Turing Instability in Pioneer/Climax Species Interactions

J. Robert Buchanan

July 12, 2005

Millersville University of Pennsylvania

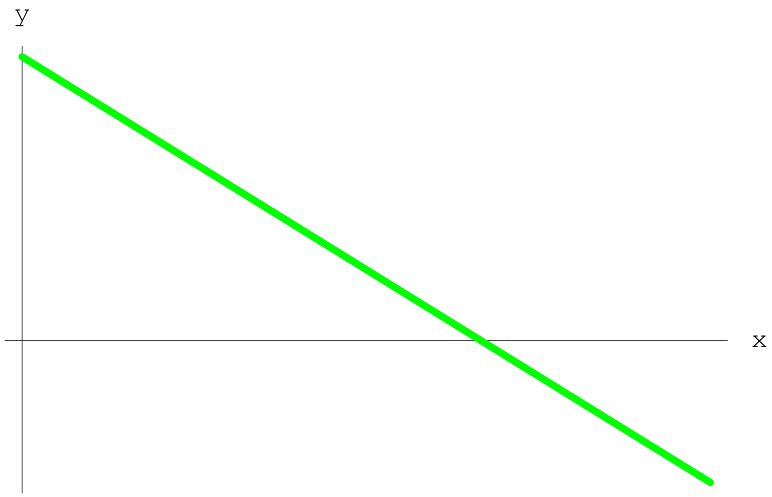
email: Bob.Buchanan@millersville.edu

Background and History

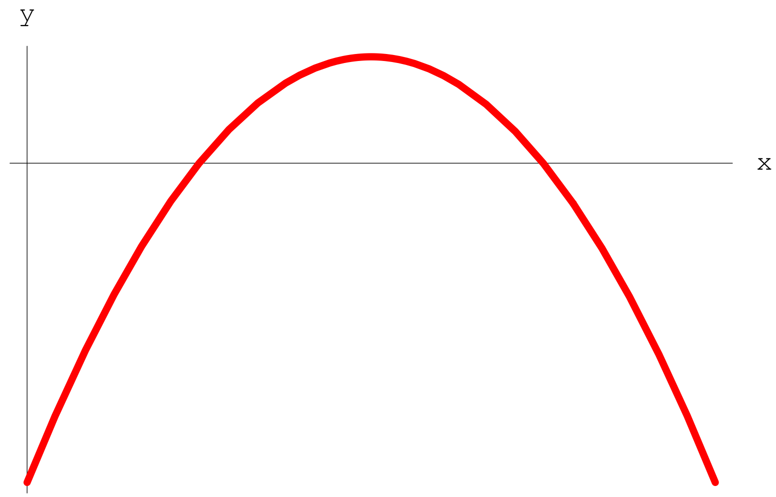
- Previous work on occurrence of Hopf bifurcations in pioneer/climax models,
- Use of constant and/or time periodic forcing functions to return a system to “near stability”,
- Current work on occurrence of Turing (diffusional) bifurcations in pioneer/climax models and the use of constant forcing to restabilize a system.

Introduction

Forestry science terms: **pioneer** and **climax** fitnesses



Pioneer



Climax

Assumptions

- Fitnesses will depend on a linear combination of species densities,
- Fitnesses are not necessarily linear (climax fitness cannot be linear),
- Diffusion rates will be adjusted to produce a bifurcation.

Model

Variables $u \equiv u(x,t)$ and $v \equiv v(x,t)$ represent pioneer and climax species respectively.

$$\begin{aligned} u_t &= uf(c_{11}u + v) + A_1 + D_1 u_{xx} \\ v_t &= vg(u + c_{22}v) + A_2 + D_2 v_{xx} \\ u(x,0) &= u_0(x), \quad v(x,0) = v_0(x) \end{aligned}$$

We will assume that the spatial domain is the one-dimensional finite interval, Ω, where $\Omega = \{x \in \mathbb{R} : 0 < x < L\}$ and that Neumann boundary conditions are in effect.

