2} A_2 + \frac{\epsilon_1}{a_c + b^2} A_2 + (a_c + b^2) B_2$$

$$+ \frac{2a_c b_c^2}{\omega_0^4} (\epsilon_1 - 2\epsilon_2) A_2 - \frac{\epsilon_1}{a_c + 2b_c^2} b_c^2 B_2$$

$$- k_c^2 A_2 + 2i k_c \cdot \nabla A_2 + \nabla^2 A_2. \quad (29)$$

At the threshold of the instability ($\epsilon_1 = 0 = \epsilon_2$), amplitudes $A_2$ and $B_2$ are related by

$$\frac{b^2 - a_c}{a_c + b^2} A_2 - k_c^2 A_2 = -(a_c + b^2) B_2. \quad (30)$$

Then eliminating $B_2$, we find

$$\frac{\partial A_2}{\partial t} = \left[ \frac{1}{2} (1 - \omega_0^4) (\epsilon_1 - 2\epsilon_2) \right] A_2$$

$$+ \left[ \frac{\epsilon_1}{a_c + b^2} + 2\epsilon_2 b_c^2 \right] \frac{D + 1}{2D} \epsilon_1 A_2$$

$$+ 2i k_c \cdot \nabla A_2 + \nabla^2 A_2$$

$$= \left[ \frac{1}{2} (1 - \omega_0^4) + \frac{2D}{(D - 1)^4} (D^2 - 6D + 1) \right] \epsilon_1 A_2$$

$$- \left[ (1 - \omega_0^4) - \frac{2D(D + 1)^2}{(D - 1)^4} \right] \epsilon_2 A_2$$

$$+ 2i k_c \cdot \nabla A_2 + \nabla^2 A_2. \quad (31)$$

As for Eq. (27), $A_2$ is linearly unstable if

$$\Delta_2 = \left[ \frac{1}{2} (1 - \omega_0^4) + \frac{2D}{(D - 1)^4} (D^2 - 6D + 1) \right] \epsilon_1$$

$$- \left[ (1 - \omega_0^4) - \frac{2D(D + 1)^2}{(D - 1)^4} \right] \epsilon_2 > 0. \quad (32)$$

Whether or not this is true depends on course on the signs and magnitudes of $\epsilon_1$ and $\epsilon_2$. Geometry of the pattern line (14) suggests that all $\epsilon_1 > 0$ with $\epsilon_2 = 0$.
should make $A_2$ linearly unstable. If $\epsilon_1 = 0$, then the appropriate sign of $\epsilon_2$ for linear instability can be decided by following the above analysis for the linear instability of $A_1$. It is straightforward to show that

$$\left[1 - \omega_D^2 - \frac{4D(D-1)^2}{(D-1)^2}\right] = 0 \text{ at } \epsilon = 1/2, \quad b_c = \sqrt{3}/8,$$

and

$$\left[1 - \omega_D^2 - \frac{4D(D-1)^2}{(D-1)^2}\right] > ( < 0) \text{ on the lower (upper) branch.}$$

Thus, in an exact analogy with the analysis for Eq. (27), the linear instability of $A_2$ ensues if $\epsilon_1 = 0$ together with $\epsilon_2 < 0$ (for $D < D_c$) and $\epsilon_2 > 0$ (for $D > D_c$). If both $\epsilon_1$ and $\epsilon_2$ are non-zero then (32) is the necessary condition for the linear instability of $A_2$. In Fig. 2 we have plotted the two inequalities (28) and (32) and mark the region where both $A_1$ and $A_2$ are linearly unstable.

We can therefore conclude that close to the point of the intersection of the Hopf line (10) and the pattern line (14), both the instabilities can independently form for the same set of (appropriately chosen) $\epsilon_1$, $\epsilon_2$. While the two instabilities do not interact at the linear level, they do so when nonlinear effects are included. This opens up the issue of the nature of the eventual steady state when both the instabilities are present. This may be answered by systematically considering the nonlinear effects that we discuss below.

