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Diffusion-driven instability in oscillating environments

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Diffusion-driven instability in systems of reaction-diffusion equations is a commonly used model for pattern formation in both embryology and ecology. In ecological applications, model parameters tend to oscillate in time, because of either daily or seasonal fluctuations in the environment. I investigate the effects of such fluctuations on diffusion-driven instability by considering analytically the possibility of Turing bifurcations when the parameter values (diffusion coefficients and kinetic parameters) oscillate in time between two sets of constant values, with a period that is either very short or very long compared to the time scale of the growth and predation kinetics. I show that oscillations in the kinetics can have quite different effects from oscillations in the dispersal terms. I also discuss the comparison between the solution forms predicted by linear theory and the numerical solutions of a simple nonlinear predator-prey model.

1 Introduction

More than 40 years ago, Turing [1] showed that in systems of reaction-diffusion equations, a homogeneous steady state can be driven unstable by diffusion, giving rise to spatial patterns. A large number of biological systems can reasonably be represented by reaction–diffusion models, and diffusion-driven instability has been proposed as a mechanism for spatial pattern formation in a number of areas of both embryology and ecology [2, 3]. Turing's [1] initial work concerned equations with no explicit dependence on space and time. However, in real biological systems, parameters may well vary with position in the domain. For example, in the developing chick limb bud, there is a spatial gradient in gap junction permeability, resulting in a gradient in the effective diffusion coefficients of chemical regulators of pattern [4]. Such a variation has important implications for the patterns predicted by reaction–diffusion models [5–7]. Similarly, in ecological applications, the terrain may vary with position, resulting in a variation in either kinetic parameters or dispersal rates, and the ecological implications of this have also been studied [6, 8, 9].

In ecological applications, model parameters may vary not only in space, but also in time. Such variations generally have the form of either a slow, seasonal variation or a much more rapid, daily variation. In each case, the model parameters oscillate as a function of time. There are a number of papers in the literature on the effects of such forcing in scalar reaction-diffusion equations [10, 11] and in excitable systems [12], but the implications for spatial pattern formation has received surprisingly little attention in the literature. The first study was by Timm & Okubo [13], who investigated numerically the formation of patterns in the planktonic predator-prey model of Levin & Segel [3], when the dispersal rate of the predators varies sinusoidally in time. Building on this numerical study, I recently derived explicit conditions for diffusion driven instability when the predator dispersal rate oscillates with a long period between two constant values [14]. Here I extend this work to the much more general case in which all the model parameters (diffusion coefficients and kinetic parameters) vary with time in a 'square-tooth' manner. The introduction of temporal variation in the kinetics significantly complicates the problem, since even stability to spatially homogeneous perturbations must be investigated by solving a Floquet problem. I derive conditions for diffusion-driven instability in the two biologically relevant limits of very fast and very slow oscillations in the model parameters. I do this by calculating explicitly the Floquet multipliers that determine the stability of the spatially homogeneous solution; in general this solution itself oscillates in time. In particular, the analysis shows that oscillations in the kinetic parameters can have quite different effects from oscillations in the dispersal rates; specifically, small, low frequency oscillations in the diffusion coefficients always stabilize the homogeneous solution, while corresponding oscillations in the kinetic parameters can have either a stabilizing or destabilizing effect.

2 The linear stability problem

I will consider diffusion driven instability in the reaction–diffusion system

$$\partial u/\partial t = D_u(t)\nabla^2 u + f(u,v,t), \tag{1a}$$

$$\partial v/\partial t = D_v(t)\nabla^2 v + g(u,v,t), \tag{1b}$$

where D_u, D_v and the parameters in f and g vary with time in a 'square-tooth' manner. That is, they have one set of constant values on $nT < t < (n+1/2)T$, and another set on $(n+1/2)T < t < (n+1)T$ ($n \in \mathbb{Z}$). Here T is the period, and I will be concerned primarily with the $T \to 0$ and $T \to \infty$ limits. Specifically, I take

$$D_u(t) \equiv D_{u,1} \quad D_v(t) \equiv D_{v,1} \quad f(u,v,t) \equiv f_1(u,v) \quad g(u,v,t) \equiv g_1(u,v) \quad \text{on} \quad nT < t < (n+1/2)T$$

$$D_u(t) \equiv D_{u,2} \quad D_v(t) \equiv D_{v,2} \quad f(u,v,t) \equiv f_2(u,v) \quad g(u,v,t) \equiv g_2(u,v) \quad \text{on} \quad (n+1/2)T < t < (n+1)T$$

($n \in \mathbb{Z}$). I assume that f_i and g_i are such that the system has a spatially homogeneous solution $(u,v) = (u_s(t), v_s(t))$ that is periodic in time with the same period T as the model parameters. Intuitively, one expects such a solution to exist for ecologically realistic models. However, I am not aware of general conditions on f_i and g_i for such a solution to exist, and for the particular nonlinear model discussed in §5, I have only numerical evidence for the existence of such a solution.

To investigate the stability of this homogeneous solution, I look for solutions of (1) of the form $(u(\boldsymbol{x},t), v(\boldsymbol{x},t)) = (u_s(t), v_s(t)) + (U(t), V(t)\exp(i\boldsymbol{k}\cdot\boldsymbol{x})$, where $|U(t)|, |V(t)| \ll 1$. On a spatial domain that is either infinite or finite with suitable boundary conditions (such as zero flux), the Fourier theorem implies that separable solutions of this form are complete for the solution space. However, I make the additional assumption that the appropriate sums of the separable solutions are termwise differentiable, giving a series that is also convergent. To leading order, the separable solution gives a system of linear ordinary differential equations for $W(t) \equiv (U(t), V(t))$ whose coefficients vary periodically in time:

$$\mathrm{d}W/\mathrm{d}t = L_i(t)\, W \quad \text{on} \quad (n+(i-1)/2)\,T < t < (n+i/2)\,T \tag{2}$$

($i = 1, 2, n \in \mathbb{Z}$). Here

$$L_i(t) = \begin{bmatrix} \partial f_i/\partial u\,|_{(u_s(t), v_s(t))} - D_{u,i} K & \partial f_i/\partial v\,|_{(u_s(t), v_s(t))} \\ \partial g_i/\partial u\,|_{(u_s(t), v_s(t))} & \partial g_i/\partial u\,|_{(u_s(t), v_s(t))} - D_{v,i} K \end{bmatrix}$$

with $K = |\boldsymbol{k}|^2$.

In a system of the form (2), whose coefficients vary periodically in time, the $W = \mathbf{0}$ steady state is stable if and only if both Floquet multipliers are less than one in absolute value. In general, the Floquet multipliers cannot be determined analytically. However, for the piecewise constant temporal variations I am considering, I will show that the leading order solutions of (2) in both the $T \to 0$ and $T \to \infty$ limits can be found analytically, enabling explicit calculation of the Floquet multipliers. Both of these limits are of particular biological relevance, since in many ecological systems the population dynamic interactions occur on a time scale that is short compared to a year but long compared to a day. The $T \to 0$ limit then corresponds to daily oscillations in the environment, while the $T \to \infty$ limit corresponds to seasonal oscillations. I will consider the two limits separately; however, the analytic approach is essentially the same in both cases.

3 Diffusion-driven instability as $T \to 0$

In this section, I will consider the limiting case as the period of the parameter oscillations tends to zero. I will show that, as one might expect intuitively, the condition for diffusion-driven instability to occur is simply that it occurs in the reaction-diffusion system given by the average of the oscillating parameters. Moreover, I will derive the leading order correction to this stability condition.

Since $(u, v) = (u_s(t), v_s(t))$ is a periodic solution of (1) with period T, $(u_s(t), v_s(t)) = (u_0, v_0) + O(T)$ as $T \to 0$, where (u_0, v_0) is a steady state of the sum of the two kinetic terms, that is $f_1(u_0, v_0) + f_2(u_0, v_0) = g_1(u_0, v_0) + g_2(u_0, v_0) = 0$. Thus $L_i(t) = A_i + O(T)$, where

$$A_i = \begin{bmatrix} a_i - D_{u,i} K & b_i \\ c_i & d_i - D_{v,i} K \end{bmatrix} \tag{3}$$

with

$$a_i = \left.\frac{\partial f_i}{\partial u}\right|_{(u_0, v_0)} \quad b_i = \left.\frac{\partial f_i}{\partial v}\right|_{(u_0, v_0)} \quad c_i = \left.\frac{\partial g_i}{\partial u}\right|_{(u_0, v_0)} \quad d_i = \left.\frac{\partial g_i}{\partial v}\right|_{(u_0, v_0)}.$$

Note that A_i is independent of t, enabling the leading-order behaviour to be calculated analytically. Specifically, any fundamental matrices of (2) (that is, matrices whose columns are a pair of linearly independent solutions) have the form

$$\Phi(t) = Z_i \Lambda_i(t)\, C_{i,n} \quad \text{on} \quad (n+(i-1)/2)\,T < t < (n+i/2)\,T$$

($i = 1, 2, n \in \mathbb{Z}$). Here $\Lambda_i(t) = \mathrm{diag}\,[\exp(\lambda_i^1 t), \exp(\lambda_i^2 t)]$, where λ_i^1 and λ_i^2 are the eigenvalues of A_i, and Z_i is a matrix whose columns are the corresponding eigenvectors. The (non-singular) matrices $C_{1,n}$ and $C_{2,n}$ are made up of constants of integration. Continuity at $t = (n+1/2)\,T$ implies $C_{2,n}$ as a function of $C_{1,n}$, and continuity at $t = (n+1)\,T$ implies $C_{1,n+1}$ as a function of $C_{2,n}$. Thus, as expected, there are four independent constants of integration, corresponding to arbitrary combinations of two linearly independent solutions for each column of $\boldsymbol{\Phi}$.

