Bifurcations in Pioneer/Climax Population Interaction Models

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Model Equations (ODE)

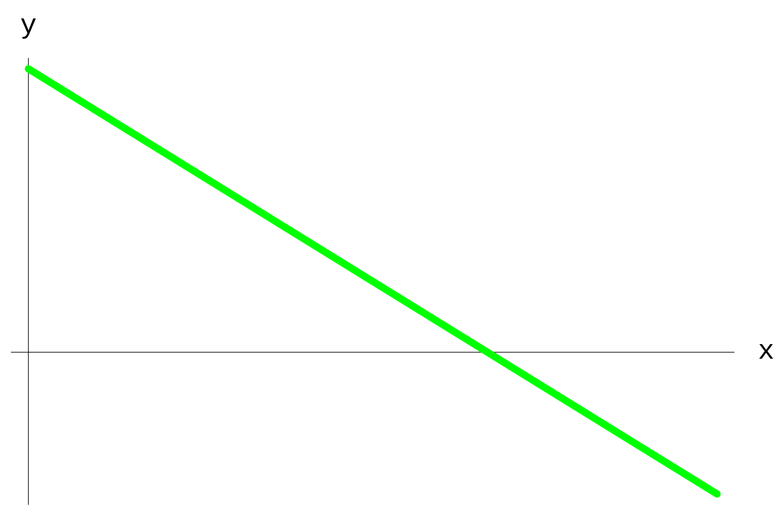
$$\begin{aligned} u_t &= uf(c_{11}u + v) + A_1 \\ v_t &= vg(u + c_{22}v) + A_2 \end{aligned}$$

Functions $f(z)$ and $g(z)$ represent the per capita reproductive response to the weighted densities of the species u and v, a pioneer and a climax species respectively.

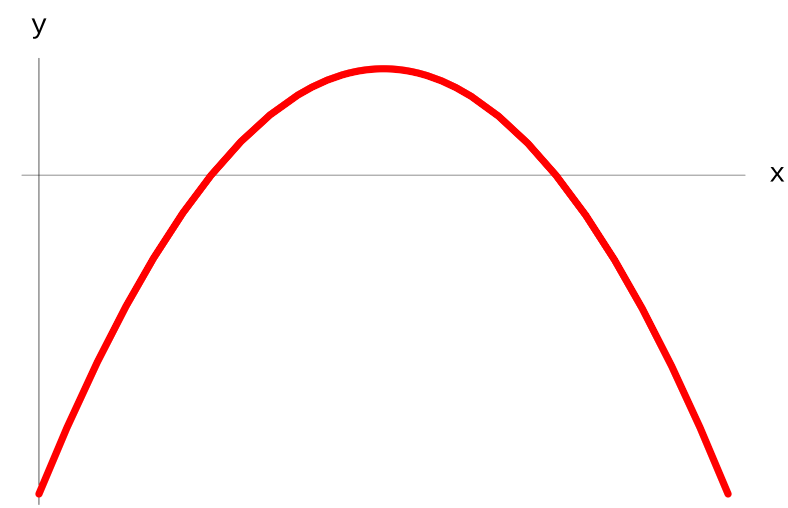
Constants A_1 and A_2 represent external forces such as stocking and harvesting.

Pioneer and Climax Fitnesses

- *Pioneer* species have continuous and monotonically decreasing reproductive rates.
- *Climax* species have continuous reproductive rates which are continuous, increasing at low average population densities and decreasing at high densities.



Pioneer



Climax

Equilibria

Standing Hypothesis A: suppose $f(z)$ has a unique positive zero at $z = z_1$ and that $f'(z_1) < 0$ while $g(z)$ has a zero at $z = z_2$ and that $g'(z_2) > 0$.

Standing Hypothesis B: suppose that $A_1 = A_2 = 0$ and the following inequalities hold:

$$1 - c_{11}c_{22} > 0, \qquad z_2 - c_{22}z_1 > 0, \qquad z_1 - c_{11}z_2 > 0,$$

Then the equilibria are distinct and lie in $\mathbb{R}^2_+$.
Consider the fixed point,

$$(e_u, e_v) = \left(\frac{z_2 - c_{22}z_1}{1 - c_{11}c_{22}}, \frac{z_1 - c_{11}z_2}{1 - c_{11}c_{22}} \right).$$

Objectives (ODE)

- Determine the values of the interaction coefficients (c_{ii}) for which the model undergoes a Hopf bifurcation.

