War of the Worlds: Modelling the spread of an invasive species and a pathogen in a host population.

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(Tree Munchers)

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Outline

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1. Background
2. Model formulation
   - Equations
   - Well-posedness
   - Stabilities of equilibria
   - Tr-Det plane
   - Stabilities
   - Numerical Simulations of 1 patch dynamics

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   - Two patch model
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5. Conclusions

Background

by forest insects.pdf

Defoliation by forest insect pests

- > 100 species
  - Gypsy moth
  - Larch bud moth
  - Spruce budworm
  - Etc.
- Costs
  - Control management
  - Loss of tree vigor and productivity

Background

by forest insects2.pdf

Objectives

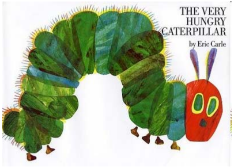
- Investigate the impact of feedback between the pest insect and the host tree (resources)
- Consider the effects of spatial structure and insect movement by a patch model
- Include tritrophic interactions (tree-insect-pathogen)

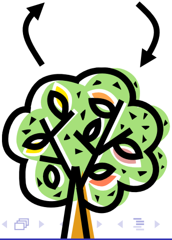
Background

by forest insects3.pdf

Our model settings

- Feedbacks
  - Carrying capacity of trees sustains the insects
  - Larvae munch on tree leaves and decrease food resource (leaves) available for them
- Trees have no defense against the pest
- The insect can move from a tree to another tree
  - Density dependent
  - The insect can only observe the condition of the tree where they are currently feeding
- Continuous reproduction of the insect and regeneration of trees
- Larvae are susceptible to the pathogen





The model

The model is described by the following system of differential equations

$$\begin{cases} \dfrac{dN(t)}{dt} = rN(t)\left(1 - \dfrac{N(t)}{K(t)}\right), \\ \dfrac{dK(t)}{dt} = cK(t)\left(1 - \dfrac{K(t)}{a}\right) - d\dfrac{N(t)K(t)}{K(t)+b}. \end{cases} \quad (1)$$

N: the number of insects
K: the "tree quality"
r, c: growth rate of insects and tree, respectively
a: maximum productivity of the tree
d: intensity of pest consumption of tree
b: saturation constant.

Dimensionless System

We let

$$\tau = rt, \quad x(t) = \frac{N(t)}{a}, \quad y(t) = \frac{K(t)}{a},$$

and get the associated dimensionless form

$$\begin{cases} \dfrac{dx(\tau)}{d\tau} = x(\tau)\left(1 - \dfrac{x(\tau)}{y(\tau)}\right), \\ \dfrac{dz(\tau)}{d\tau} = \gamma z(\tau)(1 - z(\tau)) - \delta \dfrac{x(\tau)z(\tau)}{z(\tau) + \theta}, \end{cases} \tag{2}$$

where

$$\gamma = \frac{c}{r}, \quad \delta = \frac{d}{r}, \quad \theta = \frac{b}{a}.$$

Well-posedness

For any initial value $x_0 \in R^2_+$ and initial time t_0, there is a unique bounded solution $x(t, t_0, x_0) \geq 0$ through x_0 on the interval $[t_0, +\infty)$.

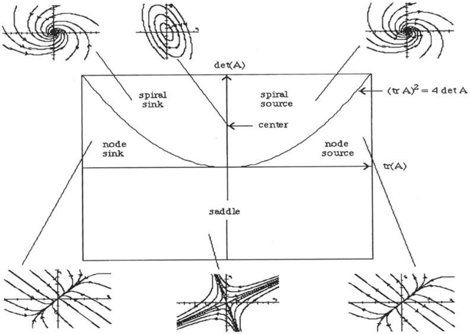
Equilibria of dimensionless system

Three equilibria: $E_0 = (0,0)$, $E_1 = (0,1)$, $E_2 = (x^*, z^*)$,

where $x^* = z^* = \dfrac{1-\theta-\dfrac{\delta}{\gamma}+\sqrt{\left(1-\theta-\dfrac{\delta}{\gamma}\right)^2+4\theta}}{2}$.

E_1: saddle source.