The Floquet multipliers are the eigenvalues of

$$\begin{aligned}
&\boldsymbol{\Phi}(nT)^{-1}\boldsymbol{\Phi}((n+1)T)\\
&\quad = \boldsymbol{C}_{1,n}^{-1}\boldsymbol{\Lambda}_1(nT)^{-1}\boldsymbol{Z}_1^{-1}\boldsymbol{Z}_2\boldsymbol{\Lambda}_2((n+1)T)\boldsymbol{C}_{2,n}\\
&\quad = \boldsymbol{C}_{1,n}^{-1}\boldsymbol{\Lambda}_1(nT)^{-1}\boldsymbol{Z}_1^{-1}\boldsymbol{Z}_2\boldsymbol{\Lambda}_2((n+1)T)\boldsymbol{\Lambda}_2((n+1/2)T)^{-1}\boldsymbol{Z}_2^{-1}\boldsymbol{Z}_1\boldsymbol{\Lambda}_1((n+1/2)T)\boldsymbol{C}_{1,n}\\
&\quad = [\boldsymbol{Z}_1\boldsymbol{\Lambda}_1(nT)\boldsymbol{C}_{1,n}]^{-1}\boldsymbol{Z}_2\boldsymbol{\Lambda}_2(T/2)\boldsymbol{Z}_2^{-1}\boldsymbol{Z}_1\boldsymbol{\Lambda}_1(T/2)\boldsymbol{Z}_1^{-1}[\boldsymbol{Z}_1\boldsymbol{\Lambda}_1(nT)\boldsymbol{C}_{1,n}].
\end{aligned}$$

Here I am using the conditions for continuity at $(n+1/2)T$. Therefore, the Floquet multipliers are the eigenvalues of $\boldsymbol{E} = \boldsymbol{M}_2\boldsymbol{M}_1$, where $\boldsymbol{M}_i = \boldsymbol{Z}_i\boldsymbol{\Lambda}_i(T/2)\boldsymbol{Z}_i^{-1}$. Note that for any two matrices $\mathscr{A}$ and $\mathscr{B}$, $\boldsymbol{e}$ is an eigenvector of $\mathscr{A}\cdot\mathscr{B} \Leftrightarrow \mathscr{B}\,\boldsymbol{e}$ is an eigenvector of $\mathscr{B}\cdot\mathscr{A}$, with the same eigenvalue. Thus, as expected intuitively, the Floquet multipliers are symmetric in the subscripts 1 and 2. It is straightforward to calculate the eigenvalues and eigenvectors of $\boldsymbol{A}_1$ and $\boldsymbol{A}_2$, enabling $\boldsymbol{E}$ to be determined. This shows that the two Floquet multipliers μ are given by

$$\mu = \tilde{\mu}\cdot\exp(-\Gamma T/4) \quad \text{where} \quad \tilde{\mu}^2 - B\tilde{\mu} + 1 = 0. \tag{4}$$

Here

$$\begin{aligned}
\Gamma &= \gamma_1+\gamma_2,\\
B &= \tfrac{1}{2}\,e^{(P_1+P_2)T/4}[(1+e^{-P_1T/2})(1+e^{-P_2T/2})\\
&\quad +(1-e^{-P_1T/2})(1-e^{-P_2T/2})(Q_1Q_2+2b_1c_2+2b_2c_1)/(P_1P_2)],
\end{aligned} \tag{5}$$

with

$$\begin{aligned}
\gamma_i &= (D_{v,i}+D_{u,i})K-(a_i+d_i),\\
Q_i &= (D_{v,i}-D_{u,i})K+a_i-d_i,\\
P_i &= \surd(Q_i^2+4b_ic_i).
\end{aligned} \tag{6}$$

The homogeneous solution $(u_s(t), v_s(t))$ is stable to perturbations with wave number $\boldsymbol{k}$ if and only if both roots for $\tilde{\mu}$ have absolute value less than $\exp(\Gamma T/4)$. Diffusion driven instability occurs if and only if the homogeneous solution is stable to homogeneous perturbations (that is $\boldsymbol{k} = \boldsymbol{0}$), and unstable to perturbations with some non-trivial $\boldsymbol{k}$.

Expanding (5) as a Taylor series about $T = 0$ gives

$$B = 2+\alpha\left(\frac{T}{4}\right)^2+\frac{\alpha^2+16\beta}{12}\left(\frac{T}{4}\right)^4,$$

where

$$\begin{aligned}
\alpha &= (Q_1+Q_2)^2+4(b_1+b_2)(c_1+c_2),\\
\beta &= (b_1Q_2-b_2Q_1)(c_1Q_2-c_2Q_1)-(b_1c_2-b_2c_1)^2.
\end{aligned}$$

Therefore

$$\tilde{\mu} = 1\pm\alpha^{1/2}\left(\frac{T}{4}\right)+\frac{\alpha}{2}\left(\frac{T}{4}\right)^2\pm\frac{\alpha^2+4\beta}{6\alpha^{1/2}}\left(\frac{T}{4}\right)^3+\ldots,$$

while

$$e^{-\Gamma T/4} = 1-\Gamma\left(\frac{T}{4}\right)+\frac{\Gamma^2}{2}\left(\frac{T}{4}\right)^2-\frac{\Gamma^3}{6}\left(\frac{T}{4}\right)^3+\ldots.$$

Thus, the two Floquet multipliers are

$$\begin{aligned}
\mu = \tilde{\mu}\,e^{-\Gamma T/4} &= 1+(\pm\alpha^{1/2}-\Gamma)\left(\frac{T}{4}\right)+\tfrac{1}{2}(\pm\alpha^{1/2}-\Gamma)^2\left(\frac{T}{4}\right)^2\\
&\quad +[\pm\tfrac{2}{3}\beta/\alpha^{1/2}+\tfrac{1}{6}(\pm\alpha^{1/2}-\Gamma)^3]\left(\frac{T}{4}\right)^3+\ldots.
\end{aligned}$$

The $O(T)$ differences between $\boldsymbol{L}_i$ and $\boldsymbol{A}_i$ make an $O(T^2)$ contribution to the Floquet multipliers. Thus if $\alpha < 0$, the Floquet multipliers are complex conjugates to leading order, with absolute value $1-\Gamma(T/4)+O(T^2)$, while if $\alpha \geqslant 0$ there are two real (positive) Floquet multipliers, with values $1+(\pm\alpha^{1/2}-\Gamma)(T/4)+O(T^2)$.