Turing (Diffusional) Instability

An equilibrium solution to the model equations exhibits Turing instability if it is stable to homogeneous perturbations, but unstable to non-homogeneous perturbations.
Non-dimensionalize model:

$$\tilde{x} = \frac{\pi}{L} x \quad \text{and} \quad \tilde{t} = D_1 \left(\frac{\pi}{L} \right)^2 t$$

$$\begin{aligned} u_{\tilde{t}} &= u\tilde{f}(c_{11}u + v) + \tilde{A}_1 + u_{\tilde{x}\tilde{x}} \\ v_{\tilde{t}} &= v\tilde{g}(u + c_{22}v) + \tilde{A}_2 + \tilde{D}_2 v_{\tilde{x}\tilde{x}} \\ u(\tilde{x}, 0) &= u_0(\tilde{x}), \quad v(\tilde{x}, 0) = v_0(\tilde{x}). \end{aligned}$$

Stability Definition I

An equilibrium solution $(\overline{u}, \overline{v})$, is **stable to homogeneous perturbations** if given any $\epsilon > 0$ there exists a $\delta = \delta(\epsilon) > 0$ such that if $(u_0, v_0) = (\overline{u} + w_1, \overline{v} + w_2)$ with $0 < w_1^2 + w_2^2 < \delta^2$ then the solution (u, v) to the reaction-diffusion equation with zero-flux boundary conditions obeys the inequality $(\overline{u} - u)^2 + (\overline{v} - u)^2 < \epsilon^2$ for all $t \geq 0$.

Stability Definition II

An equilibrium solution $(\overline{u}, \overline{v})$, is **stable to non-homogeneous perturbations** if given any $\epsilon > 0$ there exists a $\delta = \delta(\epsilon) > 0$ such that if $(u_0(x), v_0(x)) = (\overline{u} + w_1(x), \overline{v} + w_2(x))$ with $0 < w_1(x)^2 + w_2(x)^2 < \delta^2$ for all $x \in \overline{\Omega}$ then the solution (u, v) to the reaction-diffusion equation with zero-flux boundary conditions obeys the inequality $(\overline{u} - u)^2 + (\overline{v} - u)^2 < \epsilon^2$ for $x \in \overline{\Omega}$ and all $t \geq 0$.

Equilibrium Solution

$$(\overline{u}, \overline{v}) = \left(\frac{z_2 - c_{22}z_1}{1 - c_{11}c_{22}}, \frac{z_1 - c_{11}z_2}{1 - c_{11}c_{22}} \right),$$

where we assume

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

which implies $1 - c_{11}c_{22} > 0$.

Linearization

Let $(u, v) = (\overline{u} + w_1, \overline{v} + w_2)$ where w_1 and w_2 depend on (x, t) and satisfy the homogeneous Neumann boundary conditions.

Substitute into the non-dimensional model equations, and keep only the terms terms linear in w_1 and w_2.

$$\begin{bmatrix} w_{1,t} \\ w_{2,t} \end{bmatrix} = \begin{bmatrix} c_{11}\overline{u}f'(z_1) & \overline{u}f'(z_1) \\ \overline{v}g'(z_2) & c_{22}\overline{v}g'(z_2) \end{bmatrix} \begin{bmatrix} w_1 \\ w_2 \end{bmatrix} + \begin{bmatrix} w_{1,xx} \\ D_2 w_{2,xx} \end{bmatrix}.$$

Eigenvalue/Eigenvector Problem

Eigenfunctions of the linear system have the form $\phi_k(x) = (\cos kx)\mathbf{\Phi}_k$ where $\mathbf{\Phi}_k$ is a two-component, non-trivial, constant vector and $k \in \mathbb{N} \cup \{0\}$. For a fixed value of k we can look for a solution to of the form $\mathbf{w}_k(x,t) = e^{\lambda_k t}\phi_k(x)$.

By the principle of superposition, a solution to the linear system will have the form

$$\mathbf{w}(x,t) = \begin{bmatrix} w_1(x,t) \\ w_2(x,t) \end{bmatrix} = \sum_{k=0}^{\infty} \alpha_k e^{\lambda_k t} \phi_k(x).$$

Determining the Eigenvalues

Substituting $\mathbf{w}_k(x,t)$ into the linear system and rearranging terms yields

$$L(k)\mathbf{\Phi}_k = \begin{bmatrix} c_{11}\overline{u}f'(z_1) - k^2 & \overline{u}f'(z_1) \\ \overline{v}g'(z_2) & c_{22}\overline{v}g'(z_2) - D_2k^2 \end{bmatrix} \mathbf{\Phi}_k = \lambda_k \mathbf{\Phi}_k.$$