The trace determinant plane



Dynamic behavior diagram for second-order linear systems. The x-axis is tr(A) and the y-axis is det(A).

http://pse.che.ntu.edu.tw/hsp/AdvancedProcessControl/APC%202007/Phase-plane%20analysis.doc

Three cases for E_2

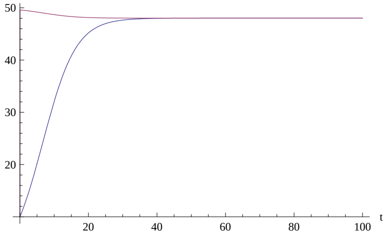
$$\text{Tr}= \gamma(1-2y^*)-1-\frac{\delta\theta y^*}{(y^*+\theta)^2}, \quad \text{Det}= \frac{\delta\theta y^*}{(y^*+\theta)^2}+\gamma y^*.$$

Case 1: if $\gamma(1-2y^*)-1-\dfrac{\delta\theta y^*}{(y^*+\theta)^2}<0$, E_2 is locally asymptotically stable;

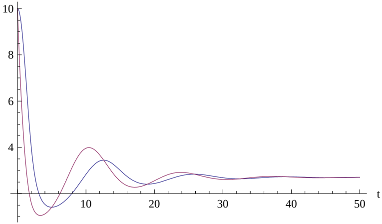
Case 2: if $\gamma(1-2y^*)-1-\dfrac{\delta\theta y^*}{(y^*+\theta)^2}=0$, two purely imaginary roots and Hopf bifurcation occurs at E_2;

Case 3: if $\gamma(1-2y^*)-1-\dfrac{\delta\theta y^*}{(y^*+\theta)^2}>0$, E_2 is unstable and limit cycle occurs.

Within 1 patch dynamics



(a) steady state



(b) Spiral sink

Within 1 patch - dynamics

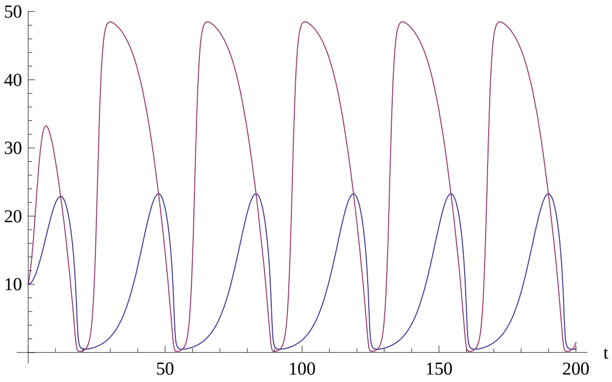


Figure: Limit Cycle

Plot of Trace = 0 for fixed δ

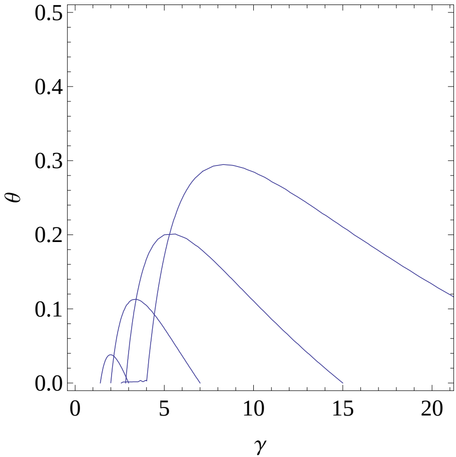


Figure: Plot of the trace of the Jacobian =0 in the $\gamma - \theta$ parameter space. As δ increases, the unstable region becomes larger.

Two patch model:

$$\begin{cases} \dfrac{dN_1}{dt} = rN_1\left(1-\dfrac{N_1}{K_1}\right) + m_{12}\left(1-\left(1-\dfrac{N_2}{K_2}\right)^q\right)N_2 \\ \qquad -m_{21}\left(1-\left(1-\dfrac{N_1}{K_1}\right)^q\right)N_1, \\ \dfrac{dK_1}{dt} = cK_1\left(1-\dfrac{K_1}{a}\right) - d\dfrac{N_1K_1}{K_1+b}, \\ \dfrac{dN_2}{dt} = rN_2\left(1-\dfrac{N_2}{K_2}\right) + m_{21}\left(1-\left(1-\dfrac{N_1}{K_1}\right)^q\right)N_1 \\ \qquad -m_{12}\left(1-\left(1-\dfrac{N_2}{K_2}\right)^q\right)N_2, \\ \dfrac{dK_2}{dt} = cK_2\left(1-\dfrac{K_2}{a}\right) - d\dfrac{N_2K_2}{K_2+b}, \end{cases} \tag{1}$$