For diffusion-driven instability, it is necessary that both Floquet multipliers have absolute value less than 1 when $K = 0$, which holds if and only if

$$\begin{aligned}(\alpha < 0 \quad \text{and} \quad \Gamma > 0) \quad \text{or} \quad (\alpha > 0 \quad &\text{and} \quad \Gamma > \alpha^{1/2}) \\ \Leftrightarrow \Gamma > 0 \quad &\text{and} \quad \Gamma^2 > \alpha \\ \Leftrightarrow \bar{a}+\bar{d} < 0 \quad &\text{and} \quad (\bar{a}+\bar{d})^2 > (\bar{a}-\bar{d})^2+4\bar{b}\bar{c} \\ \Leftrightarrow \bar{a}+\bar{d} < 0 \quad &\text{and} \quad \bar{a}\bar{d}-\bar{b}\bar{c} > 0,\end{aligned}$$

where $\bar{a} = (a_1+a_2)/2$, etc. Provided these conditions hold, diffusion-driven instability will occur if and only if one of the Floquet multipliers has absolute value greater than one for some $K > 0$,

$$\begin{aligned}&\Leftrightarrow \alpha > \Gamma^2 \quad \text{for some} \quad K > 0 \\ &\Leftrightarrow [(\bar{D}_v-\bar{D}_u)K+\bar{a}-\bar{d}]^2+4\bar{b}\bar{c} > [(\bar{D}_v+\bar{D}_u)K-\bar{a}-\bar{d}]^2 \quad \text{for some} \quad K > 0 \\ &\Leftrightarrow \bar{D}_u\bar{D}_v K^2-(\bar{a}\bar{D}_v+\bar{d}\bar{D}_u)K+(\bar{a}\bar{d}-\bar{b}\bar{c}) < 0 \quad \text{for some} \quad K > 0 \\ &\Leftrightarrow \bar{a}\bar{D}_v+\bar{d}\bar{D}_u > 0 \quad \text{and} \quad (\bar{a}\bar{D}_v+\bar{d}\bar{D}_u)^2 > 4\bar{D}_u\bar{D}_v(\bar{a}\bar{d}-\bar{b}\bar{c}).\end{aligned}$$

Here $\bar{D}_u = (D_{u,1}+D_{u,2})/2$ and $\bar{D}_v = (D_{v,1}+D_{v,2})/2$. Therefore, the condition for diffusion-driven instability to occur when the parameters oscillate very rapidly between two sets of constant values is simply that diffusion-driven instability should occur in the reaction-diffusion system given by the sum of the two sets of equations.

Suppose now that the parameters are exactly on the border between diffusion-driven instability occurring and not occurring, to first order in T. Then $\alpha \geqslant \Gamma^2$ for all $K \geqslant 0$, with equality for some $K > 0$, say $K = K_c$. The above analysis implies that

$$K_c = (\bar{a}\bar{D}_v+\bar{d}\bar{D}_u)/(2\bar{D}_u\bar{D}_v).$$

Whether or not diffusion-driven instability will occur for very small T will then depend upon higher order terms in the expansion of the Floquet multipliers as power series in T when $K = K_c$. In general, this depends upon the details of the spatially homogeneous solution $(u_s(t), v_s(t))$, since the difference between this solution and (u_0, v_0) makes a $O(T^2)$ contribution to the Floquet multipliers. However, one simple case in which the higher order terms can be determined explicitly is when the two sets of kinetics have a common steady state, so that $(u_s(t), v_s(t)) \equiv (u_0, v_0)$. In this case, $\boldsymbol{L}_i = \boldsymbol{A}_i$ ($i = 1$ and 2), and both the Floquet multipliers are real when $K = K_c$, with the larger one being

$$\mu = 1+\tfrac{2}{3}\beta/\alpha^{1/2}(T/4)^3+O(T^4).$$

Therefore, diffusion-driven instability will occur if and only if $\beta > 0$ when $K = K_c$. I have not been able to find a simple criterion that determines the sign of $\beta|_{K=K_c}$, but it is straightforward to show that the sign will be different in different parameter regimes. For example, when $b_1 \neq b_2$ and $c_1 \neq c_2$, with all other parameters constant,

$$\begin{aligned}\beta|_{K=K_c} &= 4[(\bar{D}_v-\bar{D}_u)K_c+\bar{a}-\bar{d}]^2\hat{b}\hat{c}-4(\bar{b}\hat{c}-\bar{c}\hat{b})^2 \\ &= 4\hat{c}^2\bar{c}^2\left(\frac{\hat{b}}{\hat{c}}+\frac{\bar{b}\bar{D}_u}{\bar{c}\bar{D}_v}\right)\cdot\left(\frac{\hat{b}}{\hat{c}}+\frac{\bar{b}\bar{D}_v}{\bar{c}\bar{D}_u}\right),\end{aligned}$$

which changes sign as the ratio $\hat{b}/\hat{c}$ is varied. Here I am using the notation $\hat{b} = (b_2-b_1)/2$, etc.

4 Diffusion-driven instability as $T\to\infty$

To investigate the $T\to\infty$ limit, I make an additional assumption on the two sets of kinetics, that for both $i = 1$ and $i = 2$, $f_i(u, v)$ and $g_i(u, v)$ have a unique steady state in the positive first quadrant, that is both globally attracting in this quadrant and also linearly stable; the second assumption rules out the possibility of neutral stability. I denote the steady states by $(u_{s,i}, v_{s,i})$ $(i = 1, 2)$. This assumption holds for most predator–prey systems that sustain stationary spatial patterns. Under this assumption, in the limit as $T\to\infty$, any spatially homogeneous periodic solution will have the qualitative form illustrated in Fig. 1, tending towards $(u_{s,1}, v_{s,1})$ and $(u_{s,2}, v_{s,2})$ in the first and second half of each period, respectively. That is, $(u_s(t), v_s(t)) = (u_{s,i}, v_{s,i})+(u_e(t), v_e(t))$ on $(n+(i-1)/2)T < t < (n+i/2)T$, where $u_e(t)$ and $v_e(t)\to 0$ exponentially as $t\to\infty$. I now write

$$\begin{aligned}\boldsymbol{L}_i(t) &\equiv \begin{bmatrix} \partial f_i/\partial u|_{(u_s(t),v_s(t))}-D_{u,i}K & \partial f_i/\partial v|_{(u_s(t),v_s(t))} \\ \partial g_i/\partial u|_{(u_s(t),v_s(t))} & \partial g_i/\partial u|_{(u_s(t),v_s(t))}-D_{v,i}K\end{bmatrix} \\ &= \begin{bmatrix} \partial f_i/\partial u|_{(u_{s,i},v_{s,i})}-D_{u,i}K & \partial f_i/\partial v|_{(u_{s,i},v_{s,i})} \\ \partial g_i/\partial u|_{(u_{s,i},v_{s,i})} & \partial g_i/\partial u|_{(u_{s,i},v_{s,i})}-D_{v,i}K\end{bmatrix}+\boldsymbol{L}_e(t).\end{aligned}$$

Then $\boldsymbol{L}_e(t)\to\boldsymbol{0}$ exponentially as $t\to\infty$. Therefore $\boldsymbol{L}_e(t)$ makes a contribution to the change in a fundamental matrix over one period that is $O(1)$ as $T\to\infty$; in contrast, the constant matrices $\boldsymbol{L}_i(t)-\boldsymbol{L}_e(t)$ $(i = 1, 2)$ makes a $O(T)$ contribution. Therefore, the leading-order behaviour of (2) in the limit as $T\to\infty$ is given by the solution of the piecewise constant equation $\mathrm{d}\boldsymbol{W}/\mathrm{d}t = \boldsymbol{A}_i\boldsymbol{W}$ on $(n+(i-1)/2)T < t < (n+i/2)T$ $(i = 1, 2, n\in\mathbb{Z})$. Here $\boldsymbol{A}_i$ is as given in (3), with a_i, b_i, c_i and d_i redefined as

$$a_i = \left.\frac{\partial f_i}{\partial u}\right|_{(u_{s,i},v_{s,i})} \qquad b_i = \left.\frac{\partial f_i}{\partial v}\right|_{(u_{s,i},v_{s,i})} \qquad c_i = \left.\frac{\partial g_i}{\partial u}\right|_{(u_{s,i},v_{s,i})} \qquad d_i = \left.\frac{\partial g_i}{\partial v}\right|_{(u_{s,i},v_{s,i})}.$$

I maintain these new definitions throughout this section. The Floquet multipliers of this leading order system can then be determined exactly as in the previous section, and are given by (4). Now the quantities P_1 and P_2, defined in (6), are either real and positive or pure imaginary, so that $B/\exp[(P_1+P_2)T/4] = O(1)$ as $T\to\infty$. This implies that one root for $\tilde{\mu}$ is $O(1)$ as $T\to\infty$, while the other satisfies $\tilde{\mu}/\exp[(P_1+P_2)T/4] = O(1)$. Recall that the corresponding Floquet multipliers are given by $\mu = \tilde{\mu}\cdot\exp(-\Gamma T/4)$. Therefore, the absolute values of the Floquet multipliers are either $\ll 1$ or $\gg 1$ as $T\to\infty$ (apart from at critical transition values, at which the corrections due to $\boldsymbol{L}_e$ determine stability), and