  A Hopf bifurcation occurs when an equilibrium solution loses its stability and a nearby periodic orbit appears. This occurs usually as a complex conjugate pair of eigenvalues passes through the imaginary axis.
- Determine conditions on the forcing constants that reverse a Hopf bifurcation that has already taken place.

Eigenvalues (ODE)

Linearizing the ODE about (e_u, e_v) yields

$$DF(e_u, e_v) = \begin{bmatrix} c_{11}e_u f'(z_1) & e_u f'(z_1) \\ e_v g'(z_2) & c_{22}e_v g'(z_2) \end{bmatrix}$$

The characteristic polynomial of $DF(e_u, e_v)$ is

$$\lambda^2 - (\mathrm{tr}DF(e_u, e_v))\lambda + \det DF(e_u, e_v).$$

$$\begin{aligned} \mathrm{tr}DF(e_u, e_v) &= c_{11}e_u f'(z_1) + c_{22}e_v g'(z_2) \\ \det DF(e_u, e_v) &= -e_u e_v f'(z_1) g'(z_2)(1 - c_{11}c_{22}) \end{aligned}$$

Stability of Equilibrium

The eigenvalues have negative real parts when $\mathrm{tr} DF(e_u, e_v) < 0$ and $\det DF(e_u, e_v) > 0$.

Under the standing hypothesis $(e_u, e_v) \in \mathbb{R}^2_+$ and $\det DF(e_u, e_v) > 0$, thus a Hopf bifurcation can only take place when $\mathrm{tr} DF(e_u, e_v) = 0$.

Formally,

$$\hat{c}_{11} = \frac{c_{22} z_1 g'(z_2)}{c_{22} z_2 g'(z_2) - (z_2 - c_{22} z_1) f'(z_1)} > 0 \quad \text{or}$$

$$\hat{c}_{22} = \frac{c_{11} z_2 f'(z_2)}{c_{11} z_1 f'(z_2) - (z_1 - c_{11} z_2) g'(z_2)} > 0$$

Transversality Condition

Eigenvalues cross the imaginary axis with “non-zero speed”.

$$\left.\frac{d\lambda}{dc_{11}}\right|_{\hat{c}_{11}} = \frac{(c_{22}z_2g'(z_2) - (z_2 - c_{22}z_1)f'(z_1))^2}{2(z_2 - c_{22}z_1)(f'(z_1) - c_{22}g'(z_2))} < 0$$

$$\left.\frac{d\lambda}{dc_{22}}\right|_{\hat{c}_{22}} = \frac{(c_{11}z_1f'(z_1) - (z_1 - c_{11}z_2)g'(z_2))^2}{2(z_1 - c_{11}z_2)(g'(z_2) - c_{11}f'(z_1))} > 0$$

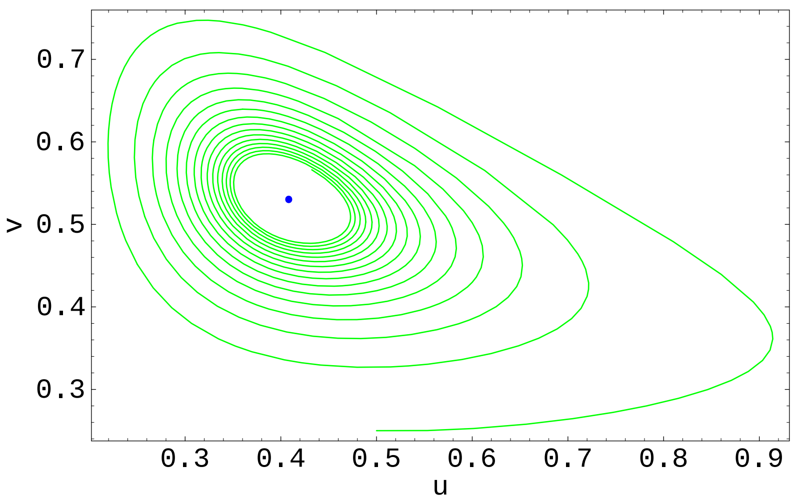
Thus (e_u, e_v) destabilizes as c_{11} decreases or c_{22} increases.

