Bifurcations in Pioneer/Climax Population Interaction Models

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Model Equations (ODE)

\[
\begin{align*}
  u_t &= uf(c_{11}u + v) + A_1 \\
  v_t &= vg(u + c_{22}v) + A_2
\end{align*}
\]

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.
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:

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

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

\[
\lambda^2 - (\text{tr} DF(e_u, e_v))\lambda + \det DF(e_u, e_v).
\]

\[
\text{tr} DF(e_u, e_v) = c_{11} e_u f'(z_1) + c_{22} e_v g'(z_2)
\]

\[
\det DF(e_u, e_v) = -e_u e_v f'(z_1) g'(z_2)(1 - c_{11} c_{22})
\]
Stability of Equilibrium

The eigenvalues have negative real parts when $\text{tr}DF(e_u, e_v) < 0$ 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 $\text{tr}DF(e_u, e_v) = 0$.

Formally,

\[
\hat{c}_{11} = \frac{c_{22}z_1g'(z_2)}{c_{22}z_2g'(z_2) - (z_2 - c_{22}z_1)f'(z_1)} > 0 \quad \text{or} \quad \\
\hat{c}_{22} = \frac{c_{11}z_2f'(z_2)}{c_{11}z_1f'(z_2) - (z_1 - c_{11}z_2)g'(z_2)} > 0
\]
Transversality Condition

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

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

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

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.

\[ c_{22} = 0.41 \]

\[ c_{22} = 0.43 \]
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,

\[
\begin{align*}
c_{11}u + v &= z_1 \\
v g(u + c_{22}v) + A_2 &= 0
\end{align*}
\]

Linearizing system of ODEs about this fixed point yields

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

Solving the first equilibrium equation for $u = (z_1 - v)/c_{11}$, we eliminate $u$ from $\text{tr} \, DF(u, v) = 0$ 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{align*}
G_2(v, c_{22}, A_2) &= \quad vg \left( \frac{z_1 - v}{c_{11}} + c_{22}v \right) + A_2 \\
H_2(v, c_{22}, A_2) &= \quad (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{align*}
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

\[
\begin{vmatrix}
\frac{\partial G_2}{\partial A_2} & \frac{\partial G_2}{\partial v} \\
\frac{\partial G_2}{\partial H_2} & \frac{\partial H_2}{\partial v}
\end{vmatrix}
\neq 0
\]

we have \(A_2 = A_2(c_{22})\).

\[
\frac{dA_2}{dc_{22}} \bigg|_{\hat{c}_{22}} = - \frac{\begin{vmatrix}
\frac{\partial G_2}{\partial c_{22}} & \frac{\partial G_2}{\partial v} \\
\frac{\partial G_2}{\partial H_2} & \frac{\partial H_2}{\partial v}
\end{vmatrix}}{\begin{vmatrix}
\frac{\partial G_2}{\partial A_2} & \frac{\partial G_2}{\partial v} \\
\frac{\partial G_2}{\partial H_2} & \frac{\partial H_2}{\partial v}
\end{vmatrix}} (e_v, \hat{c}_{22}, 0)
\]
Example of Restabilization

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

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)

\[ u_t = uf(c_{11}u + v) + A_1 + D_1 u_{xx} \]
\[ v_t = vg(u + c_{22}v) + A_2 + D_2 v_{xx} \]

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 \(k = 0, 1, 2, \ldots\).

\[
\text{tr} L(k) = -k^2(D_1 + D_2) + c_{11}e_u f'(z_1) + c_{22}e_v g'(z_2)
\]

\[
\det L(k) = D_1 D_2 k^4 - k^2(D_1 c_{22} e_v g'(z_2) + D_2 c_{11} e_u f'(z_1)) - e_u e_v f'(z_1) g'(z_2)(1 - c_{11} c_{22})
\]

The eigenvalues have negative real parts when \(\text{tr} L(k) < 0\) 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

$$c_{22} < \min \left\{ \frac{1}{c_{11}}, \frac{c_{11}z_2f'(z_1)}{c_{11}z_1f'(z_1) - (z_1 - c_{11}z_2)g'(z_2)} \right\}$$