4.2 Nonlinear effects

We now consider the nonlinear effects that eventually lead to saturation of the amplitudes in the long time limit [44]: see Ref. [45,46] for general discussions on nonlinear amplitude equations. We start by expanding the model equations (1) and (2) about the fixed points (3) up to the cubic orders. Truncation at the cubic order is justified for small $\epsilon_1$, $\epsilon_2$. We note that in the presence of the nonlinearities $u_0$ and $v_0$ no longer satisfy the resulting nonlinear equations. We find

$$\frac{\partial u}{\partial t} = \frac{b_2}{b_2} - a + (a + b_2)v + \nabla^2 u + N_u, \quad (33)$$

$$\frac{\partial v}{\partial t} = -(a + b_2)v - 2a \frac{b_2^2}{a + b_2} + D\nabla^2 v + N_v, \quad (34)$$

where $N_u$ and $N_v$ are the nonlinear terms:

$$N_u = 2bu + \frac{u^2 b}{a + b_2} + u^2 v = -N_v \equiv N, \quad (35)$$

retaining up to the cubic contributions. In order to obtain the nonlinear amplitude equations systematically, we write

$$u = u_0 + u_1, \quad v = v_0 + v_1, \quad (36)$$

where $u_1$ and $v_1$ are small and assumed to be slowly varying functions of $x$ and $t$. Zeroth-order contributions $u_0$ and $v_0$ are continued to be given by (23) and (24). Periodic boundary condition is still used on the system, which again ensures that (33) and (34) can be expanded in a Fourier series. Nonlinearities in (33) and (34) lead to coupling of the different Fourier modes. Nonetheless, sufficiently close to $(\epsilon_1, \epsilon_2)$, i.e. with vanishingly small $\epsilon_1$, $\epsilon_2$ in the unstable side, only the modes with $k = k_c$ and/or $\omega = \omega_D$ grow. Retention of only these modes however necessarily generate the higher harmonics. Keeping this in mind, we expand $u_1$ and $v_1$ as follows:

$$u_1(x, t) = C_1e^{2i\omega_D t} + D_1e^{i(k_c x)} + F_1 + G_1e^{i(\omega_D - k_c) x} + H_1e^{i(\omega_D + k_c) x} + e_c, \quad (37)$$

$$v_1(x, t) = C_2e^{2i\omega_D t} + D_2e^{i(k_c x)} + F_2 + G_2e^{i(\omega_D - k_c) x} + H_2e^{i(\omega_D + k_c) x} + e_c. \quad (38)$$

In a perturbative approach which we adopt here, (37) and (38) suffice to the lowest order in nonlinearities, or in $\epsilon_1$, $\epsilon_2$. Coefficients $C_1$, $C_2$, $D_1$, $D_2$, $F_1$, $F_2$, $G_1$, $G_2$, $H_1$, $H_2$ are in general complex functions of $D$ which
we find below. Substituting (37) and (38) in (33) and (34) and matching coefficients of \( \exp(i\omega_0 t) \) and \( \exp(i\mathbf{k}_e \cdot \mathbf{x}) \), we obtain the nonlinear amplitude equations. The Hopf amplitude \( A_1 \) follows the nonlinear amplitude equation

\[
\frac{\partial A_1}{\partial t} = \Delta_1 A_1 - (a_c \epsilon_1 + 2b_c^2 \epsilon_2) \frac{i \omega_0}{\omega_0^2} A_1 + \nabla^2 A_1 + 2b_c \left[ A_1^* C_2 + A_1 F_2 + A_2 G_2 \right. \\
\left. + A_2^* H_2 + B_1 F_1 + B_1^* C_1 + B_2 G_1 + B_2^* H_1 \right] + \frac{2b_c}{\omega_0} \left[ A_1 F_1 + A_2 G_1 + A_1^* C_1 + A_2^* H_1 \right] \\
- (4 + \frac{2}{D}) |A_1|^2 - 3A_1 |A_1|^2 + A_1 |A_1|^2 \frac{i}{\omega_0},
\]

(39)

Likewise, the pattern mode amplitude \( A_2 \) follows the nonlinear amplitude equation

\[
\frac{\partial A_2}{\partial t} = \Delta_2 A_2 + 2b_c \left[ A_1 G_3 + A_1^* H_2 + F_2 A_2 \right. \\
\left. + D_2 A_2^* + B_2 F_1 + B_1 G_1 + B_1^* H_1 + B_2^* D_1 \right] + \frac{2b_c}{\omega_0} \left[ A_1 G_1^* + A_2 F_1 + A_1^* H_1 + A_2^* D_1 \right] \\
- (5 + \frac{1}{D}) |A_2|^2 - \frac{3}{2}(1 + \frac{1}{D}) |A_2|^2. 
\]

(40)