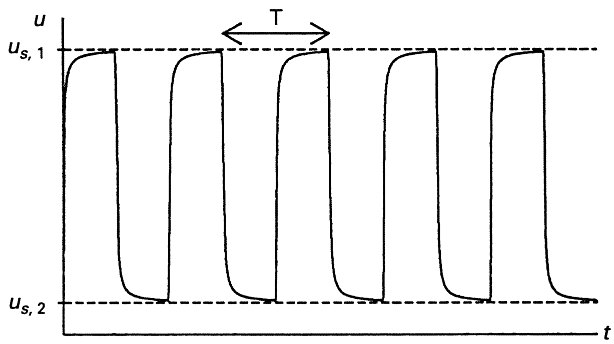

FIGURE 1. The qualitative form of a spatially homogeneous, temporally periodic solution of (1) for $T \gg 1$, under the assumption that both sets of kinetics (that is, for $i = 1$ and 2) have a unique steady state in the first quadrant, that is globally attracting within that quadrant. The solution tends towards the steady states $(u_{s,1}, v_{s,1})$ and $(u_{s,2}, v_{s,2})$ on the first and second halves of the period, respectively.

homogeneous solution $(u_s(t), v_s(t))$ is stable to perturbations with wave number $\boldsymbol{k}$ if and only if both of the Floquet multipliers are $\leqslant 1$, that is if and only if

$$\Gamma > \mathrm{Re}(P_1) + \mathrm{Re}(P_2). \tag{7}$$

I consider briefly the autonomous equations

$$\partial u/\partial t = D_{u,i} \nabla^2 u + f_i(u, v) \tag{8a}$$

$$\partial v/\partial t = D_{v,i} \nabla^2 v + g_i(u, v), \tag{8b}$$

which have a steady state

$$(u, v) = (u_{s,i}, v_{s,i}). \tag{9}$$

This steady state is stable to perturbations of wave number $\boldsymbol{k}$ if and only if $\gamma_i > \mathrm{Re}(P_i)$. (Recall that $\Gamma = \gamma_1 + \gamma_2$.) Thus, as expected intuitively, the homogeneous solution $(u_s(t), v_s(t))$ of (1) is stable/unstable to a perturbation of wave number $\boldsymbol{k}$ whenever the steady state (9) of (8) is stable/unstable to that perturbation for both $i = 1$ and $i = 2$. However, in general (9) may be stable to the perturbation for one i and unstable for the other, and this requires a more detailed investigation of the Floquet multipliers. I will now show that (7) holds if and only if all of the following conditions hold:

(i) $\Gamma^2 > P_1^2$;
(ii) $\Gamma^2 > P_2^2$;
(iii) $(\Gamma^2 - P_1^2 - P_2^2)^2 > 4P_1^2 P_2^2$;
(iv) $\Gamma > 0$.

(7) ⇒ (i), (ii), (v): These implications are trivial, since $\mathrm{Re}(P_i) \geqslant 0$.

(7) ⇒ (iii): If $P_1 \in \mathbb{R}$ and $P_2 \notin \mathbb{R}$, or *vice versa*, then $P_1^2 P_2^2 < 0$, so that (iii) holds trivially. Expanding the right-hand side of (iii) gives the condition as

$$\Gamma^4 - 2(P_1^2 + P_2^2)\Gamma^2 + (P_1^2 - P_2^2)^2 > 0,$$

so that (iii) also holds trivially if both P_1 and P_2 are pure imaginary. It remains to consider the case P_1, $P_2 \in \mathbb{R}$. Then (7) is

$$\Gamma > P_1 + P_2 \Rightarrow \Gamma^2 > P_1^2 + P_2^2 + 2P_1 P_2 \Rightarrow \Gamma^2 - P_1^2 P_2^2 > 2P_1 P_2,$$

which implies (iii), since P_1 and P_2 are positive when they are real.

(i)–(iv) ⇒ *(7)*: I consider four cases separately:

$P_1 \notin \mathbb{R}, P_2 \notin \mathbb{R}$: then (iv) ⇒ (7).

$P_1 \in \mathbb{R}, P_2 \notin \mathbb{R}$: then (i) ⇒ (7).

$P_1 \notin \mathbb{R}, P_2 \in \mathbb{R}$: then (ii) ⇒ (7).

$P_1 \in \mathbb{R}, P_2 \in \mathbb{R}$: then $P_1^2 P_2^2 > 0$, so that (iii) $\Rightarrow \Gamma^2 > (P_1 + P_2)^2 \Rightarrow$ (7).

4.1 Stability to homogeneous perturbations

I require that the homogeneous solution $(u_s(t), v_s(t))$ is stable to homogeneous perturbations, so that conditions (i)–(iv) must hold when $K = 0$. I write $\tau_i = a_i + d_i$ and $\Delta_i = a_i d_i - b_i c_i$, denoting the trace and determinant of the equation matrix A_i when $K = 0$. Then conditions (i)–(iv) simplify to the following expressions:

$$\text{(i)}\,|_{K=0} \qquad \tau_2(2\tau_1 + \tau_2) + 4\Delta_1 > 0, \tag{10a}$$

$$\text{(ii)}\,|_{K=0} \qquad \tau_1(2\tau_2 + \tau_1) + 4\Delta_2 > 0, \tag{10b}$$

$$\text{(iii)}\,|_{K=0} \qquad (\tau_2 \Delta_1 + \tau_1 \Delta_2)(\tau_1 + \tau_2) + (\Delta_1 - \Delta_2)^2 > 0 \tag{10c}$$

$$\text{(iv)}\,|_{K=0} \qquad \tau_1 + \tau_2 < 0. \tag{10d}$$

These conditions simplify greatly when $\tau_1 = \tau_2 = \tau$, say, giving

$$\left(\frac{\Delta_1}{\tau^2} - \frac{\Delta_2}{\tau^2}\right)^2 + 2\left(\frac{\Delta_1}{\tau^2} + \frac{\Delta_2}{\tau^2}\right) > 0 \quad \text{and} \quad \frac{\Delta_1}{\tau^2} > -3/4 \quad \text{and} \quad \frac{\Delta_2}{\tau^2} > -3/4, \tag{11}$$

which defines a parameter space that is illustrated in Fig. 2. When $\tau_1 \neq \tau_2$, I have been unable to simplify (10) significantly.

4.2 Conditions (i) and (ii) for instability

Since all the diffusion coefficients are positive, (10d) implies that (iv) holds for all $K > 0$. Therefore, the homogeneous solution $(u_s(t), v_s(t))$ will be unstable to a suitable inhomogeneous perturbation if and only if one or more of conditions (i), (ii) and (iii) fail to hold for some $K > 0$. I begin by considering condition (i), which fails if and only if $0 > \Gamma^2 - P_1^2 = q_1(K)$, where $q_1(\cdot)$ is a quadratic. The problem is symmetric in u and v, and thus I can assume without loss of generality that $D_{v,1} \geqslant D_{u,1}$; I make this assumption within this subsection only. The expression for $q_1(K)$ is then simplified by writing

$$\delta = (D_{v,1} - D_{u,1})/(2D_{u,1} + D_{u,2} + D_{v,2})\,(> 0),$$

$$\tilde{K} = (2D_{u,1} + D_{u,2} + D_{v,2})\,K,$$

$$\alpha = 2a_1 + a_2 + d_2,$$

$$\beta = a_1 - d_1.$$

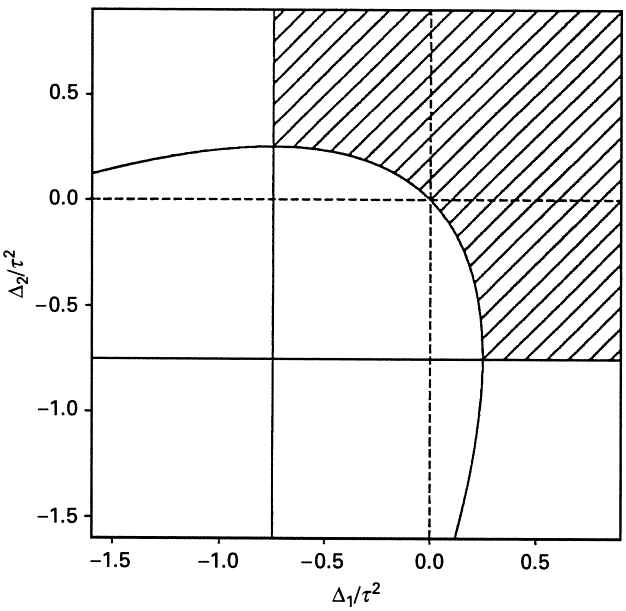

FIGURE 2. An illustration of the parameter space defined in (11). The shaded region is that in which all three inequalities in (11) hold. When $\tau_1 = \tau_2 = \tau$, the kinetic parameters must lie in this region for the homogeneous solution $(u_s(t), v_s(t))$ to be stable to homogeneous perturbations in the limit as $T \to \infty$.

