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Appendix from J. B. Xavier et al., "Social Evolution of Spatial Patterns in Bacterial Biofilms: When Conflict Drives Disorder"

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Stability Analysis for the Single-Species Model

Finding Stable Fixed Points by Linear Analysis

Our model is based on the system of ordinary differential equations

$$\frac{\partial S}{\partial t} = Q(S_0 - S) - \frac{\mu}{Y}\frac{S}{S+K}X,$$
$$\frac{\partial X}{\partial t} = \mu\frac{S}{S+K}X - mX. \qquad \text{(A1)}$$

The system was made dimensionless by normalizing time by $1/Q$ and length by $(D/Q)^{1/2}$. The resulting system of dimensionless equations is

$$\dot{s} = g(s,x), \qquad \text{where } g(s,x) = (1-s) - \phi^2\frac{s}{s+k}x,$$
$$\dot{x} = q(s,x), \qquad \text{where } q(s,x) = \gamma\left(\frac{s}{s+k} - f\right)x. \qquad \text{(A2)}$$

The dimensionless parameters k, f, and ϕ^2 were defined in the main text, and $\gamma = \mu/Q$. Note that the equations are written for dimensionless concentration of nutrient, $s = S/S_0$, and dimensionless biomass, $x = X/\rho$.

The system has two fixed points, which are determined by solving $g(s^*, x^*) = 0$ and $q(s^*, x^*) = 0$. The first fixed point is a trivial steady state where $s^* = 1$ and $x^* = 0$. The second fixed point, here called the nontrivial steady state, is

$$s^* = k\frac{f}{1-f},$$
$$x^* = \frac{1-s^*}{\phi^2 f}. \qquad \text{(A3)}$$

Stability is determined by linearizing equation (A2) at each fixed point and evaluating the solution of the linearized system. That solution has the form

$$\mathbf{W}(t) \propto e^{\lambda t}, \qquad \text{(A4)}$$

where $\mathbf{W}$ represents the matrix of small variations about a fixed point $\dot{\mathbf{W}} = \mathbf{AW}$, where

$$\mathbf{W} = \begin{pmatrix} s - s^* \\ x - x^* \end{pmatrix},$$

$$\mathbf{A} = \begin{pmatrix} \partial q/\partial s & \partial q/\partial x \\ \partial g/\partial s & \partial g/\partial x \end{pmatrix}. \tag{A5}$$

Matrix **A** is the Jacobian and is evaluated at the fixed point (s^*, x^*). Equation (A5) is an eigenvalue problem, and its solution is obtained from solving

$$\det(\mathbf{A} - \lambda\mathbf{I}) = 0, \tag{A6}$$

where **I** is the identity matrix. The stability of the fixed points is then evaluated as follows: a fixed point is stable if values of λ are negative and unstable if any value of λ is greater than 0. Determining λ produces the quadratic equation with the form

$$\lambda^2 - \tau\lambda + \Delta = 0, \tag{A7}$$

and the solution is best assessed through the values of $\tau = \mathrm{tr}(\mathbf{A})$ and $\Delta = \det(\mathbf{A})$. The conditions that ensure stability are $\tau < 0$ and $\Delta > 0$. For the steady state $(s^*, b^*) = (1, 0)$, these conditions are, respectively,

$$\gamma \frac{1 - f - fk}{1 + k} < 1, \tag{A8}$$

and

$$\gamma \frac{1 - f - fk}{1 + k} < 0. \tag{A9}$$

For the nontrivial steady state, the same conditions become, respectively,

$$\frac{(1 - f - fk)(1 - f)}{kf} > 0, \tag{A10}$$

and

$$\gamma \frac{(1 - f - fk)(1 - f)}{kf} > 0. \tag{A11}$$

The nontrivial steady state is not possible when the nutrient concentration necessary for $x^* \geq 0$ is $s^* \geq 1$. This is equivalent to

$$s^* = k \frac{f}{1 - f} \geq 1 \Leftrightarrow 1 - f - fk \leq 0. \tag{A12}$$

Under such conditions, only the steady state $(s^*, x^*) = (1, 0)$ is possible. When the system is within the range in equation (A12), the conditions for stability are valid for the fixed point (1, 0). When the nontrivial steady state is also possible (i.e., when we are outside the range in eq. [A12]), we have $1 - f - fk > 0$ and condition (A9) no longer holds. Therefore, the trivial steady state is unstable under those conditions, which means that the system will move away from that state. On the other hand, conditions (A10) and (A11) are fulfilled. Hence, the nontrivial steady state is stable (fig. A1). In summary, the linear analysis concludes that the stable fixed points are

$$(s^*, x^*) = \begin{cases} (1, 0) & \text{if } k\dfrac{f}{1-f} \geq 1 \\ \left(k\dfrac{f}{1-f}, \dfrac{1 - k[f/(1-f)]}{\phi^2 f}\right) & \text{if } k\dfrac{f}{1-f} < 1 \end{cases}. \tag{A13}$$