The coefficients are given by

\[
C_1 = -\tilde{C}_1 A_1^2, \quad C_2 = \tilde{C}_2 A_1^2, \\
D_1 = \tilde{D}_1 A_2^2, \quad D_2 = -\tilde{D}_2 A_2^2, \\
F_1 = 0, \quad F_2 = -\tilde{F}_2 |A_1|^2 + |A_2|^2, \\
G_1 = \tilde{G}_1 A_1 A_2^*, \quad G_2 = -\tilde{G}_2 A_2 A_2^*, \\
H_1 = \tilde{H}_1 A_1 A_2^*, \quad H_2 = -\tilde{H}_2 A_1 A_2^*.
\]

(41-45)

Coefficients \( C_1, \tilde{C}_2, \tilde{D}_1, \tilde{D}_2, \tilde{F}_2, \tilde{G}_1, \tilde{G}_2, \tilde{H}_1, \tilde{H}_2 \) are all functions of \( D \), whose explicit forms are rather lengthy and are given in Appendix. We note that redefining the coefficient \( A_1 \) to be real does not make the coefficients in (39) real; they are in general complex, whereas redefining the coefficient \( A_2 \) to be real does make the coefficients in (40) real. We thus set \( A_2 \) to be real without any loss of generality. In order to proceed further, we neglect the spatial dependences of \( A_1 \) and \( A_2 \) and set \( A_1 = R \exp(i\phi) \). The governing equation of motion for \( R \) can be obtained from Eq. (39) by extracting equations of the real and imaginary parts of (39). Coupled equations for \( R \) and \( A_2 \) have the general structure

\[
\dot{R} = \Delta_1 R + l_1 R^3 + l_2 R A_2^2, \\
\dot{A}_2 = \Delta_2 A_2 + l_3 A_2^3 + l_4 R^2 A_2,
\]

(47)

where the effective coefficients \( \mu_1, \mu_2, l_1, l_2, l_3, l_4 \) are all functions of \( D \). The full expressions of these coefficients are given in Appendix. We notice that if either of \( A_1 \) (i.e. \( R \)) or \( A_2 \) vanishes, the coefficients \( G_1, G_2, H_1, H_2 \) vanish identically. Before proceeding further, we make a technical comment. Notice that we have originally started with two PDEs (1) and (2), which admit infinite number modes. However, very close to the instability threshold and on the unstable side of the stability diagram, the model is reduced to solving two amplitude equations (39) and (40), which allow us to infer about the eventual steady states stemming from the linear instabilities very close to the instability threshold. This procedure is standard; see, for example, Ref. [45, 46] for more details.

We now consider the fixed points (FP) \( (R^2, A_2^2) \). There are in principle four of them: FP1 with \( (R^2 = 0, A_2^2 = 0) \), FP2 with \( (R^2 = 0, A_2^2 > 0) \), FP3 with \( (R^2 > 0, A_2^2 = 0) \) and FP4 with \( (R^2 > 0, A_2^2 > 0) \). Fixed point FP1 is unstable globally anywhere within the unstable region. Let us now analyse FP2 and FP3, and study their linear stability properties. To obtain FP2, we set \( A_2 = 0 \) and \( R = 0 \) in (47), i.e. we take Eq. (40) and set \( A_2 = 0 \) with \( R = 0 \). This gives a fixed point \( FP2(0, A_2^2) \), where

\[
(A_2^*)^2 = \Delta_2 \left[ \frac{1}{\omega_0^2} + \frac{(D + 7)(D - 1)}{72D} \right]^2 + \frac{2}{9} \left[ \frac{D + 1}{(D - 1)^2} - \frac{2}{9} \frac{D - 1}{\omega_0^2} \right]^{-1} \frac{1}{2b_c}.
\]

(48)

This exists only if \( 2(D - 1)(4 + D) < 27D^2 \), i.e. \( D < 5 \), as can be seen from (B1) in Appendix, which is less than \( D_{min} = 5.83 \), below which the pattern cannot exist as we have argued above. Thus, this FP is ruled out. Nonetheless, \( A_2 > 0, R = 0 \) remains unstable for all \( A_2 \), which is unphysical. To ensure stability, higher-order terms with stabilising signs are needed to stop the instability. While higher-order perturbation theory would indeed produce higher-order terms in the amplitude equations, we refrain from extending the perturbative analysis to higher-order terms. Instead, assuming that such stabilising higher-order terms would be generated by higher-order perturbative expansions, we note that if there is a \( -\Gamma A_2^3 \) term in (40) with a positive \( \Gamma \), then there should be a hysteric transition to a state with a non-zero \( A_2^* \). If so, this would be a backward bifurcation, a direct analogue of first-order phase transitions