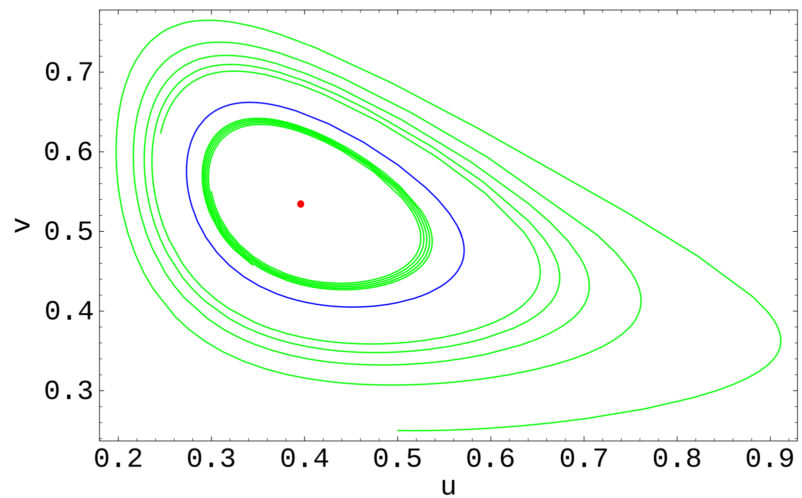
Example of Hopf Bifurcation

$$u_t = u\left(e^{2/3-u/3-v} - 1\right)$$

$$v_t = v\left(\frac{2}{3}(u + c_{22}v)e^{3/2-u-c_{22}v} - 1\right)$$

When $c_{22} \approx 0.420426$, a Hopf bifurcation occurs.





$c_{22} = 0.41$ $c_{22} = 0.43$

Effects of Forcing (ODE)

Consider the situation in which $A_1 = 0$ and $A_2 \neq 0$.

The constant A_2 represents an external force such as stocking or harvesting of the climax species.

The equilibrium (u, v) solves the system,

$$\begin{aligned} c_{11}u + v &= z_1 \\ vg(u + c_{22}v) + A_2 &= 0 \end{aligned}$$

Linearizing system of ODEs about this fixed point yields

$$DF(u, v) = \begin{bmatrix} c_{11}uf'(z_1) & uf'(z_1) \\ vg'(u + c_{22}v) & c_{22}vg'(u + c_{22}v) - A_2/v \end{bmatrix}$$

Simultaneous Equations

Solving the first equilibrium equation for $u = (z_1 - v)/c_{11}$, we eliminate u from $\mathrm{tr} DF(u, v) = 0$ and $vg(u + c_{22}v) + A_2 = 0$.

This yields a system of two equations in three unknowns (v, c_{22}, A_2):

$$
\begin{aligned}
G_2(v, c_{22}, A_2) &= vg\left(\frac{z_1 - v}{c_{11}} + c_{22}v\right) + A_2 \\
H_2(v, c_{22}, A_2) &= (z_1 - v)f'(z_1) + c_{22}vg'\left(\frac{z_1 - v}{c_{11}} + c_{22}v\right) - \frac{A_2}{v}
\end{aligned}
$$

Implicit Function Theorem

A Hopf bifurcation occurs when $(G, H)(v, c_{22}, A_2) = (0, 0)$.

Using the Implicit Function Theorem we know that when

$$\left| \begin{array}{cc} \frac{\partial G_2}{\partial A_2} & \frac{\partial G_2}{\partial v} \\ \frac{\partial H_2}{\partial A_2} & \frac{\partial H_2}{\partial v} \end{array} \right|_{(e_v, \hat{c}_{22}, 0)} \neq 0$$

we have $A_2 \equiv A_2(c_{22})$.

$$\left. \frac{dA_2}{dc_{22}} \right|_{\hat{c}_{22}} = - \frac{\left| \begin{array}{cc} \frac{\partial G_2}{\partial c_{22}} & \frac{\partial G_2}{\partial v} \\ \frac{\partial H_2}{\partial c_{22}} & \frac{\partial H_2}{\partial v} \end{array} \right|_{(e_v, \hat{c}_{22}, 0)}}{\left| \begin{array}{cc} \frac{\partial G_2}{\partial A_2} & \frac{\partial G_2}{\partial v} \\ \frac{\partial H_2}{\partial A_2} & \frac{\partial H_2}{\partial v} \end{array} \right|_{(e_v, \hat{c}_{22}, 0)}}.$$

