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STUDENT VERSION
Climate Change Effects on Insect Outbreaks

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Motivation

Before class,

1. Watch the following short videos about mountain pine beetle (MPB) outbreaks:
    - *National Geographic*: https://www.youtube.com/watch?v=vR30qlK0-Cw [7]
    - *The YEARS Project*: https://www.youtube.com/watch?v=FzrfzQG6YD0 [9]
2. Read Sections 1 and 2 of this project.
3. Read Sections 1 and 2 (Subsections 2.1 and 2.2 only) of [5].

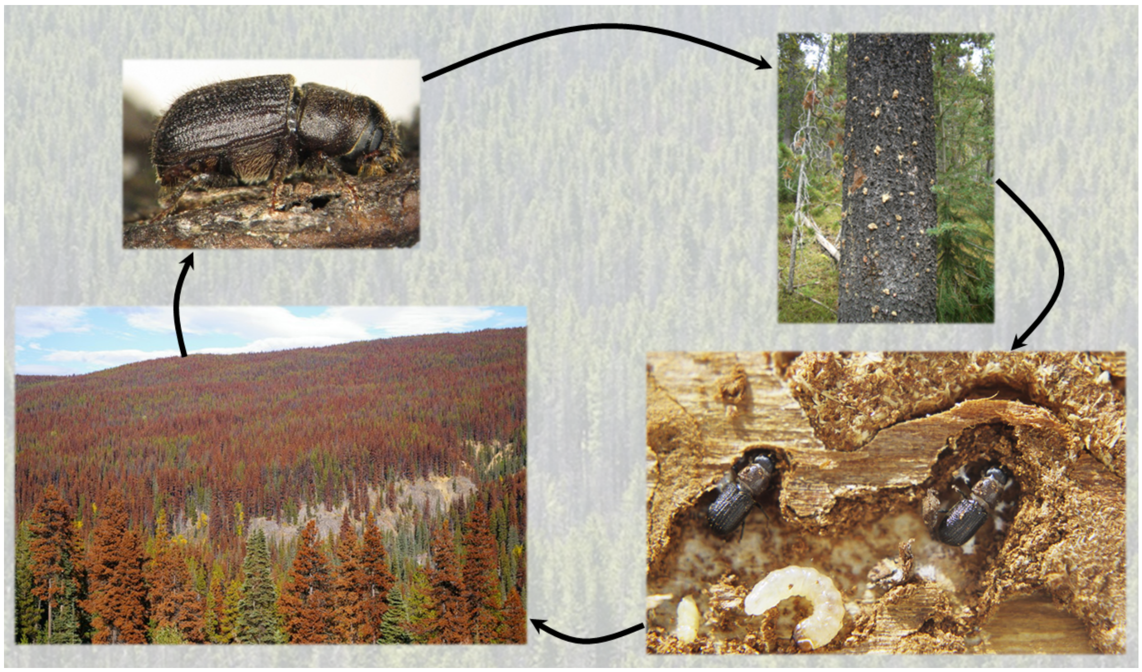

Figure 1. Relationship between MPB life-cycle and lodgepole pine forests.

SCENARIO DESCRIPTION

1 Introduction

The mountain pine beetle (MPB, *Dendroctonus ponderosae*), a tree-killing bark beetle, has historically been part of the normal disturbance regime in lodgepole pine (*Pinus contorta*) forests. In recent years, however, warmer weather has allowed MPB populations to achieve synchronous emergence and successful attacks, resulting in widespread population outbreaks and resultant tree mortality across western North America [2].

In late spring and summer, MPB emerge from infested trees and search for new trees to colonize. MPB attack adult pine trees *en masse* in order to overcome the tree's defensive mechanisms [3]. Once colonized, MPB lay eggs beneath the bark of the tree. In spring, eggs hatch and larvae feed on the tree's phloem layer, which kills the tree. Once larvae have molted into adult MPB, they emerge from the tree in summer and the cycle begins again [1] (see Figure 1).