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in equilibrium systems. With a $-\Gamma A^3_2$ being added to (40), the latter gives a quadratic equation in $A^2_2$ at the fixed point with $A^2_2 = 0$. The fixed point solutions are given by

$$A^2_2 = \frac{1}{2\Gamma} \left[ l_3 \pm \sqrt{l_3^2 + 4\Gamma\Delta_2} \right].$$

(49)

If $\Delta_2 > 0$, this leads to only one possibility:

$$A^2_2 = \frac{1}{2\Gamma} \left[ l_3 + \sqrt{l_3^2 + 4\Gamma\Delta_2} \right].$$

(50)

In contrast, for $\Delta_2 < 0$ both the solutions given in (49) exist, which would give rise to metastability. However, $\Delta_2 < 0$ will place $a = a_c(1 - \epsilon_1), b = b_c(1 - \epsilon_2)$ outside the unstable region, where a pattern with a preferred wavevector $k_c$ cannot exist, as $k_c$ itself is not defined outside the unstable region. Thus, only (50) is the physically acceptable solution. It should be noted that since $l_3 > 0$, as soon as $D$ reaches the threshold $D_{\text{min}}$ (for the codimension-two point $D > D_{\text{min}}$) we have a backward bifurcation for the reaction-diffusion system with a steady pattern of $O(1)$ amplitude appearing out of nothing.

Likewise, to study FP3 it is sufficient to consider Eq. (39) and set $\dot{R} = 0$ with $A_2 = 0$. This gives

$$R^* = \left( \frac{2a_c^2b_c^2}{a_0^4} + a_c \right) \epsilon_1 - \left( \frac{4a_c^2b_c^2}{a_0^4} - 2b_c^2 \right) \epsilon_2 + \frac{\omega_0^2}{2b_c} \left( \frac{1}{2} + \frac{2}{\omega_0^2} \right)^{-1}.$$

Clearly, $R$ scales as the square root of the “distance” (i.e. $\epsilon_1, \epsilon_2$) from the threshold of the instability; as $\epsilon_1, \epsilon_2$ decrease, $R$ decreases continuously, eventually vanishing smoothly for $\epsilon_1 = 0 = \epsilon_2$, which is a hallmark of a forward bifurcation.

Lastly, there could be a fourth fixed point FP4, where both $R^2$ and $A^2_2$ are nonzero. Evaluation of this fixed point requires considerably more algebra. At this fixed point, we have the relations

$$l_2 R^2 + l_2 A^2_2 + \Delta_1 = 0,$$

$$l_3 A^2_2 + l_4 R^2 - \Gamma A^2_2 = 0.$$

(52)

(53)

Solving we obtain

$$A^2_2 = \frac{1}{2l_1 \Gamma} \left[ l_1 l_3 + l_2 l_4 \right.$$}

$$\pm \sqrt{l_1 l_3 + l_2 l_4 - 4l_1 \Gamma(l_4 \Delta_1 - l_1 \Delta_2))}.$$ 

(54)

The solution (54) gives one for $A^2_2$ if $l_4 \Delta_1 - l_1 \Delta_2 < 0$, else there are two solutions for $A^2_2$, if $l_4 \Delta_1 - l_1 \Delta_2 > 0$ and $(l_1 l_3 + l_2 l_4)^2 > 4l_1 \Gamma l_4 \Delta_1 - l_1 \Delta_2$ are simultaneously satisfied. Further, there are no solutions for $A^2_2$ at all for $(l_1 l_3 + l_2 l_4)^2 < 4l_1 \Gamma l_4 \Delta_1 - l_1 \Delta_2$. Once $A^2_2$ is found, $R^2$ may be calculated; this exists only if $\Delta_1 > l_2 A^2_2$.

Having argued for the existence of the four fixed points, we now discuss the linear stability of these FPs. Before we embark on the linear stability analysis, an important technical comment is in order. We have truncated the amplitude equations up to cubic order nonlinearities. Retaining up to this order does not clearly stabilise the $A_2$ dynamics. Systematically going beyond the cubic order, one would have generated fifth-order nonlinear terms in the $A_2$-equation having forms $A^5_2, A^3_2 R^2, A_2 R^4$. We do not do that here. The $-\Gamma A^3_2$-term that stabilises the dynamics of the amplitude $A_2$ (and in turn produces fixed points) is added in an ad hoc manner. This makes $\Gamma$ a free parameter unlike all other coefficients which are functions of $D$. Thus, any linear stability analysis would be sensitive to the numerical value of $\Gamma$, making us only able to speculate about the general flow topology around the fixed points.