Example of Restabilization

$$\begin{aligned} u_t &= u\left(e^{2/3-u/3-v}-1\right) \\ v_t &= v\left(\frac{2}{3}(u+c_{22}v)e^{3/2-u-c_{22}v}-1\right)+A_2 \end{aligned}$$

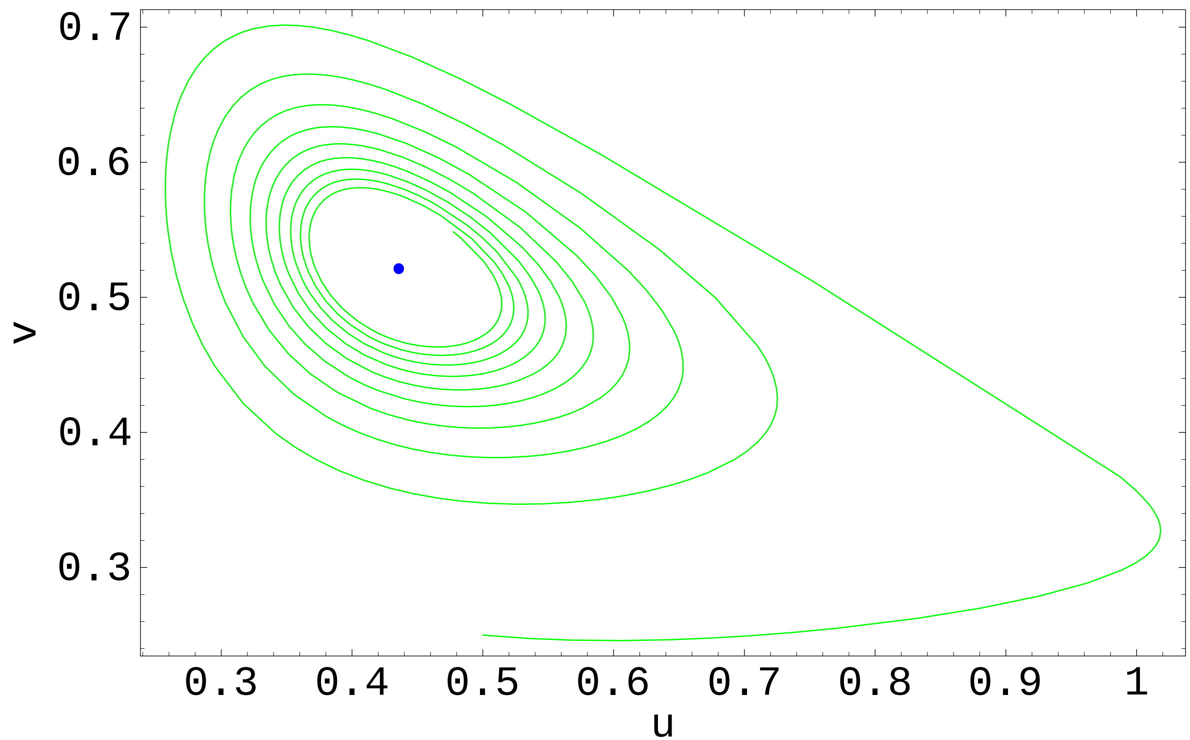
When $c_{22}=0.43$, a Hopf bifurcation has occurred. Since

$$\left.\frac{dA_2}{dc_{22}}\right|_{\hat{c}_{22}} \approx -0.0196686 < 0$$

harvesting the climax species (*i.e.* $A_2 < 0$) will restabilize the equilibrium.

Verification

Model parameters: $c_{22} = 0.43$, $A_2 = -0.01$



Model Equations (PDE)

$$
\begin{aligned}
u_t &= uf(c_{11}u + v) + A_1 + D_1 u_{xx} \\
v_t &= vg(u + c_{22}v) + A_2 + D_2 v_{xx}
\end{aligned}
$$

Functions $f(z)$ and $g(z)$ represent the per capita reproductive response to the weighted densities of the species u and v.

Constants A_1 and A_2 represent external forces such as stocking and harvesting.

Constants D_1 and D_2 are the diffusion rates of the species.

Neumann (zero flux) boundary conditions are assumed.

Objectives (PDE)

- Determine the values of the diffusional coefficients for which the model undergoes a Turing bifurcation.