One year following an infestation, a tree's needles turn red (the tree is then called a red snag). Two years following an infestation, the needles turn gray (gray snag). Finally, three years after infestation, the needles fall off of the tree completely. This opens up the forest floor (which will typically be littered with heat-dependent serotinous pine cones) to the sun's thermal radiation, generating new juvenile tree growth. Juvenile trees are not susceptible to MPB attacks until they have a big enough phloem layer to support a colonization (around 50 to 80 years of age) [1].

In this project, we will use a system of difference equations that incorporates temperature-dependent

MPB population growth rate to model the outbreak and recovery cycle in MPB-infested forests. We then explore analytical methods, applied to the model, to predict outbreak severity in terms of the climate-sensitive growth rate parameter. These model-based predictions elucidate the connection between warming climate and increased severity of recent MPB outbreaks.

2 The SIJ Model

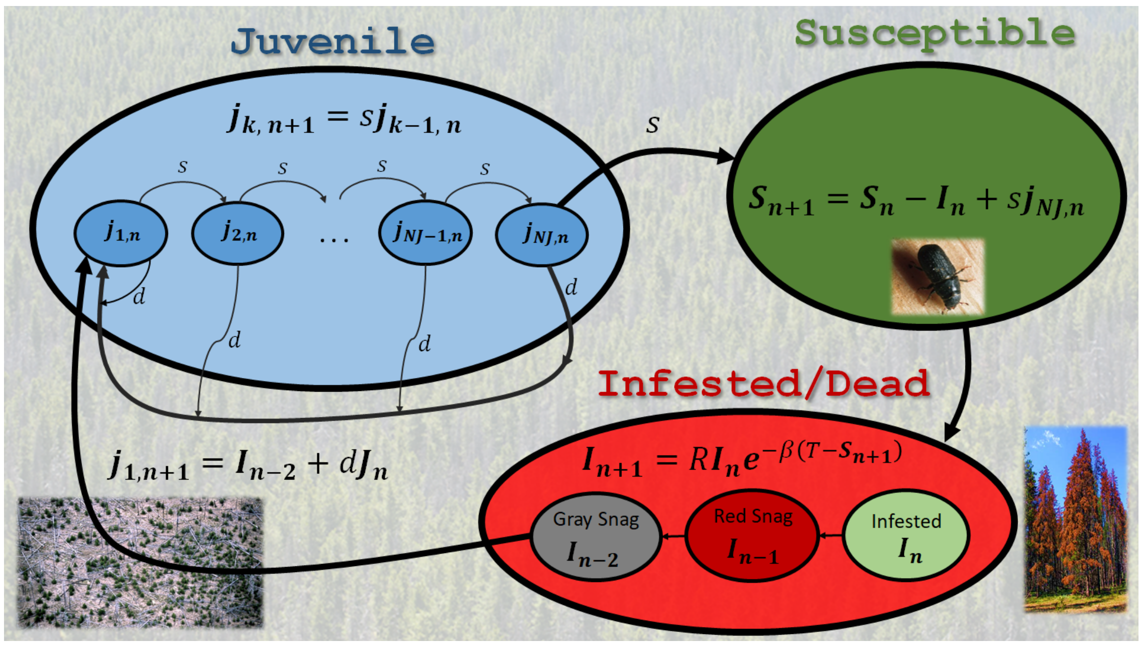

Figure 2. The SIJ model.

The SIJ model of [5] is a system of difference equations that tracks yearly populations of susceptible trees S_n, infected trees I_n, and juvenile trees J_n (see Figures 2 and 3). Natural juvenile mortality, d, opens up forest floor space to new seedling growth. Likewise, infestation mortality translates to seedling growth (after a once infested tree spends 2 years as a snag). Juvenile age class survivorship $s = 1 - d$ is constant. A tree spends NJ years as a juvenile before graduating (maturing) to the susceptible class. Susceptible trees in the forest become infested at a rate proportional to last year's population of infested trees. The constant of proportionality is the MPB population growth rate. The rate of infestation also depends on how easily MPB are able to find susceptible trees, and can be characterized by $e^{-\beta(T-S_{n+1})}$, where β is a parameter measuring the efficiency with which MPB search out and find new host trees to colonize. The total population of trees in the forest is denoted by T. The equation modeling infested trees is

$$I_{n+1} = RI_n e^{-\beta(T-S_{n+1})}, \tag{1}$$

where R represents the MPB population growth rate parameter. Note that R implicitly depends on temperature since MPB developmental rates are driven by ambient thermal energy as they progress through their life stages [2].