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

Since $\text{tr}L(k) < \text{tr}L(0) < 0$ for all $k = 1, 2, \ldots$ then instability can occur when $\det L(k) = 0$ for some $k$. 
The eigenvalues of $L(k)$ are real and simple. One eigenvalue becomes 0 as $D_2$ changes. $\det L(k) = 0$ is equivalent to

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

Thus when

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

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

Since

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

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

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

\[ v_t = -v(1 - u - \frac{9}{20}v)(\frac{3}{2} - u - \frac{9}{20}v) + D_2v_{xx} \]

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

\[ L(k) = \begin{bmatrix} -11/51 - 2k^2 & -11/17 \\ 20/51 & 3/17 - D_2k^2 \end{bmatrix} \]

\[ \text{det } L(1) = 0 \text{ when } D_2 = 7/113. \]
Non-homogeneous Perturbations

\[ D_2 = 1/10, \quad u(x, 0) = 11/17 + B(x; \pi/3, 2\pi/3), \]
\[ v(x, 0) = 40/51 + B(x; \pi/4, \pi/2) \]
Instability to Perturbation

\[ D_2 = \frac{1}{20}, \quad u(x, 0) = \frac{11}{17} + B(x; \pi/3, 2\pi/3), \]

\[ v(x, 0) = \frac{40}{51} + B(x; \pi/4, \pi/2) \]
Homogeneous Perturbations

\[ D_2 = \frac{1}{20}, \ u(x, 0) = 0.7471, \ v(x, 0) = 0.8843 \]
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,

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

Linearizing the system about this fixed point gives us

$$L(k; A_1) = \begin{bmatrix}
c_{11}uf'(c_{11}u + v) - D_1 k^2 - \frac{A_1}{u} & uf'(c_{11}u + v) \\
v g'(z_2) & c_{22}vg'(z_2) - D_2 k^2
\end{bmatrix}$$
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.

\[
G_1(u, A_1, D_2) = uf(c_{11}u + \frac{z_2 - u}{c_{22}}) + A_1
\]

\[
H_1(u, A_1, D_2) = D_1D_2k^4 - \frac{A_1}{u}(z_2 - u)g'(z_2) - k^2(D_1(z_2 - u)g'(z_2) + D_2c_{11}uf'(c_{11}u + \frac{z_2 - u}{c_{22}}) - \frac{A_1}{u}) - \left(\frac{1}{c_{22}} - c_{11}\right)u(z_2 - u)f'(c_{11}u + \frac{z_2 - u}{c_{22}})g'(z_2)
\]
Implicit Function Theorem

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

Using the Implicit Function Theorem we know that when

$$
\begin{vmatrix}
\frac{\partial G_1}{\partial A_1} & \frac{\partial G_1}{\partial u} \\
\frac{\partial H_1}{\partial A_1} & \frac{\partial H_1}{\partial u}
\end{vmatrix}
\neq 0
$$

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

$$
d\frac{A_1}{dD_2} \bigg|_{D_2} = -
\begin{vmatrix}
\frac{\partial G_1}{\partial A_1} & \frac{\partial G_1}{\partial u} \\
\frac{\partial H_1}{\partial A_1} & \frac{\partial H_1}{\partial u}
\end{vmatrix}
\bigg|_{(e_u, 0, \hat{D}_2)}.
$$
Another Example

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

\[ v_t = -v(1 - u - \frac{9}{20}v)(\frac{3}{2} - u - \frac{9}{20}v) + D_2v_{xx} \]

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

if \( k \in \mathbb{N} \cup \{0\} \).

\[
\frac{dA_1}{dD_2} = \frac{2486k^2(11 + 102k^2)}{5763 + 93738k^2} > 0.
\]
$D_2 = 1/20, \ A_1 = -1/25, \ u(x, 0) = 11/17 + B(x; \pi/3, 2\pi/3),$
$v(x, 0) = 40/51 + B(x; \pi/4, \pi/2)$