n patch model:

$$\begin{cases} \dfrac{dN_i}{dt} = rN_i\left(1-\dfrac{N_i}{K_i}\right) + \sum\limits_{j=1}^{p} m_{ij}\left(1-\left(1-\dfrac{N_j}{K_j}\right)^q\right)N_j \\ \qquad - \sum\limits_{j=1}^{p} m_{ji}\left(1-\left(1-\dfrac{N_i}{K_i}\right)^q\right)N_i, \\ \dfrac{dK_i}{dt} = cK_i\left(1-\dfrac{K_i}{a}\right) - d\dfrac{N_iK_i}{K_i+b}, \quad i=1,2,...,n. \end{cases} \tag{2}$$

Within n patch - dynamics

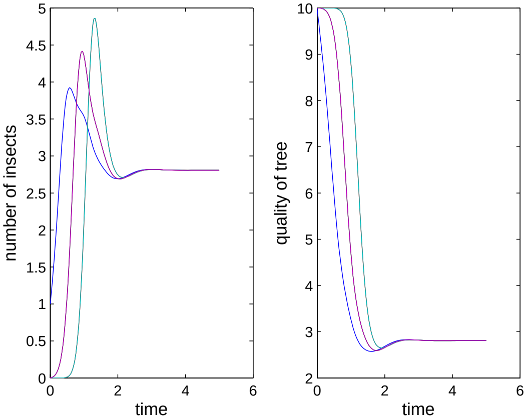


Figure: 5 patch model, with the quality of the tree equal in each patch and initial population of insects introduced into one patch.

Within n patch - dynamics

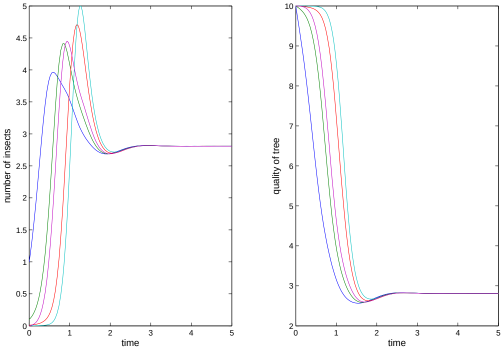


Figure: 5 patch model, with the quality of the tree equal in each patch and initial population of insects is distributed among the patches at decreasing values.

Within n patch - dynamics

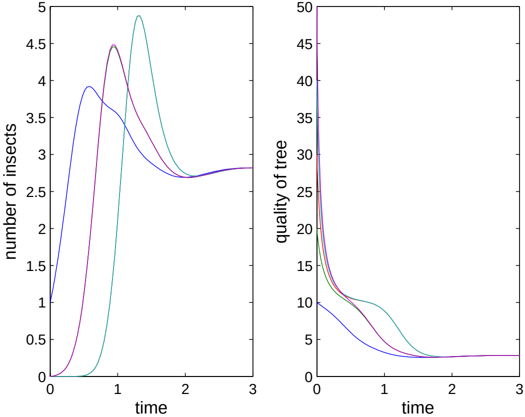


Figure: 5 patch model, with the initial quality of the tree different in each patch and initial population of insects introduced into one patch.

Within 1 patch - dynamics

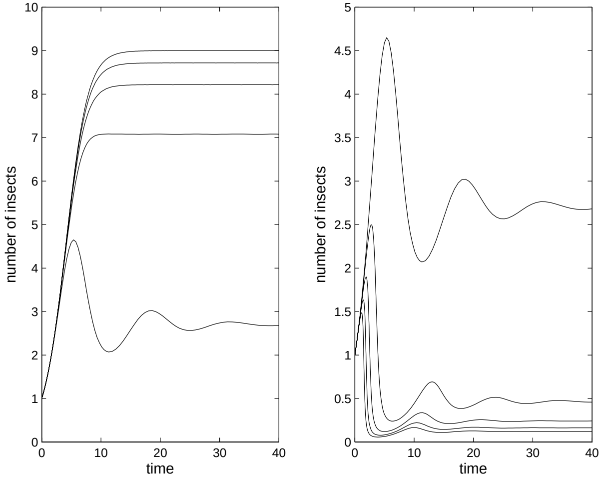


Figure: Within patch : On the left hand side, effect of increasing c and on the right hand side, effect of increasing d.