If the real parts of all the λ_ks are negative then $\lim_{t\to\infty} \mathbf{w}(x,t) \to (0,0)$

Trace and Determinant

$$\begin{aligned} \mathrm{tr} L(k) &= -k^2(1+D_2) + c_{11}\overline{u}f'(z_1) + c_{22}\overline{v}g'(z_2) \\ \det L(k) &= D_2k^4 - (c_{11}D_2\overline{u}f'(z_1) + c_{22}\overline{v}g'(z_2))k^2 \\ &\quad - (1 - c_{11}c_{22})\overline{uv}f'(z_1)g'(z_2) \end{aligned}$$

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

- $\mathrm{tr} L(k) < \mathrm{tr} L(0) < 0$ for all $k \in \mathbb{N}$,
- eigenvalues of $L(k)$ are real and simple and one eigenvalue can be made zero.

Making $\det L(k) = 0$

$$
\begin{aligned}
k^2_{\min} &= \frac{c_{11} D_2 \overline{u} f'(z_1) + c_{22} \overline{v} g'(z_2)}{2D_2} \\
\det L(k_{\min}) &= -\frac{(c_{11} D_2 \overline{u} f'(z_1) + c_{22} \overline{v} g'(z_2))^2}{4D_2} \\
&\quad - (1 - c_{11} c_{22}) \overline{uv} f'(z_1) g'(z_2).
\end{aligned}
$$

$\det L(k_{\min}) = 0$ **when**

$$
D_2 = \hat{D}_2 = -\frac{\overline{v} g'(z_2)}{c_{11}^2 \overline{u} f'(z_1)} \left(1 + \sqrt{1 - c_{11} c_{22}}\right)^2 .
$$

Example

$$
\begin{aligned}
u_t &= u(1 - \frac{1}{2}u - v) + A_1 + u_{xx} \\
v_t &= -v(1 - u - \frac{3}{5}v)(\frac{3}{2} - u - \frac{3}{5}v) + A_2 + D_2 v_{xx}
\end{aligned}
$$

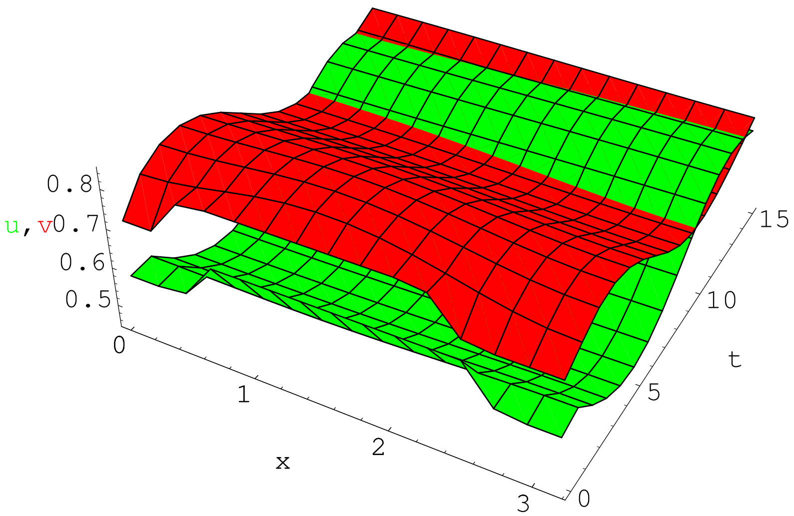
When $A_1 = A_2 = 0$ the equilibrium solution is $(\frac{4}{7}, \frac{5}{7})$ and

$$
L(k) = \begin{bmatrix} -2/7 - k^2 & -4/7 \\ 5/14 & 3/14 - D_2 k^2 \end{bmatrix}.
$$