  A Turing bifurcation occurs when an equilibrium solution becomes unstable to perturbations which are non-homogeneous in space but remains stable to spatially homogeneous perturbations.
- Determine conditions on the forcing constants that reverse a Turing bifurcation that has already taken place.

Eigenvalues

$$L(k) = \begin{bmatrix} c_{11}e_u f'(z_1) - D_1 k^2 & e_u f'(z_1) \\ e_v g'(z_2) & c_{22}e_v g'(z_2) - D_2 k^2 \end{bmatrix}$$

The eigenvalues of the Laplacian operator on the interval $(0, \pi)$ are $-k^2$ for $k = 0, 1, 2, \ldots$.

$$\begin{aligned} \mathrm{tr} L(k) &= -k^2(D_1 + D_2) + c_{11}e_u f'(z_1) + c_{22}e_v g'(z_2) \\ \det L(k) &= D_1 D_2 k^4 - k^2(D_1 c_{22} e_v g'(z_2) + D_2 c_{11} e_u f'(z_1)) - \\ &\qquad e_u e_v f'(z_1) g'(z_2)(1 - c_{11}c_{22}) \end{aligned}$$

The eigenvalues have negative real parts when $\mathrm{tr} L(k) < 0$ and $\det L(k) > 0$.

Spatially Homogeneous Perturbations

For a fixed c_{11} we have (e_u, e_v) is isolated when $c_{22} < \min\{1/c_{11}, z_2/z_1\}$.

Then when

$$c_{22} < \min\left\{\frac{1}{c_{11}}, \frac{c_{11} z_2 f'(z_1)}{c_{11} z_1 f'(z_1) - (z_1 - c_{11} z_2) g'(z_2)}\right\}$$

we have $\mathrm{tr} L(0) < 0$ and $(e_u, e_v) \in \mathbb{R}^2_+$ and asymptotically stable.

Since $\mathrm{tr} L(k) < \mathrm{tr} L(0) < 0$ for all $k = 1, 2, \ldots$ then instability can occur when $\det L(k) = 0$ for some k.

Turing Bifurcation

The eigenvalues of $L(k)$ are real and simple. One eigenvalue becomes 0 as D_2 changes. $\det L(k) = 0$ is equivalent to

$$c_{22} = \frac{D_1 D_2 k^4 - z_2 f'(z_1)\left(c_{11} D_2 k^2 + (z_1 - c_{11} z_2) g'(z_2)\right)}{(D_1 k^2 - z_1 f'(z_1))\,(c_{11} D_2 k^2 + (z_1 - c_{11} z_2) g'(z_2))} > 0.$$

Thus when

$$D_2 < \hat{D}_2 = \frac{z_2 f'(z_1) g'(z_2)\left(c_{11} D_1 k^2 - (z_1 - c_{11} z_2) g'(z_2)\right)}{D_1 k^4\,(c_{11} f'(z_1) - g'(z_2)) + c_{11} k^2 z_2 f'(z_1) g'(z_2)}$$

the fixed point becomes unstable to perturbations which are not homogeneous in space.

Loss of Stability

Since

$$\left.\frac{d\lambda_k}{dD_2}\right|_{\hat{D}_2} = \frac{D_1 k^4 - c_{11} e_u f'(z_1) k^2}{\mathrm{tr} L(k)} < 0,$$

the equilibrium loses stability when D_2 decreases through $\hat{D}_2$ causing an eigenvalue to increase through 0.

Example

$$
\begin{aligned}
u_t &= u(1 - \frac{1}{3}u - v) + 2u_{xx} \\
v_t &= -v(1 - u - \frac{9}{20}v)(\frac{3}{2} - u - \frac{9}{20}v) + D_2 v_{xx}
\end{aligned}
$$