(i) The FP1=$(0,0)$ is linearly unstable for all $\Delta_1 > 0, \Delta_2 > 0$. This establishes the instability of spatially uniform and temporally constant states for all $\Delta_1 > 0, \Delta_2 > 0$.

(ii) The FP2=$(A^2_2 = 0, R^2 = \Delta_1/\lambda_1)$: Small fluctuations $\delta R = \delta A_2$ about $R^*$, $A^2_2$ follow the linearised equations:

$$\delta \dot{R} = -2\Delta_1 \delta R,$$

$$\delta \dot{A}_2 = \frac{1}{l_1}(l_1 A_2 - l_2 A_1) \delta A_2.$$

(55)

(56)

This would be globally stable for $l_1 \Delta_2 < l_4 \Delta_1$. This condition can be satisfied by appropriately choosing $\Delta_1$ and $\Delta_2$ (i.e. by choosing $\epsilon_1$ and $\epsilon_2$).

(iii) Let us now consider the fixed point FP3=$(R = 0, A^2_2 > 0)$. The small fluctuations $\delta R, \delta A_2$ follow

$$\delta \dot{R} = (\Delta_1 - l_2 A^2_2) \delta R,$$

$$\delta \dot{A}_2 = (\Delta_2 + 3l_3 A^2_2 - 2\Gamma A^2_2) \delta A_2.$$

(57)

(58)

Thus, stability is ensured for $l_2 A^2_2 > \Delta_1$ and $\Delta_2 + 3l_3 (A^2_2)^2 - 2\Gamma (A^2_2)^2 < 0$. This can be achieved for appropriately chosen $\epsilon_1, \epsilon_2$ and also for a large $\Gamma$.

(iv) Finally, we consider the stability of the non-trivial FP4, where $R^* \neq 0, A^2_2 \neq 0$. Small fluctuations
Flow lines around the fixed points in the $A^2 - R^2$ plane, that are expected only in a small region of the parameter space. Filled blue circles represent linearly unstable fixed points and filled black circles represent linearly stable fixed points; FP2 and FP3 are the globally stable fixed points. The broken red line is the separatrix. Arrows denote directions of the flows around this fixed point follow the linearised equations

$$\delta \dot{R} = (\Delta_1 - 3l_1(R^*)^2 - l_2(A^2_2)^2)\delta R - 2R^*A^3_2\delta A_2,$$

$$\delta \dot{A}_2 = -2l_4 A^4_2 R^* \delta R + (\Delta_2 + 3l_3(A^2_2)^*) - l_4(R^*)^2 - 5\Gamma(A^4_2)^* \delta A_2.$$  

The eigenvalues of the corresponding stability matrix now depend upon $\Gamma$. We do not write their explicit forms. We, however, argue that by varying $\Gamma$, two distinct possible scenarios can be constructed.

### 4.2.1 Absence of mixed states

This scenario holds when FP2 and FP3 are globally stable, with FP4 being globally unstable. This means there are no mixed states. One would either have a steady pattern, or oscillations of spatially uniform states. The non-trivial unstable FP at $(R^*)^2, (A^2_2)^2$ provides equation of the separatrix in the $A^2_2 - R^2$ plane: it is a straight line with a slope $m = (R^*)^2/(A^2_2)^*$. The flow diagram around the fixed points are shown in Fig. 3.

The instability of the fixed point FP4 corresponding to mixed states implies that while the linear stability analysis predicts joint occurrence of both the instabilities for appropriate values of $\epsilon_1$ and $\epsilon_2$ (see the light green region in Fig. 2), the nonlinear amplitude equations rule out such a possibility; see Fig. 4 which is the analogue of Fig. 2 for the nonlinear theory. Instead, the light green region in Fig. 2 is now split by the separatrix into two regions, with one part displaying only spatially uniform oscillatory instability identical to the Hopf bifurcation in the diffusionless model (vertical banded region in Fig. 4), and the other region showing steady patterns without any oscillation (checkerboard region in Fig. 4).