Turing Instability Analysis

Next, we perform analysis of Turing instabilities and show that there are no biologically relevant conditions under which these fixed points become unstable to spatial perturbations. This means that no true Turing instabilities (Turing 1952) exist. For simplicity, we refer to the analysis outlined by Murray (2004).

To make our model amenable to Turing instability analysis, we first assume that both nutrients and cells can spread on the surface by diffusion processes. With this assumption, system (A1) becomes

$$\begin{aligned} \frac{\partial S}{\partial t} &= Q(S_0 - S) - \frac{\mu}{Y}\frac{S}{S + K}X + D\nabla^2 S, \\ \frac{\partial X}{\partial t} &= \mu\frac{S}{S + K}X - mX + D_X\nabla^2 X, \end{aligned} \tag{A14}$$

where D_X is the diffusivity of cells. The nondimensional form of equation (A14) is

$$\begin{aligned} \dot{s} &= g(s, x) + \nabla^2 s, \\ \dot{x} &= q(s, x) + \beta\nabla^2 x, \end{aligned} \tag{A15}$$

where $\beta = D_X/D$.

The analysis of Turing instabilities follows through a series of derivations that we skip here. The reader may refer to Murray (2004) for a step-by-step derivation. The following conditions must be met for a steady state (s^*, x^*) to be a Turing instability:

$$\beta\frac{\partial q}{\partial s} + \frac{\partial g}{\partial x} > 0, \tag{A16}$$

$$\beta\left(\frac{\partial q}{\partial s} + \frac{\partial g}{\partial x}\right)^2 - 4\beta\left(\frac{\partial q}{\partial s}\frac{\partial g}{\partial x} + \frac{\partial q}{\partial x}\frac{\partial g}{\partial s}\right) > 0. \tag{A17}$$

Again, partial derivatives are evaluated at the steady state.

Next, we show that conditions (A16) and (A17) are never fulfilled for biologically relevant parameter ranges. For the fixed point (1, 0), condition (A16) becomes

$$\gamma\frac{1 - f - fk}{1 + k} < \beta, \tag{A18}$$

which is in disagreement with condition (A9), since $\beta > 0$. For the nontrivial steady state, condition (A16) is

$$\beta\frac{(1 - f - fk)(1 - f)}{kf} < 0. \tag{A19}$$

Conditions (A10) and (A19) are mutually exclusive because $\beta > 0$. Therefore, we conclude that the fixed point is not unstable in the strict sense of Turing instabilities.

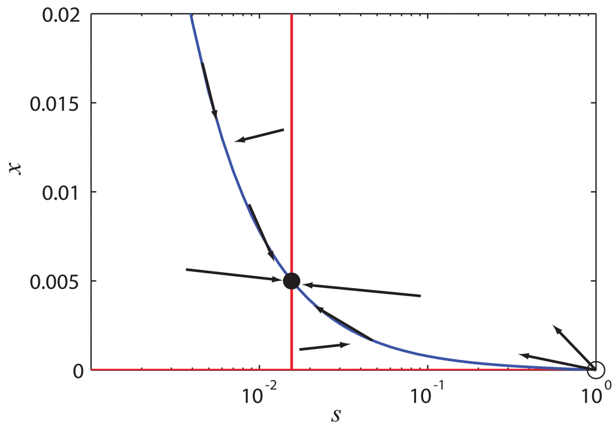

Figure A1: Fixed points and isoclines for the system within the range in condition (A12). Red lines are the isoclines $\partial x/dt = 0$, and the blue line is the isocline $\partial s/dt = 0$. The fixed point $(s^*, x^*) = (1, 0)$, represented by an open circle, is unstable, as evaluated by the linear stability analysis. The nontrivial fixed point (*filled circle*) is stable. Arrows represent trends of system dynamics within the regions delimited by isoclines, as evaluated by $\partial s/dx$.