This gives $q_1(K) \equiv q_2(\tilde{K})$, where

$$q_2(\tilde{K}) = (2\delta+1)\tilde{K}^2 - 2(\alpha\delta+\alpha-\beta)\tilde{K} + (\alpha^2 - 2\alpha\beta - 4b_1 c_1).$$

Condition (i) fails for some $K > 0$ if and only if $q_2(\tilde{K}) < 0$ for some $\tilde{K} > 0$. Now (10a) implies that $q_2(0) > 0$, and thus $q_2(\tilde{K}) < 0$ for some $\tilde{K} > 0$

$$\begin{aligned} &\Leftrightarrow (\alpha\delta+\alpha-\beta) > 0 \\ &\quad \text{and} \quad (\alpha\delta+\alpha-\beta)^2 - (2\delta+1)(\alpha^2 - 2\alpha\beta - 4b_1 c_1) > 0, \\ &\Leftrightarrow \alpha\delta > \beta - \alpha \\ &\quad \text{and} \quad q_3(\delta) \equiv \alpha^2\delta^2 + 2(\alpha\beta + 4b_1 c_1)\delta + (\beta^2 + 4b_1 c_1) > 0. \end{aligned} \tag{12}$$

Now $\beta - \alpha = -(a_1 + a_2 + d_1 + d_2) > 0$ using (10d), and thus $\alpha\delta + \beta - \alpha > 0$ if and only if $\alpha > 0$ and $\delta > (\beta/\alpha) - 1$. Moreover,

$$\begin{aligned} q_3(\beta/\alpha - 1) &= (1 - 2\beta/\alpha)(\alpha^2 - 2\alpha\beta + 4) \\ &= (1 - 2\beta/\alpha)[\tau_2(2\tau_1 + \tau_2) + 4\Delta_1]. \end{aligned}$$

We have $\beta > \alpha$, and thus when $\alpha > 0$, $1 - 2\beta/\alpha < 0$. Together with (10a), this implies that $q_3(\beta/\alpha - 1) < 0$. Therefore, condition (i) fails for some $K > 0$ if and only if $\alpha > 0$ and $\delta > \delta_c$, where δ_c is the larger root of (12), that is

$$\delta_c = -\left(\frac{\beta}{\alpha}\right) - \left(\frac{4b_1 c_1}{\alpha^2}\right) + \left[\left(\frac{4b_1 c_1}{\alpha^2}\right)^2 + 2\left(\frac{4b_1 c_1}{\alpha^2}\right)\left(\frac{\beta}{\alpha}\right) - \left(\frac{4b_1 c_1}{\alpha^2}\right)\right]^{1/2}. \tag{13}$$

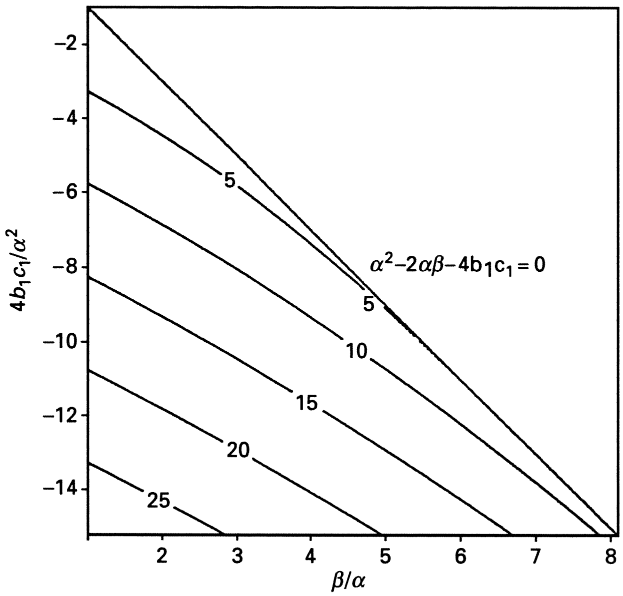

FIGURE 3. The variation of δ_c, defined in (13), with the kinetic parameter values. Stability to homogeneous perturbations requires $\beta > \alpha$ and $\alpha^2-2\alpha\beta-4b_1c_1 > 0$, and δ_c is only defined when $\alpha > 0$. I plot contours of δ_c in the parameter space defined by these constraints. The kinetic parameters must satisfy other conditions for the homogeneous solution to be stable to homogeneous perturbations, but these depend upon b_2c_2, which has no effect on δ_c. Provided that these conditions are also satisfied, and under the assumption that $D_{v,1} > D_{u,1}$, diffusion-driven instability will occur if and only if $(D_{v,1}-D_{u,1})/(2D_{u,1}+D_{u,2}+D_{v,2}) > \delta_c$.

The variation in δ_c with the kinetic parameters is illustrated in Fig. 3. Diffusion-driven instability can also occur by condition (ii) failing, and the parameter regime in which this occurs is given by interchanging the subscripts 1 and 2 in the expressions for δ, α, β and δ_c.

4.3 Condition (iii) for instability

Diffusion driven instability will also occur if condition (iii) fails for some $K > 0$. This requires $(\Gamma^2-P_1^2-P_2^2)^2 < 4P_1^2P_2^2$, which simplifies to

$$F(K)+G(K) < 0 \quad \text{for some} \quad K > 0, \tag{14}$$

where

$$F(K) \equiv \bar{D}_u\bar{D}_vK^2-(\bar{a}\bar{D}_v+\bar{d}\bar{D}_u)K+(\bar{a}\bar{d}-\overline{bc}) \tag{15}$$

and

$$G(K) \equiv -[\{\bar{D}_vK-\bar{d}\}\{(\hat{D}_v-\hat{D}_u)K+(\hat{a}-\hat{d})\}+\widehat{bc}][\{\bar{D}_uK-\bar{a}\}\{(\hat{D}_v-\hat{D}_u)K+(\hat{a}-\hat{d})\}-\widehat{bc}][(\bar{D}_u+\bar{D}_v)K-(\bar{a}+\bar{d})]^{-2}. \quad (16).$$

Here, $\overline{bc} = (b_1c_1+b_2c_2)/2$ and $\widehat{bc} = (b_2c_2-b_1c_1)/2$. When all the parameters are constant, $G(K) \equiv 0$, so this gives the well known condition for diffusion-driven instability in a constant environment (see [15] for review). In some cases, conditions (i) and (ii) also fail when all the parameters are constant, but I have shown previously [14] that this only occurs when condition (iii) also fails.

To investigate the implications of this dispersion relation more generally, I begin by considering the case in which only the diffusion coefficients vary temporally, so that $\hat{a} = \hat{b} = \hat{c} = \hat{d} = 0$. Then

$$F(K)+G(K) = -\overline{bc}+[\bar{D}_u K-\bar{a}]\cdot[\bar{D}_v K-\bar{d}]\cdot[(D_{u,1}+D_{v,2})K-(\bar{a}+\bar{d})]$$
$$[(D_{u,2}+D_{v,1})K-(\bar{a}+\bar{d})]\cdot[(\bar{D}_u+\bar{D}_v)K-(\bar{a}+\bar{d})]^{-2}. \quad (17)$$

When the kinetic parameters are constant, (10) imply that $\bar{a}+\bar{d} < 0$ and $\bar{a}\bar{d} > \overline{bc}$. Therefore,

$$F(K)+G(K) > -\bar{a}\bar{d}+[\bar{D}_u K-\bar{a}]\cdot[\bar{D}_v K-\bar{d}]\cdot[(D_{u,1}+D_{v,2})K-(\bar{a}+\bar{d})]$$
$$[(D_{u,2}+D_{v,1})K-(\bar{a}+\bar{d})]\cdot[(\bar{D}_u+\bar{D}_v)K-(\bar{a}+\bar{d})]^{-2},$$

and simplifying this shows that $F(K)+G(K) > 0\,\forall\, K > 0$ when $\bar{a}$ and $\bar{d}$ are both negative. Therefore, $\bar{a}$ and $\bar{d}$ must have opposite signs whenever (14) holds, and so $\overline{bc} < \bar{a}\bar{d} < 0$. Equation (17) then implies that a necessary condition for $F(K)+G(K) < 0$ is $(\bar{D}_u K-\bar{a})(\bar{D}_v K-\bar{d}) < 0$, so that

$$G(K) = -K^2(\hat{D}_v-\hat{D}_u)^2(\bar{D}_u K-\bar{a})(\bar{D}_v K-\bar{d})[(\bar{D}_u+\bar{D}_v)K-(\bar{a}+\bar{d})]^{-2} \geqslant 0.$$

That is, $G(K) \geqslant 0$ whenever (14) holds. Therefore, when the kinetic parameters are constant, (iii) will fail if and only if the conditions for diffusion driven instability in a constant environment are satisfied by $\bar{D}_u$ and $\bar{D}_v$, and $|\hat{D}_v-\hat{D}_u|$ is less than a critical value that depends upon $\bar{D}_u, \bar{D}_v$ and the kinetic parameters. This result is a simple extension of the condition I derived previously [14] for the case of only one diffusion coefficient varying in time.