Initial conditions lying below the separatrix flow towards FP3, whereas those lying above flow towards FP2. Thus, the precise initial conditions determine the ensuing final states for small $\epsilon_1, \epsilon_2$ near $(a_c, b_c)$, which is either a uniform state with oscillation (Hopf state controlled by FP2), or a steady pattern (controlled by FP3). When the system is controlled by FP2, the eventual final state should display spirals, targets, etc, [45–48], whereas when it is controlled by FP3, the system...
When Hopf meets saddle: bifurcations in the diffusive

Fig. 5 Flow lines around the fixed points in the $A^2 - R^2$ plane, that are expected in a small region of the parameter space. Filled blue circles represent linearly unstable fixed points and the filled black circle represents linearly stable fixed point; FP4 is the only globally stable fixed point. The broken red line is the separatrix. Arrows denote directions of the flows should display steady patterns of a given periodicity [49,50].

4.2.2 Existence of mixed states

This is observed when only FP4 is globally stable; see Fig. 5. This corresponds to mixed states. What is the nature of these mixed states? From our perturbation theory, we can only say these correspond to traveling waves with a phase velocity $\omega_0/k_c$. Results of Refs. [51,52] provide further clue.

Within our theory, one would observe the traveling waves in whole the checkerboard region in Fig. 6 that covers the area $\Delta_1 > 0, \Delta_2 > 0$ in the $\epsilon_1 - \epsilon_2$ plane.

In the above, we have studied the nature of the steady states inside the unstable region at a point $a = a_c(1-\epsilon_1), b = b_c(1-\epsilon_2)$. This point could be reached by a variety of paths in the phase space starting from some points outside of the unstable region. The theory that we described above is only valid for those paths that pass through the codimension-two point. Only these paths cross the two boundaries of the Hopf bifurcation and saddle-node instability, respectively, simultaneously. This evidently raises the question what one might observe if one crosses the boundaries away from $(a_c, b_c)$. In this case, one either crosses the boundary of the Hopf bifurcation first, or of the saddle-node instability first. Consider the case, when one crosses the boundary of the saddle-node instability first. Upon crossing this boundary and before crossing the Hopf bifurcation boundary, the state is a patterned state with a given periodicity or a wavevector. At the boundary of the Hopf bifurcation, this state actually does not undergo a further instability, for only a uniform state undergoes a Hopf bifurcation at this boundary. Similarly, if one crosses the Hopf bifurcation boundary first, a uniform oscillatory instability sets in. Upon meeting the saddle-node instability boundary, this oscillatory state does not undergo another instability as at the saddle-node instability boundary only a non-oscillatory uniform state undergoes an instability. Thus, depending upon which boundary the system meets first starting from a uniform state, a particular final state will be generated. For $D < D_{min}$ as one approaches from the uniform steady state, one necessarily meets the Hopf bifurcation boundary leading to a Hopf bifurcation to a uniform oscillatory state; for $D < D_{min}$ there are no patterned states. Of course, very far from the boundaries and near to the origin, there can be further instabilities of period or time scale doubling type, leading

Fig. 6 Possibility of traveling waves in the $\epsilon_1 - \epsilon_2$ plane. When FP4 is the globally stable fixed point, the checkerboard board region corresponds to the phase space region with traveling waves. Its boundaries are given by $\Delta_1 > 0, \Delta_2 > 0$, which is identical to the light green region in Fig. 2.
ultimately to spatio-temporal chaos. We do not discuss this here.

As a function of $D$, we find that for $0 \leq D \leq D_{min}$, only a Hopf bifurcation is possible. For $D > D_{min}$ the system can generally undergo two possible bifurcations - a forward to an oscillatory but spatially uniform state, and a backward to a steady pattern, to be decided on the initial conditions on the amplitudes. For some choices of $D > D_{min}$, the system can also display traveling waves. It is interesting to find out the stable fixed points for $D \rightarrow \infty$, in particular, whether FP4 can exist. The codimension-two point in this case lies on the lower branch of the Hopf boundary (10) and approaches the origin. In the limit $D \rightarrow \infty$, (54) gives $A_2^2 \sim D / \Gamma \sim O(1)$, assuming $\Gamma$ scaling as $D$. This scaling is not unreasonable, as without it (i.e. if $\Gamma \sim O(1)$), $A_2^2$ diverges, which is not an acceptable solution. Since $R$ always undergoes a second-order transition, (52) cannot be satisfied for $A_2^2 \sim O(1)$. Thus, FP4 with $A_2^2 > 0$, $R^2 > 0$ does not exist in this limit. Only possible solutions are FP2 with $A_2^2 > 0$, $R = 0$, or FP3 with $R^2 > 0$, $A_2 = 0$. We speculate that for a large enough $D > D_h$ (a threshold not explicitly obtained here), FP4 ceases to exist. Thus, mixed states are not expected for $D > D_h$. This is summarised in Fig. 7.