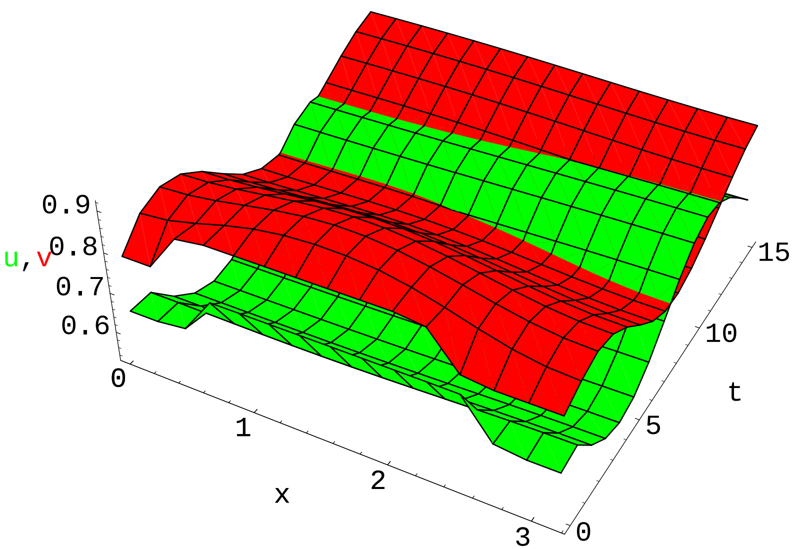
Equilibrium: $(e_u, e_v) = (11/17, 40/51)$

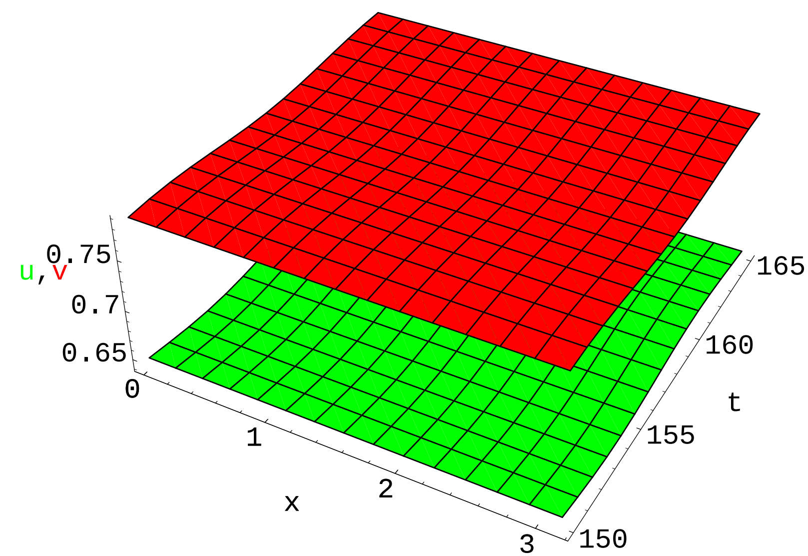
$$
L(k) = \begin{bmatrix} -11/51 - 2k^2 & -11/17 \\ 20/51 & 3/17 - D_2 k^2 \end{bmatrix}
$$

$\det L(1) = 0$ when $D_2 = 7/113$.

Non-homogeneous Perturbations

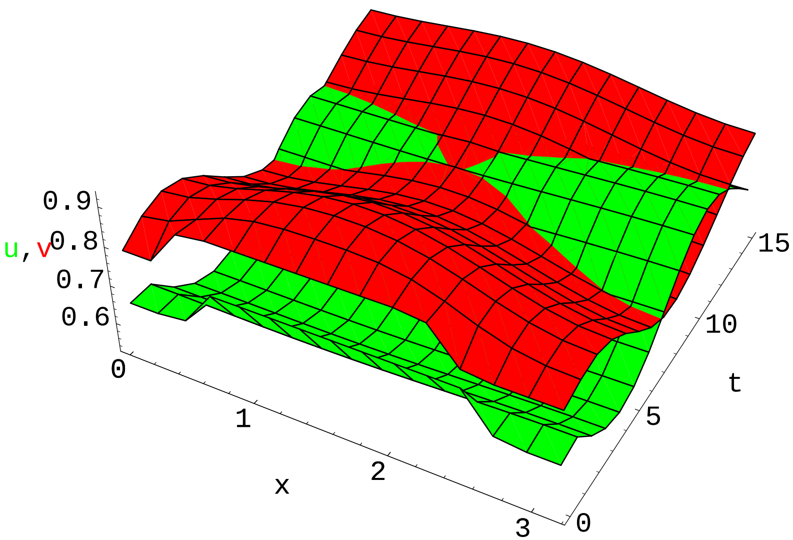
$D_2 = 1/10$, $u(x,0) = 11/17 + B(x; \pi/3, 2\pi/3)$,
$v(x,0) = 40/51 + B(x; \pi/4, \pi/2)$