When the kinetic parameters also vary in time, I have been unable to derive simple conditions on the parameters for (14) to hold. However, a special case that can be solved analytically is when there are small oscillations in the parameter values. When all the parameters are constant, the dispersion relation (14) is a simple quadratic with a minimum at $K = K_c \equiv (a\bar{D}_v+\bar{d}\bar{D}_u)/(2\bar{D}_u\bar{D}_v)$. I suppose that the parameters have constant values such that (10) holds for the kinetic parameters, and $\bar{a}\bar{D}_v+\bar{d}\bar{D}_u > 0$, so that $K_c > 0$, with $F(K_c) = 0$. The system is then on the borderline between diffusion-driven instability occurring and not occurring. I consider whether the introduction of a small temporal variation in parameter values will stabilize or destabilize the homogeneous solution. This depends upon the sign of $G(K_c)$, since all the other conditions will continue to hold for sufficiently small variations. Straightforward substitution shows that

$$G(K_c) = \left[2\bar{D}_u\bar{D}_v(\hat{a}-\hat{d})+(\bar{a}\bar{D}_v+\bar{d}\bar{D}_u)(\hat{D}_v-\hat{D}_u)+\left(\frac{4\bar{D}_u\bar{D}_v^2}{\bar{a}\bar{D}_v-\bar{d}\bar{D}_u}\right)\widehat{bc}\right]$$
$$\times\left[2\bar{D}_u\bar{D}_v(\hat{a}-\hat{d})+(\bar{a}\bar{D}_v+\bar{d}\bar{D}_u)(\hat{D}_v-\hat{D}_u)+\left(\frac{4\bar{D}_u^2\bar{D}_v}{\bar{a}\bar{D}_v-\bar{d}\bar{D}_u}\right)\widehat{bc}\right]$$
$$\times[4\bar{D}_v\bar{D}_u(\bar{D}_v-\bar{D}_u)^2]^{-1}. \quad (18)$$

I have shown that $\bar{a}$ and $\bar{d}$ have opposite signs, and, without loss of generality, I assume, for the case of small variations only, that $\bar{a} > 0$ and $\bar{d} < 0$. This implies that $\bar{D}_v > \bar{D}_u$. Then (18) implies that $G(K_c) < 0$, so that the small temporal parameter variation destabilizes the homogeneous solution, if and only if

$$\frac{-2\bar{D}_v}{\bar{a}\bar{D}_v-\bar{d}\bar{D}_u} < \left(\frac{\hat{a}-\hat{d}}{\widehat{bc}}\right)+\left(\frac{\bar{a}\bar{D}_v+\bar{d}\bar{D}_u}{2\bar{D}_u\bar{D}_v}\right)\cdot\left(\frac{\hat{D}_v-\hat{D}_u}{bc}\right) < \frac{-2\bar{D}_u}{\bar{a}\bar{D}_v-\bar{d}\bar{D}_u}. \quad (19)$$

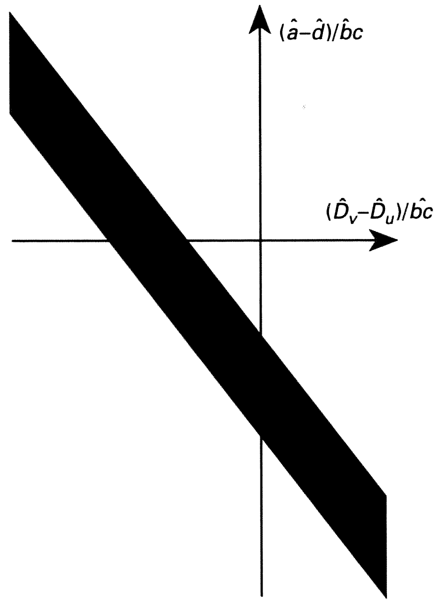

FIGURE 4. An illustration of the parameter domain defined in (19) (shaded). A small temporal oscillation in parameter values will destabilize a system that is on the borderline between stability and instability provided that the parameters satisfy (19).

This condition is illustrated in Fig. 4. Note, in particular, that a small variation in the diffusion coefficients alone always stabilizes the homogeneous solution, while small variations in the kinetics alone can either stabilize or destabilize the homogeneous solution.

5 The form of the solution

To investigate the parameter regions in which the spatially homogeneous solution $u_s(t)$, $v_s(t)$) will be driven unstable by diffusion, I have solved (using separation of variables) the linear partial differential equations governing the leading order behaviour of small perturbations to this homogeneous solution, for both $T \ll 1$ and $T \gg 1$. However, in the case of diffusion-driven instability in a constant environment, this linear theory is in fact rather more powerful than simply the determination of conditions for diffusion-driven instability to occur. For a wide range of systems of non-linear partial differential equations, numerical solutions with parameter values close to a Turing bifurcation point evolve to patterns that vary in space, but are constant in time, with qualitative form very similar to the sinusoidal solution predicted by the linear theory (reviewed in [15]). That is, the nonlinear patterns for the two species u and v are approximately sinusoidal, and both the spatial wavelength and the amplitude ratio of the u and v waves are very similar to that predicted by the linear theory. Of course, the linear solutions grow without bound (but with a limiting shape), whereas the nonlinearities keep the solution of the full system bounded.

I now consider whether a similar correspondence between linear and nonlinear solutions applies when the parameter values oscillate in a square-tooth manner. Investigation of this is only possible numerically, and thus requires the specification of a particular system of

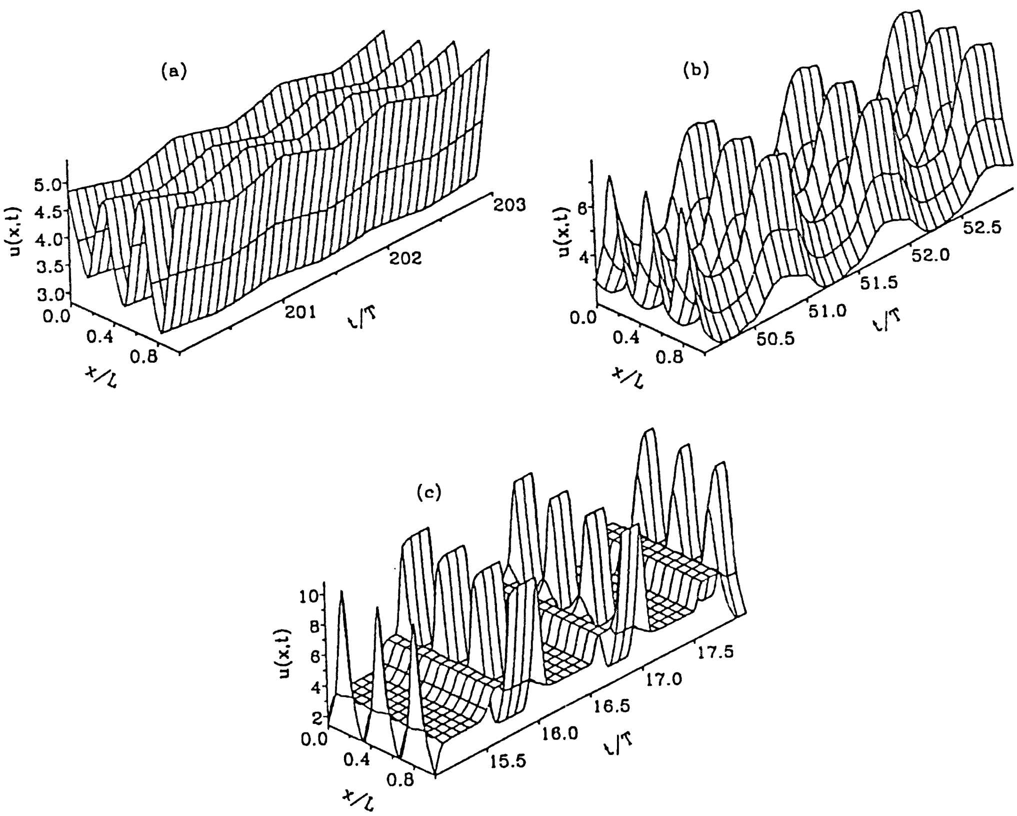

FIGURE 5. Numerical solutions of the reaction-diffusion system with kinetics given in (20). I show the variation of $u(x, t)$ with position x and time t once sufficient time has elapsed for transients to decay. The period T is (a) $T = 0.5$, (b) $T = 5$, (c) $T = 400$; all the other parameters are the same in the three parts, with values $D_{u,1} = 1$, $D_{u,2} = 0.75$, $D_{v,1} = 8$, $D_{v,2} = 6$, $\mu_1 = 0.8$, $\mu_2 = 0.7$, $\kappa_1 = \kappa_2 = 0.5$, $\sigma_1 = \sigma_2 = 1$. I solved the equations on $0 < x < L = 20$, with zero flux boundary conditions at $x = 0$ and $x = L$. At $t = 0$, u and v consisted of small, random perturbations about $u_{s,1}$ and $v_{s,1}$, and the final solutions are not sensitive to the details of the perturbations. The numerical solution used the method of lines, with the resulting ordinary differential equation system integrated using Gear's method.