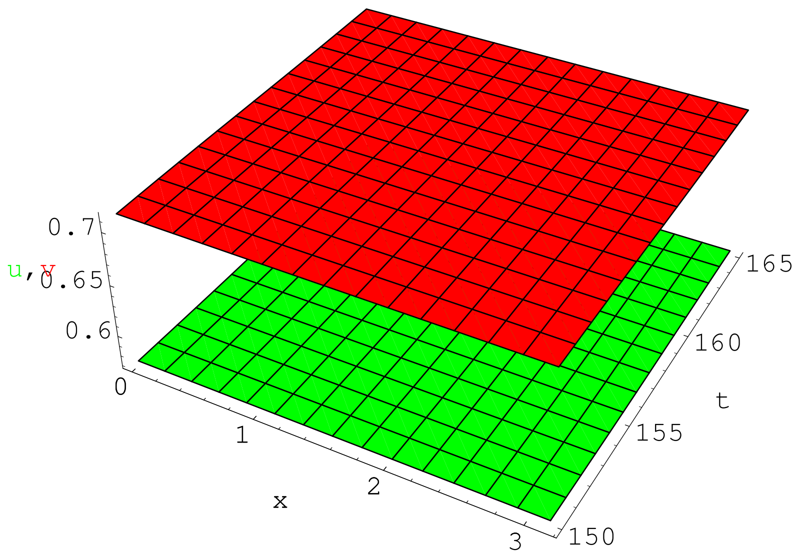
Since $\mathrm{tr} L(0) = -1/14$ and $\det L(0) = 1/7$, the eigenvalues negative real parts.