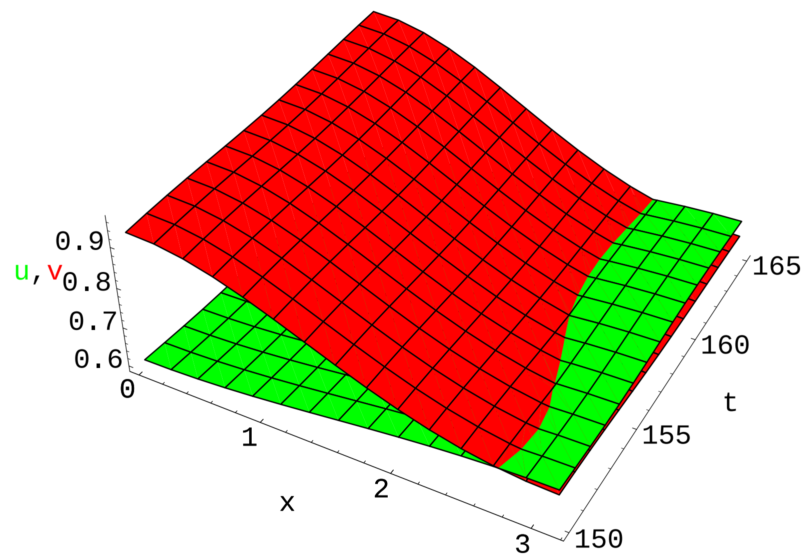




Instability to Perturbation

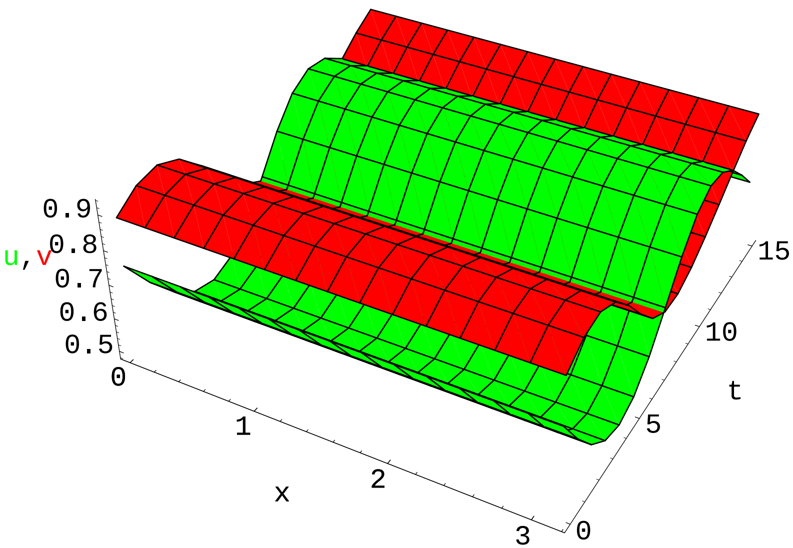
$D_2 = 1/20$, $u(x,0) = 11/17 + B(x;\pi/3, 2\pi/3)$,
$v(x,0) = 40/51 + B(x;\pi/4, \pi/2)$

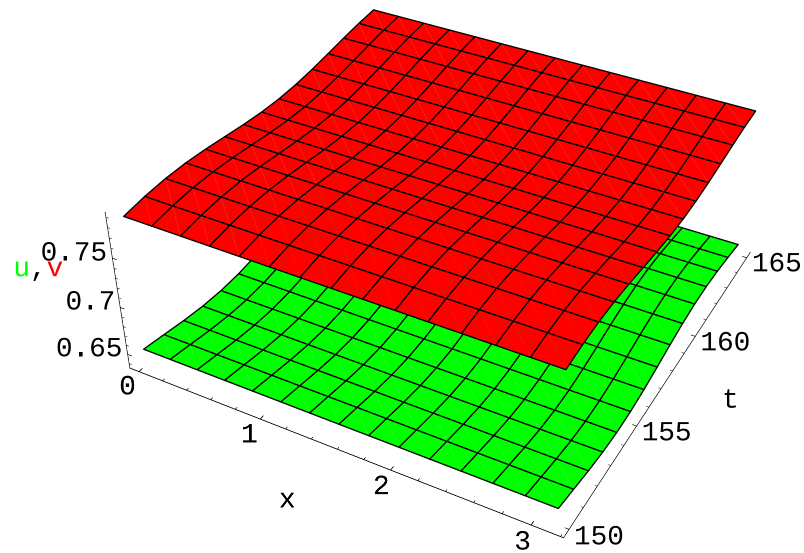




Homogeneous Perturbations

$D_2 = 1/20$, $u(x,0) = 0.7471$, $v(x,0) = 0.8843$





Effects of Forcing

Consider the situation in which $A_1 \neq 0$ and $A_2 = 0$.