Within n patch - dynamics: Change of movement

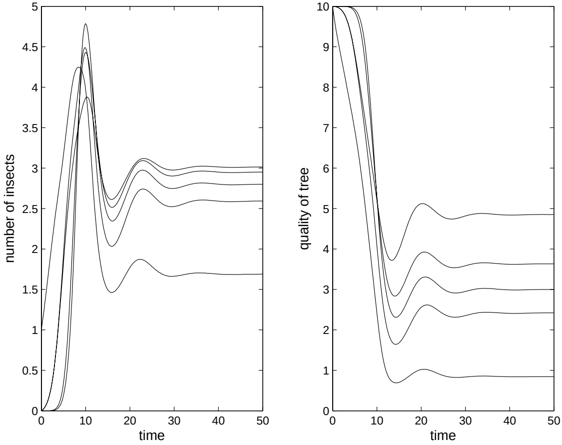


Figure: 5 patch model, with the movement equal in all directions. The quality of the tree equal in each patch and initial population of insects introduced into one patch only.

Within n patch - dynamics: Limit Cycle in each Patch

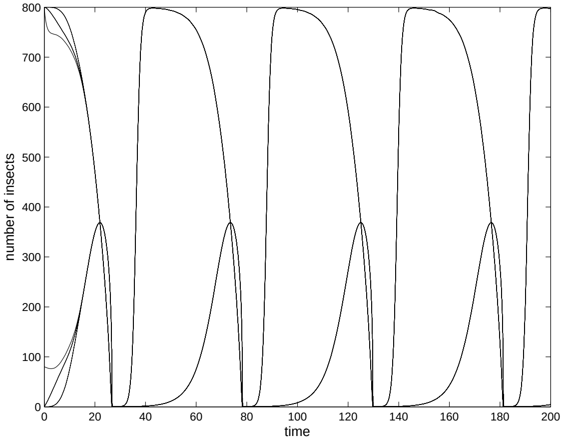


Figure: 5 patch model, with the movement equal in each direction. The quality of the tree equal in each patch and initial population of insects introduced into one patch only.

Within n patch - dynamics: Change of movement

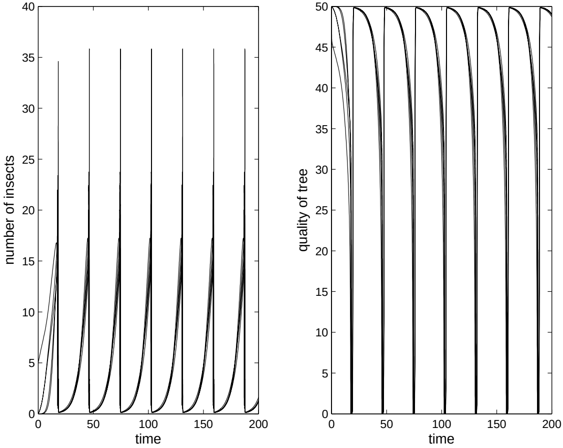


Figure: 5 patch model, with the movement predominant in one direction. The quality of the tree equal in each patch and initial population of insects introduced into one patch only.

Introduction of Pathogen to Pest-Host System

Assume direct pest to pest transmission of the pathogen. The model equations are:

$$\begin{cases} \dfrac{dS}{dt} = rS\left(1 - \dfrac{S+I}{K}\right) - \beta SI, \\ \dfrac{dI}{dt} = \beta SI - rI\dfrac{S+I}{K} - \alpha I, \\ \dfrac{dK}{dt} = cK\left(1 - \dfrac{K}{a}\right) - d\dfrac{K(S+I)}{K+b}. \end{cases} \quad (1)$$

Let $x = \frac{S}{a}$, $y = \frac{I}{a}$, $z = \frac{K}{a}$, and $\tau = rt$, then we get the dimensionless form as

$$\begin{cases} \frac{dx}{d\tau} = x(1 - \frac{x+y}{z}) - \varepsilon xy, \\ \frac{dy}{d\tau} = \varepsilon xy - \frac{x+y}{z} y - \zeta y, \\ \frac{dz}{d\tau} = \gamma z(1-z) - \delta \frac{z(x+y)}{z+\theta}, \end{cases} \tag{2}$$

where $\varepsilon = \frac{\beta a}{r}, \quad \zeta = \frac{\alpha}{r}, \quad \gamma = \frac{c}{r}, \quad \delta = \frac{d}{r}, \quad \theta = \frac{b}{a}.$