Critical Value of Diffusion: $\hat{D}_2 = (17 - 2\sqrt{70})/4$

Simulation, $D_2 > \hat{D}_2$

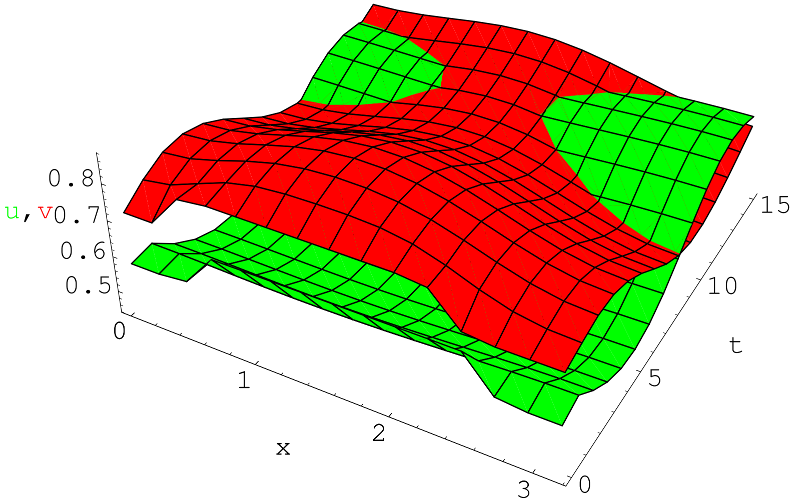


Initial conditions

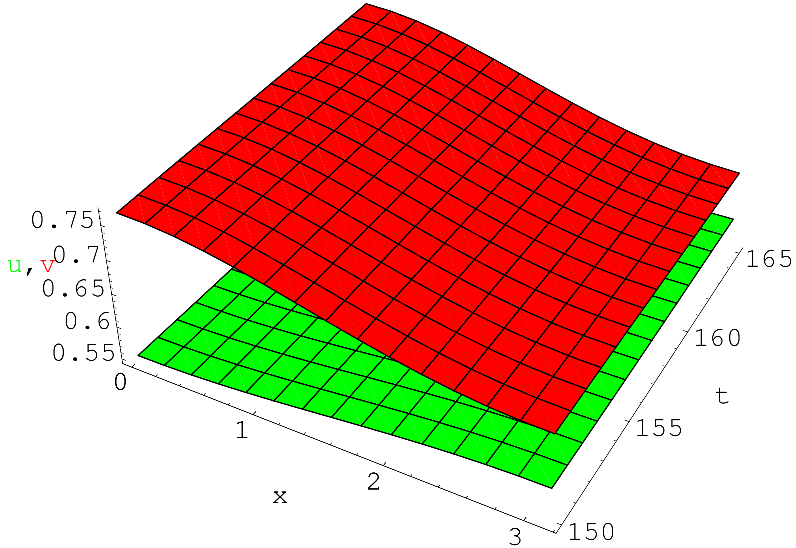


Asymptotic behavior

Simulation, $D_2 < \hat{D}_2$

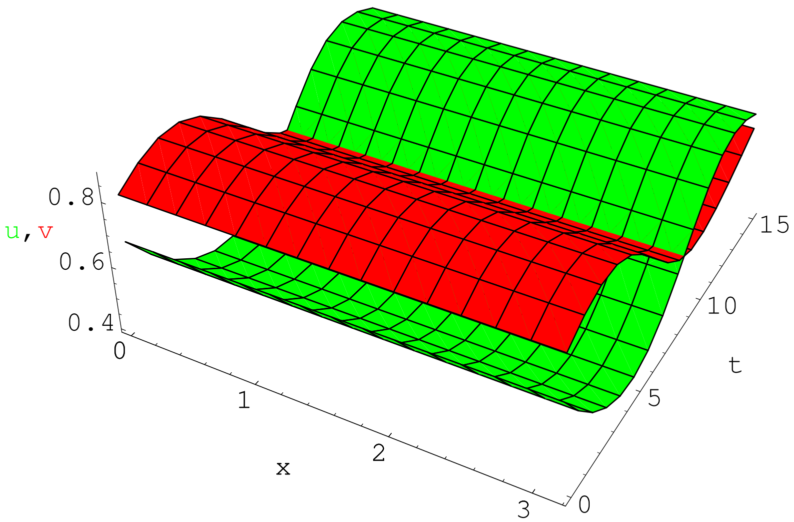


Initial conditions

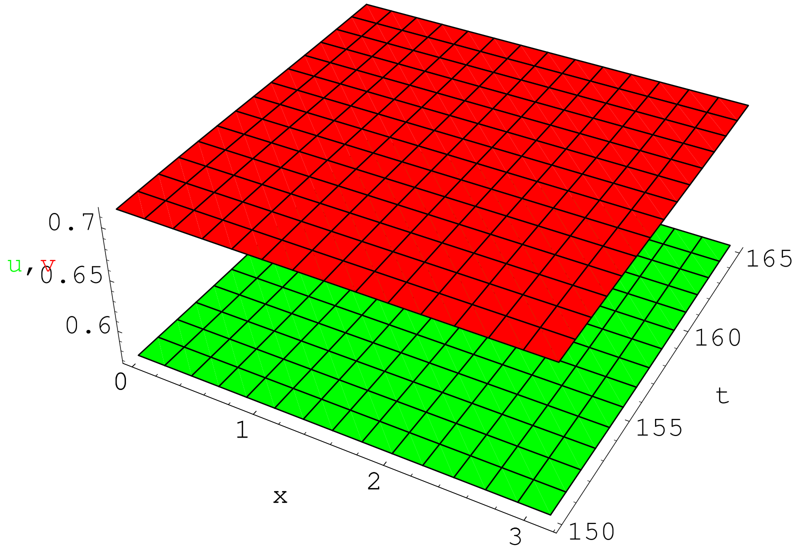


Asymptotic behavior

Homogeneous Perturbation



Initial conditions



Asymptotic behavior

Add Forcing

Assume $A_1 \neq 0$ and $A_2 = 0$.

Equilibrium solution must satisfy:

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

Linearized system becomes:

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

Finding Critical Value of A_1

Again, onset of diffusional instability occurs when $\det L(k; A_1) = 0$.

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

Implicit Function Theorem

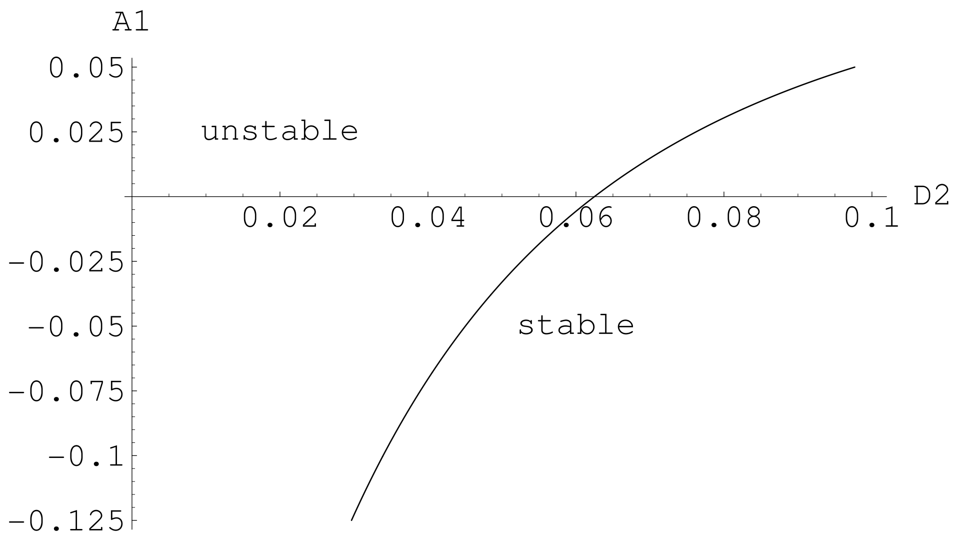
The monotonicity of A_1 as a function of D_2 at $\hat{D}_2$ is given by