equations. For this purpose, I use the predator–prey model proposed by Segel & Jackson [16], for which the kinetics are

$$f_i(u, v) = u + \kappa_i u^2 - \mu_i uv, \tag{20a}$$

$$g_i(u, v) = \sigma_i uv - v^2 \tag{20b}$$

($i = 1, 2$), where the parameters σ_i, κ_i and μ_i satisfy $0 < \kappa_i < \min(\mu_i \sigma_i, \sigma_i)$. Numerical investigation suggests that for a given set of parameters, these kinetics have a unique spatially homogeneous, temporally periodic solution; however, in view of the large number of parameters, I have not attempted a systematic search of parameter space. Moreover, each set of kinetics (that is $i = 1$ and $i = 2$ considered separately) has a unique, globally attracting steady state in the first quadrant. Numerical solutions of the partial differential equations in one space dimension suggest that when the homogeneous solution is driven

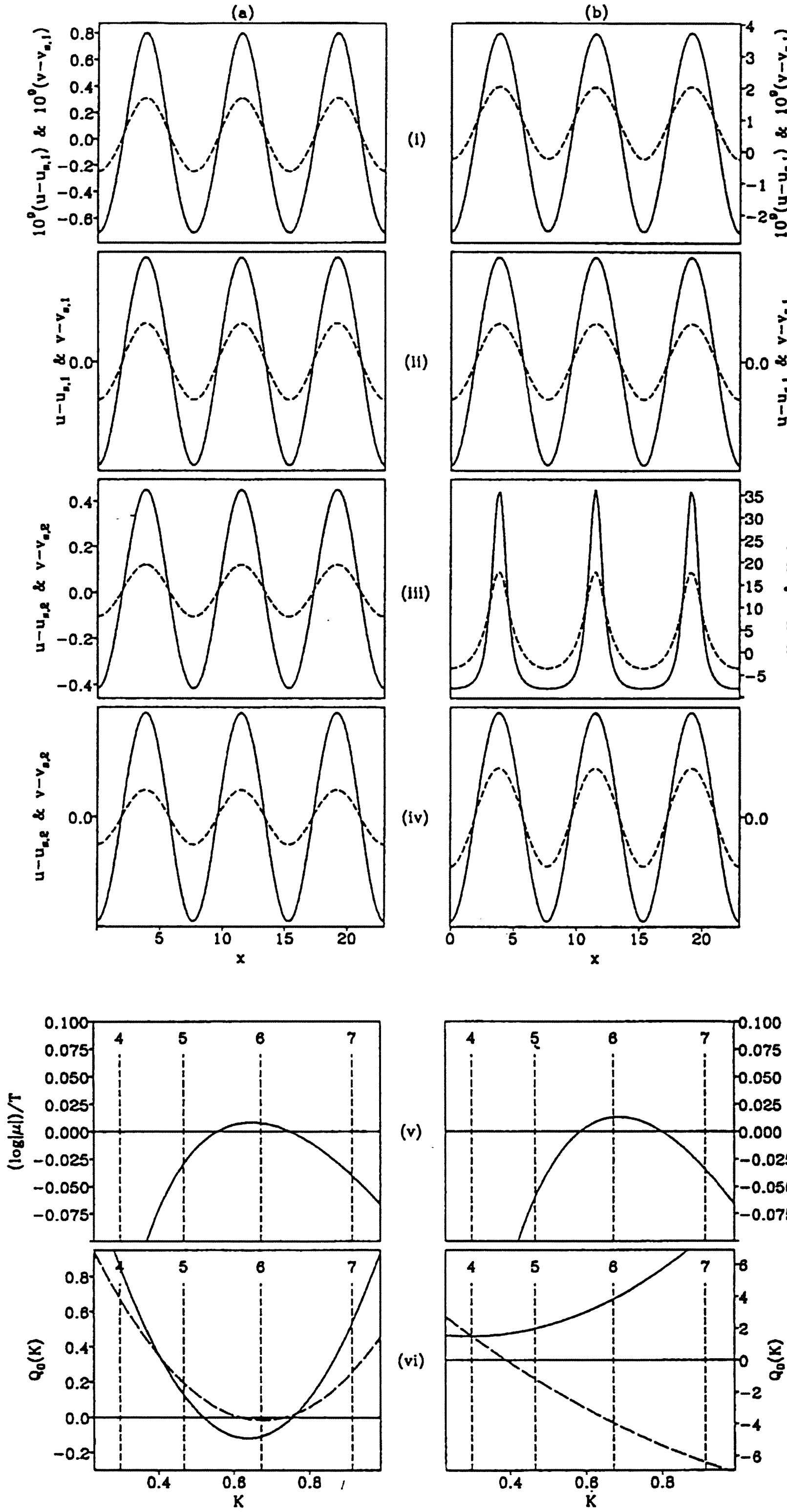

FIGURE 6. For legend see opposite.

unstable by diffusion, the model solutions evolve to spatial patterns that vary periodically in time, with the same period T as the model parameters. For small T, the solution has the form of small, rapid oscillations about a mean spatial pattern, while for very large T, the solution settles down to a different spatial pattern on each half of the period (Fig. 5).

For both $T \ll 1$ and $T \gg 1$, the leading order behaviour of the separable solution predicted by the linear theory, corresponding to a particular value of K, is sinusoidal in space, with the form $(\tilde{u}, \tilde{v}) = \boldsymbol{W}^*(t) \exp(i\boldsymbol{k} \cdot \boldsymbol{x})$. Here $\boldsymbol{W}^*$ is the solution of the linear system (2) corresponding to the (unique) Floquet multiplier, μ^* say, that is greater than one in absolute value; I take a_i, b_i, c_i and d_i to be the appropriate partial derivatives, according to whether the $T \to 0$ or $T \to \infty$ limit is being considered. I denote by $\boldsymbol{e}^*$ the normalized eigenvector of $\boldsymbol{E} \equiv \boldsymbol{M}_2 \boldsymbol{M}_1$ corresponding to eigenvalue μ^*. Then the eigenvector of $\boldsymbol{\Phi}(nT)^{-1} \boldsymbol{\Phi}((n+1)T)$ corresponding to the eigenvalue μ^* is $[\boldsymbol{Z}_1 \boldsymbol{\Lambda}_1(nT) \boldsymbol{C}_{n,1}]^{-1} \boldsymbol{e}^*$. The corresponding solution of the linear differential equation is simply the product of the solution matrix $\boldsymbol{\Phi}(t)$ and the eigenvector of $\boldsymbol{\Phi}(nT)^{-1} \boldsymbol{\Phi}((n+1)T)$, giving

$$\boldsymbol{W}^*(t) = \begin{cases} \boldsymbol{Z}_1 \boldsymbol{\Lambda}_1(t-nT) \boldsymbol{Z}_1^{-1} \boldsymbol{e}^* & nT < t < (n+1/2)T \\ \boldsymbol{Z}_2 \boldsymbol{\Lambda}_2(t-(n+1/2)T) \boldsymbol{Z}_2^{-1} \boldsymbol{Z}_1 \boldsymbol{\Lambda}_1(T/2) \boldsymbol{Z}_1^{-1} \boldsymbol{e}^* & (n+1/2)T < t < (n+1)T. \end{cases}$$

Since I have an expression for the leading order behaviour of μ^* in the $T \to 0$ and $T \to \infty$ limits, $\boldsymbol{W}^*(t)$ can be determined explicitly. This in turn gives the leading order form of the