We have neglected diffusion of the amplitudes $R$ and $A_2$, and instead treated them as spatially constant. This is of course an approximation. How good is this? At the linear order, a diffusive term would necessary add a damping at $O(k^2)$. This means as $\epsilon_1$, $\epsilon_2 \rightarrow 0$, all non-zero $k$-modes of $R$ and $A_2$ having the form $\exp(ik \cdot x)$ do not grow but decay in time. This justifies our dropping the spatial gradient terms in the amplitudes equations for $R$ and $A_2$. Sufficiently away from the threshold of the instability and inside the unstable region (i.e. when $\epsilon_1$, $\epsilon_2$ are no longer “vanishingly small”), finite $k$-modes of $R$ and $A_2$ are expected to grow. Studying the implications of those growing modes is beyond the scope of the present work. On the other hand, it is known that in a forward Hopf bifurcation, there are spatially inhomogeneous states in the form of spirals and targets forming as a result of the instabilities. This means when the steady states of the diffusive Selkov model is controlled by FP3, the steady states should accommodate spirals and targets [47]. Likewise, for $D < D_{min}$ for which steady patters are ruled out, spirals and targets should generically exist for any initial condition.

5 Summary and outlook

We have developed a theoretical description for bifurcations near a codimension-two point in the Selkov model for glycolysis with diffusion by using a perturbative treatment, and used that to sketch out the generic steady states closed to the codimension-two point. Linear stability analysis is used to show that the model equations admit two independent linear instabilities for $D > D_{min}$, a threshold for the diffusivity ratio - (i) a zero wavevector Hopf bifurcation from a uniform state to a uniform oscillatory state, and (ii) a finite wavevector saddle-node instability from a uniform steady state to a patterned state at zero frequency. We obtain the phase diagram spanned by the two model parameters. The thresholds of these two instabilities can be made to superpose on the same point in the phase diagram by tuning the diffusion constant $D$, which is a codimension-two point. In the linear theory of the instability amplitudes, these two instabilities do not mix. As a consequence, the linear theory predicts that for appropriately chosen $\epsilon_1$ and $\epsilon_2$, the measure of “distances” from the instability threshold, either of the two instabilities can exist in some regions, whereas in some other regions, the two instabilities can co-exist, as depicted in Fig. 2. We have asked what the nature of the final state is very close to the threshold. To analyse this, we have set up the lowest order nonlinear amplitude equa-
tions for the Hopf and pattern modes, which are no longer independent, but are now coupled by the nonlinear effects. We then show that the amplitude equations that we derive generally admit four fixed points. For most of the parameter values, two fixed points corresponding to either a pure steady pattern or a pure Hopf bifurcation are globally stable. Thus, depending upon the initial conditions, very close to the common instability threshold the model is to undergo either a Hopf bifurcation akin to the model without diffusion, or a saddle-node bifurcation, with no trace of the other being observed in experiments on representative physical systems. Interestingly, the Hopf bifurcation is a forward bifurcation, whereas the pattern is formed via a backward bifurcation with a sudden jump in the amplitude of the pattern that forms. For $D < D_{\text{min}}$ the Hopf bifurcation to an oscillatory state remains the only possibility. These results could also be verified by numerically solving the model partial differential equations.

To our knowledge, there have only been a few attempts to study the nature of the states near codimension-two points in laboratory experiments. Notable experimental studies include those reported in Refs. [51,52], which agree qualitatively with the results we have obtained above. In these experimental studies a mixed state with both the modes is found to be present in a small region near the threshold, which is speculated by the authors to be due to the two modes actually forming at different positions in the third dimension. Our results are expected to be generic and should hold for any pair of amplitude equations having similar structure. Numerical simulations of this model, useful in obtaining results for finite $\epsilon_1, \epsilon_2$, i.e. far away from the codimension-two point, should give a more complete picture of the instabilities and spatially or temporally non-uniform steady states anywhere in the unstable region of the phase space. Lastly, we have not considered the effect of noise in this work. It is well known [53,54] that the Hopf bifurcation is robust against the existence of weak noise and the same qualitative result holds for the pattern formation in reaction diffusion systems as well [55]. Based on these works, we expect the same qualitative results to hold near the codimension-two point as well. For the Hopf bifurcation it has been pointed out that a backward bifurcation can be made forward by the addition of noise [56]. Whether this can hold for the reaction diffusion system considered here is an issue worth exploring in future. We hope our theoretical results will inspire more detailed experimental and numerical results on relevant systems in future, which may be used to validate and improve our results beyond low-order perturbation expansions here.