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

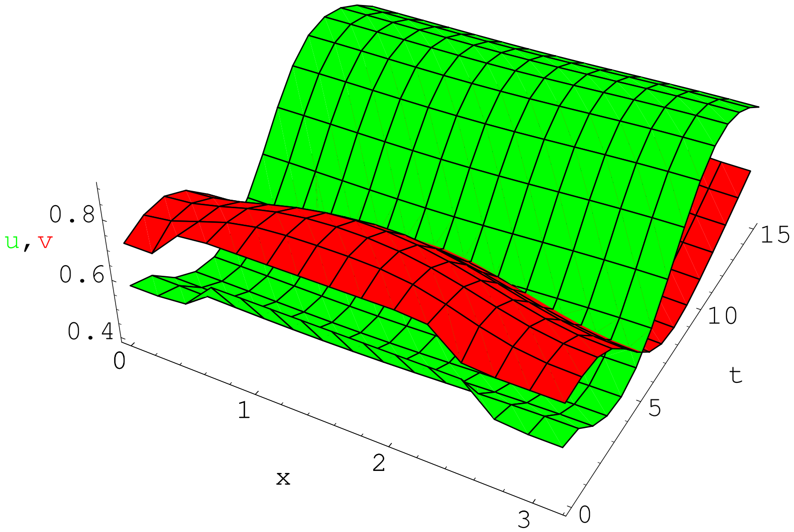
Re-stabilization Example

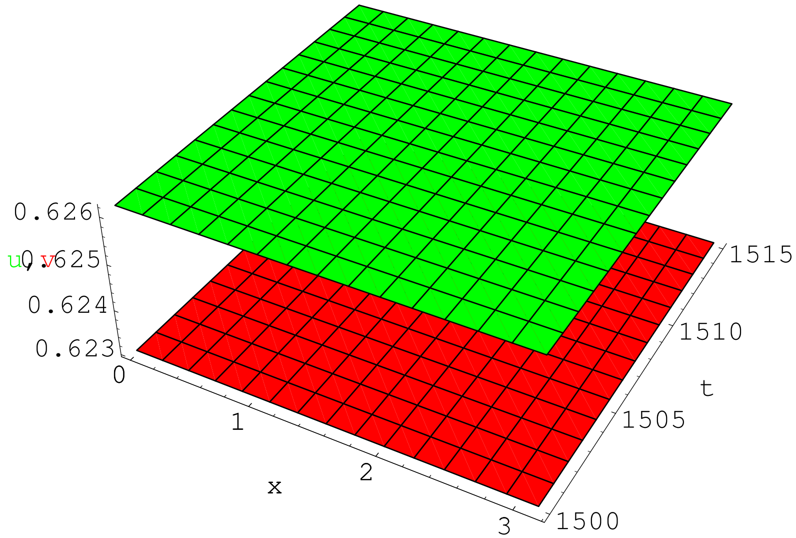
Keeping $A_2 = 0$ and allowing A_1 to vary in the earlier example we have

$$\left.\frac{dA_1}{dD_2}\right|_{D_2=\hat{D}_2} = \frac{54k^2(2+7k^2)}{7(15+28k^2)} > 0.$$



Re-stabilization Simulation, $D_2 < \hat{D}_2$





Initial conditions

Asymptotic behavior

Open Questions and Reference

- Will harvesting the pioneer species or stocking the climax species always re-stabilize the equilibrium solution of a two-species pioneer/climax model?
- Can time-varying stocking and/or harvesting be used to bring a system to “near equilibrium”?
- Can spatially non-uniform stocking and/or harvesting be used to re-stabilize the equilibrium?

“Turing Instability in Pioneer/Climax Species Interactions”, J. Robert Buchanan, *Mathematical Biosciences*, Volume 194, Number 2, (April 2005), pp. 199-216.