FIGURE 6. An illustration of the comparison between the solution forms predicted by linear theory and those observed in numerical solutions of the non-linear system with kinetics given by (20), for $T \gg 1$. Corresponding pictures are illustrated in (a) and (b), for two different sets of parameters. In (i) and (iii) I plot reaction-diffusion solutions for u (——) and v (-----) as a function of x at (i) $t = (n+1/2)T$, (iii) $t = (n+1)T$. Here $n \in \mathbb{Z}$ is sufficiently large that transients have decayed. I solved the reaction-diffusion system numerically on $0 < x < L = 23$, with zero flux boundary conditions, using the method of lines and Gear's method. At $t = 0$, u and v consisted of small, random perturbations about $u_{s,1}$ and $v_{s,1}$, and the final solutions are not sensitive to the details of the perturbations. In (ii) and (iv) I plot the corresponding solution forms predicted by linear theory, which are derived as discussed in the text. The actual values of u and v has no significance in these solutions. The comparison between the linear and nonlinear solutions is very good in (a) and in (bi, ii), but is poor in (biii, iv). In (v) I plot the leading order term in the expansion of the Floquet multiplier with larger absolute value. This is obtained by explicit solution of (4). I plot the real part of the Floquet exponent, which is $(1/T)\log|\mu|$, as a function of K. The homogeneous solution is stable to a perturbation of wave number $k \Leftrightarrow (1/T)\log|\mu| < 0$ for $K = |k|^2$. I also indicate (-----) the values of K that are admissible for the linear solution to satisfy zero flux boundary conditions on $[0, L]$, namely $(m\pi/L)^2$ $(m \in \mathbb{Z})$; the corresponding mode number m is indicated. For both sets of parameters (that is, (a) and (b)), mode 6 perturbations are just unstable, with all other perturbations stable. Correspondingly, the spatial patterns that evolve in the nonlinear model have a wavelength equal to a third of the domain length. In (vi), I plot the dispersion relations governing the stability of (9) as a steady state of (8), for $i = 1$ (——) and $i = 2$ (-----). This dispersion relation is $Q_0(K) \equiv D_{u,i} D_{v,i} K^2 - (a_i D_{v,i} + d_i D_{u,i})K + (a_i d_i - b_i c_i)$, and (9) is stable to perturbations of wave number $k \Leftrightarrow Q_0(|k|^2) > 0$ [14]. In (a), (9) is just unstable for both $i = 1$ and $i = 2$, whereas in (b), (9) is very stable for $i = 1$ and very unstable for $i = 2$. As discussed in the text, it is this difference in stability that causes that poor comparison between the nonlinear and linear solutions in (b). The parameter values are: $T = 100$ and (a) $D_{u,1} = 1$, $D_{v,1} = 8.5$, $\kappa_1 = 0.5$, $\mu_1 = 0.8$, $\sigma_1 = 1$, $D_{u,2} = 0.6$, $D_{v,2} = 8.05$, $\kappa_2 = 0.4$, $\mu_2 = 0.9$, $\sigma_2 = 0.9$; (b) $D_{u,1} = 1.55$, $D_{v,1} = 10.6$, $\kappa_1 = 0.55$, $\mu_1 = 0.8$, $\sigma_1 = 1.2$, $D_{u,2} = 1$, $D_{v,2} = 7$, $\kappa_2 = 0.45$, $\mu_2 = 0.7$, $\sigma_2 = 0.8$.

solution predicted by linear theory. Note that numerical solutions must be performed on a finite spatial domain, in which case the boundary conditions will determine a discrete set of admissible wave numbers. For parameter values sufficiently close to a Turing bifurcation point, only one of these modes will be unstable, and thus the solution predicted by linear theory will be a simple sinusoidal wave.

For $T \ll 1$, and for parameter values close to a Turing bifurcation point, solutions of the nonlinear system with kinetics given by (20) do have an approximately sinusoidal form in space, with the maximum and minimum values oscillating in time with period T (see Fig. 5a). Moreover, the spatial wavelength of the solution is exactly as predicted by the linear theory, corresponding to the unique unstable mode. However, as expected intuitively, the amplitude of the oscillations in u and v decreases with T, and appears to be $O(T)$ as $T \to 0$. This is of the same order as the oscillations of the homogeneous solution $(u_s(t), v_s(t))$ about (u_0, v_0), and thus the leading-order linear solution does not give a good indication of the quantitative form of the nonlinear solution in the $T \to 0$ limit.

For $T \gg 1$, the linear solution may or may not be a good approximation to the form of the nonlinear solution, depending on parameter values (Fig. 6), and I now discuss the conditions under which the approximation will be good. As $T \to \infty$, the form of the solution of any nonlinear model will depend crucially upon the stability of (9) as a steady state of (8), for $i = 1$ and 2, to perturbations with the wave number corresponding to the unique mode that is unstable for (1). If (9) if just unstable for both $i = 1$ and $i = 2$, then the solutions of (1) with (20) compare well with the linear theory (Fig. 6a). However, if (9) is significantly unstable for one i, say $i = 2$, then on the second half of each period, the solution will evolve to a pattern of (8) that is far from a Turing bifurcation in those equations, and will thus tend to be non-sinusoidal. Moreover, when this is the case, (9) must be stable for $i = 1$ in order that the oscillating system be close to a Turing bifurcation point. Then u and v will tend towards $u_{s,1}$ and $v_{s,1}$ on the first half of each period, with the differences $|u - u_{s,1}|$ and $|v - v_{s,1}|$ at the end of the half period tending to zero exponentially as $T \to \infty$. Thus the solution alternates between a large amplitude, non-sinusoidal pattern, and an exponential decay towards the homogeneous solution. A case of this type is illustrated in Fig. 6b.

Explicit calculation of $\boldsymbol{W}^*$ shows that the ratio of the amplitudes of the oscillations of $u(x, (n + i/2)T)$ and $v(x, (n + i/2)T)$ in the linear solutions, to leading order as $T \to \infty$, is

$$\frac{2b_i}{P_i - Q_i} \tag{21}$$

($n \in \mathbb{Z}$). It is this expression that I have used to calculate the linear solutions plotted in Fig. 6. The corresponding ratio for $u(x, (n + 1/2)T)$ and $u(x, (n + 1)T)$ tends to 0 or ∞ as $T \to \infty$, according to which of the two sets of kinetics gives the larger growth rate. This is reflected in the nonlinear solutions when (9) is stable as a steady state of (8) for one i, and unstable for the other i, as discussed above. However, when (9) is unstable for both $i = 1$ and $i = 2$, the nonlinearities in the system keep the solution bounded in both halves of the period as $T \to \infty$, and thus the ratio remains finite.

One curious aspect of the expression (21) for the ratio of the species amplitudes is that it is complex when P_i is pure imaginary. This means that the linear solution consists of sinusoidal waves for u and v, as functions of x, with a phase difference that is not an integer multiple of π. Such an intermediate phase difference is never observed in reaction–diffusion systems with constant parameters. However, $P_i \notin \mathbb{R}$ implies that the steady state (9) of (8) is stable to perturbations with that wave number, and thus the solution will decay towards the homogeneous solution during that half of the period. Numerical investigation suggests that an intermediate phase difference only occurs for values of T that are so large that the amplitude of the waves is far too small to have any ecological significance.

6 Conclusion

In this paper I have investigated diffusion-driven instability in situations in which the environment oscillates in time, corresponding to periodic forcing of the model parameters. In the particular case of square tooth forcing, I have derived conditions on the diffusion coefficients and the linearization of the reaction kinetics for spatial pattern formation to occur via diffusion-driven instability. I have considered only the limits of very high and very low frequency forcing, because the calculations are not analytically possible more generally; both these limits are relevant in ecological applications, corresponding to daily and seasonal variations in parameters, respectively. In the case of high frequency oscillations, I have shown that the condition for pattern formation is simply that the unforced reaction–diffusion system given by the average of all parameter values exhibits diffusion-driven instability. In the low frequency case, there is not a single simple condition, but I have shown how a parameter domain for diffusion-driven instability can be determined for any given kinetics. In particular, small low frequency oscillations can either stabilize or destabilize the homogeneous state, depending on the condition given explicitly in (19).

I have set the work in this paper in the context of ecological interactions. However, a number of chemical systems amenable to reaction diffusion modelling have also been studied with periodic forcing. In particular, Steinbock et al. [17] have recently shown that periodic illumination of the light sensitive Belousov–Zhabotinsky reaction results in rich set of modulations to the spiral tip paths, and Gáspár et al. [18] have studied the propagation of chemical waves in narrow channels via forced excitation. In both these studies, one of the main motivations for the introduction of forcing is to improve the understanding of the unforced case. In a very general sense, the work I have described in this paper suggests a way in which models of such experiments could be investigated analytically, namely the determination of Floquet multipliers, essentially by explicit calculation, in the case of square tooth forcing. This approach has, in fact, now been applied to another situation in which periodic forcing arises: the formation of fingering patterns during the aggregation of *Dictyostelium* amoebae [19]. In this case, the calculation of a stability condition for square tooth forcing in a caricature model gives an analytical understanding of a phenomenon that is otherwise simply observable in experiments and corresponding numerical simulations.

In summary, I have shown that the use of square took parameter oscillations enables the effects of periodic forcing on diffusion-driven instability, and in some cases on the resulting spatial pattern, to be determined analytically.

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