The constant A_1 represents an external force such as stocking or harvesting.

The equilibrium (e_u, e_v) solves the system,

$$\begin{aligned} uf(c_{11}u + v) + A_1 &= 0 \\ u + c_{22}v &= z_2 \end{aligned}$$

Linearizing the system about this fixed point gives us

$$L(k; A_1) = \begin{bmatrix} c_{11}uf'(c_{11}u + v) - D_1k^2 - \frac{A_1}{u} & uf'(c_{11}u + v) \\ vg'(z_2) & c_{22}vg'(z_2) - D_2k^2 \end{bmatrix}$$

Simultaneous Equations (PDE)

Solving the second equation for $v = (z_2 - u)/c_{22}$, eliminate v from $\det L(k; A_1) = 0$ and $uf(c_{11}u + v) + A_1 = 0$.

This yields a system of two equations in three unknowns.

$$
\begin{aligned}
G_1(u, A_1, D_2) &= uf(c_{11}u + \frac{z_2 - u}{c_{22}}) + A_1 \\
H_1(u, A_1, D_2) &= D_1 D_2 k^4 - \frac{A_1}{u}(z_2 - u)g'(z_2) - \\
&\quad k^2(D_1(z_2 - u)g'(z_2) + \\
&\qquad D_2 c_{11} u f'(c_{11}u + \frac{z_2 - u}{c_{22}}) - \frac{A_1}{u}) - \\
&\quad (\frac{1}{c_{22}} - c_{11})u(z_2 - u)f'(c_{11}u + \frac{z_2 - u}{c_{22}})g'(z_2)
\end{aligned}
$$

Implicit Function Theorem

Instability occurs when $(G,H)(u,A_1,D_2)=(0,0)$.

Using the Implicit Function Theorem we know that when

$$\left|\begin{array}{cc} \frac{\partial G_1}{\partial A_1} & \frac{\partial G_1}{\partial u} \\ \frac{\partial H_1}{\partial A_1} & \frac{\partial H_1}{\partial u} \end{array}\right|_{(e_u,0,\hat{D}_2)} \neq 0$$

we have $A_1 \equiv A_1(D_2)$.

$$\left.\frac{dA_1}{dD_2}\right|_{\hat{D}_2} = -\frac{\left|\begin{array}{cc} \frac{\partial G_1}{\partial D_2} & \frac{\partial G_1}{\partial u} \\ \frac{\partial H_1}{\partial D_2} & \frac{\partial H_1}{\partial u} \end{array}\right|_{(e_u,0,\hat{D}_2)}}{\left|\begin{array}{cc} \frac{\partial G_1}{\partial A_1} & \frac{\partial G_1}{\partial u} \\ \frac{\partial H_1}{\partial A_1} & \frac{\partial H_1}{\partial u} \end{array}\right|_{(e_u,0,\hat{D}_2)}}.$$

Another Example

$$u_t = u(1 - \frac{1}{3}u - v) + A_1 + 2u_{xx}$$

$$v_t = -v(1 - u - \frac{9}{20}v)(\frac{3}{2} - u - \frac{9}{20}v) + D_2 v_{xx}$$

$$\left| \begin{array}{cc} \frac{\partial G_1}{\partial A_1} & \frac{\partial G_1}{\partial u} \\ \frac{\partial H_1}{\partial A_1} & \frac{\partial H_1}{\partial u} \end{array} \right|_{(11/17,0,7/113)} = \frac{113 + 1838k^2}{2034} \neq 0$$

if $k \in \mathbb{N} \cup \{0\}$.

$$\frac{dA_1}{dD_2} = \frac{2486k^2(11 + 102k^2)}{5763 + 93738k^2} > 0.$$

With Harvesting

$D_2 = 1/20$, $A_1 = -1/25$, $u(x, 0) = 11/17 + B(x; \pi/3, 2\pi/3)$, $v(x, 0) = 40/51 + B(x; \pi/4, \pi/2)$