Acknowledgements AB thanks the SERB, DST (India) for partial financial support through the MATRICS scheme [file no.: MTR/2020/000406].

Funding The work was supported by Science and engineering research board (Grant No. MTR/2020/000406).

Availability of data and material Not applicable.

Declarations

Conflicts of interest None.

Code availability Not applicable.

Appendix A: Explicit values of the different coefficients

The coefficients $\tilde{C}_1, \tilde{C}_2, \tilde{D}_1, \tilde{D}_2, \tilde{F}_2, \tilde{G}_1, \tilde{G}_2, \tilde{H}_1, \tilde{H}_2$ are given by

\[
\tilde{C}_1 = -\frac{i \omega_0}{3 \omega_0^2} (1 + \omega_0^2), \quad \tilde{C}_2 = \frac{(1 + 2i \omega_0)}{6\omega_0^2} (1 + \omega_0^2), \tag{A1}
\]

\[
\tilde{D}_1 = \frac{(D - 1)}{9} (1 + \omega_0^2), \tag{A2}
\]

\[
\tilde{D}_2 = -\frac{(D + 7)(D - 1)}{72D} (1 + \omega_0^2), \tag{A3}
\]

\[
\tilde{F}_1 = 0, \quad \tilde{F}_2 = -\frac{(1 + \omega_0^2)}{\omega_0^2}, \tag{A4}
\]

\[
\tilde{G}_1 = \frac{i \omega_0 + 2D/(D - 1)}{-\omega_0^2 + 2i \omega_0(D + 1)/(D - 1)} (1 + \omega_0^2)
\]

\[
\left[ 1 + \omega_0^2 \left( -\frac{3D + 1}{2D} + \frac{i \omega_0}{\omega_0^2} \right) \right], \tag{A5}
\]

\[
\tilde{G}_2 = -\frac{i \omega_0 + 1 + 2/(D - 1)}{-\omega_0^2 + 2i \omega_0(D + 1)/(D - 1)} (1 + \omega_0^2)
\]

\[
\left[ 1 + \omega_0^2 \left( -\frac{3D + 1}{2D} + \frac{i \omega_0}{\omega_0^2} \right) \right], \tag{A6}
\]

\[
\tilde{H}_1 = \frac{i \omega_0 + 2D/(D - 1)}{-\omega_0^2 + 2i \omega_0(D + 1)/(D - 1)} (1 + \omega_0^2)
\]

\[
\left[ 1 + \omega_0^2 \left( -\frac{3D + 1}{2D} + \frac{i \omega_0}{\omega_0^2} \right) \right], \tag{A7}
\]

\[
\tilde{H}_2 = \frac{i \omega_0 + 1 + 2/(D - 1)}{-\omega_0^2 + 2i \omega_0(D + 1)/(D - 1)} (1 + \omega_0^2)
\]
The linear stability of FP2 can be easily ascertained by taking Eq. (40) and setting $R = 0$. This gives

$$
\dot{A}_2 = \left[ \frac{1}{2} (1 - \omega_0^4) + \frac{2D}{(D-1)^4} (D^2 - 6D + 1) \right] \epsilon_1 A_2
- \left[ (1 - \omega_0^4) + \frac{4D(D + 1)^2}{(D-1)^4} \right] \epsilon_2 A_2
+ 2b_c A_3^2 (1 + \omega_0^2) \left[ - \frac{1}{\omega_0^2} - \frac{(D + 7)(D - 1)}{72D} \right]
+ 2 \frac{D - 1}{9\omega_0^2} \frac{D + 1}{(D - 1)^2}
+ 2 \frac{D - 1}{\omega_0^2} \frac{D + 1}{(D - 1)^2}
- \frac{3}{2D}(D + 1)A_3^2.
$$

Including the fifth-order term, the dynamical equation for $A_2$ is given by ($R = 0$)

$$
\dot{A}_2 = \left[ \frac{1}{2} (1 - \omega_0^4) + \frac{2D}{(D-1)^4} (D^2 - 6D + 1) \right] \epsilon_1 A_2
- \left[ (1 - \omega_0^4) + \frac{4D(D + 1)^2}{(D-1)^4} \right] \epsilon_2 A_2
+ l_3 A_3^2 - \Gamma A_3^2,
$$

with $\Gamma > 0$.

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