Equilibria

$$\hat{E}_0 = (0,0,0), \quad \hat{E}_1 = (0,0,1), \quad \hat{E}_2 = (z^*, 0, z^*), \quad \hat{E}_3 = (x_e, y_e, z_e).$$

where

$$x_e = \frac{1+\zeta+\varepsilon\zeta z_e}{\varepsilon^2 z_e}, \quad y_e = \frac{\varepsilon z_e - 1 - \zeta}{\varepsilon^2 z_e},$$

and z_e is the root(s) of the following equation

$$z^2 - (1-\theta)z + \frac{\delta(1-\zeta)}{\gamma\varepsilon} - \theta = 0.$$

We use Descartes Rule of signs to get the following cases for z_e:

Case 1: if $1 \leq \theta \leq \frac{\delta(1-\zeta)}{\gamma\varepsilon}$, or $\theta < \min\left(1, \frac{\delta(1-\zeta)}{\gamma\varepsilon}\right)$ and

$$\Delta := (1+\theta)^2\gamma\varepsilon - 4\delta(1-\zeta) < 0,$$

there is no positive real roots;

Case 2: if $\theta > \frac{\delta(1-\zeta)}{\gamma\varepsilon}$, there is one positive root;

Case 3: if $\theta < \min\left(1, \frac{\delta(1-\zeta)}{\gamma\varepsilon}\right)$ and

$$\Delta := (1+\theta)^2\gamma\varepsilon - 4\delta(1-\zeta) > 0,$$

there are two positive real roots.

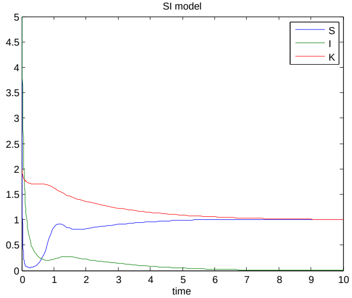


Figure: Convergence to the disease free equilibrium.

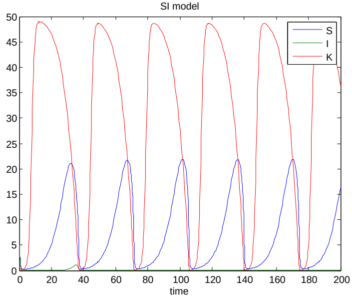


Figure: The infectious population dies out, while the susceptible population oscillates.

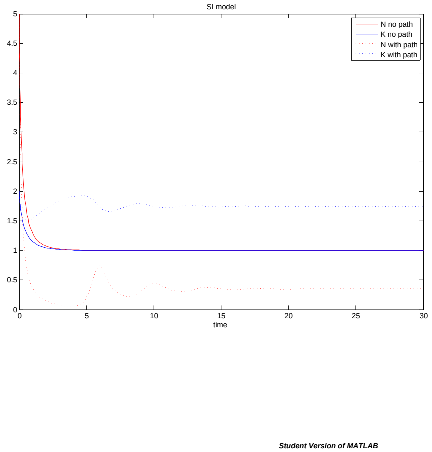


Figure: Convergence to endemic equilibrium with a pathogen, compared to the positive equilibrium of the populations that are not infected by the pathogen.

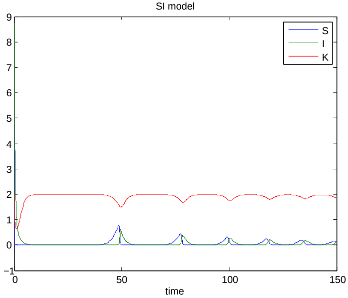


Figure: Intermittent outbreaks of infection.

Conclusions

- Patch dynamics are affected by many factors such as parameters related to insect entry characteristics and movement rates;
- In some regions of parameter space, oscillations bring insect population close to zero where stochastic effects may be important.
- Introducing a pathogen that infects the pest can reduce pest population and improve the health of the host trees.

Future Work

- Allow heterogeneity in host, i.e., different parameter values on each patch;
- Consider more complicated spatial arrangements of trees;
- Allow movement beyond neighbours, possibly as a function of distance;
- Investigate tritrophic dynamics more thoroughly;
- Consider evolution of host defences and insect resistance to pathogen;
- Consider vector based transmission.

Thank you very much!