Variables	Description	Units
S_n	Susceptible (to MPB colonization) tree population in year n	Number of stems
I_n	Infested (by MPB) tree population in year n	Number of stems
$j_{k,n}$	Juvenile tree population of the kth age class in year n	Number of stems (in adult equivalents)
J_n	Total juvenile tree population (age NJ or younger)	Number of stems (in adult equivalents)
Parameters	**Description**	**Units/nominal values**
T	Total number of trees in the forest	$T = 110{,}000$ stems (in adult equivalents)
NJ	Number of juvenile age classes	NJ $= 50$ age classes
d	Natural mortality rate for juveniles	$d = 0.01$ per year
$s = 1 - d$	Natural juvenile survivorship	$s = 0.99$ per year
R	Temperature-dependent MPB pop. growth rate	$R = 1.8$ per year
β	Failure rate for MPB host search process	$\beta = 10.8 \times 10^{-6}$ per stem

Figure 3. Model variables, parameters, and estimated parameter values from [8].

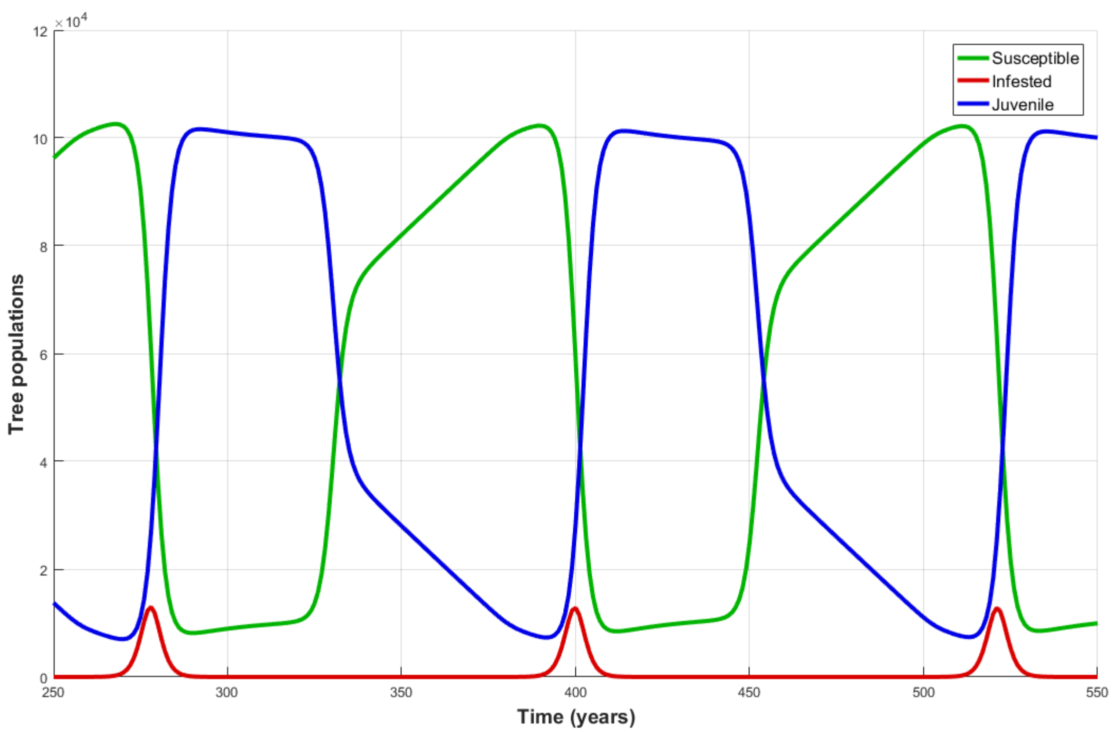

Figure 4. The outbreak-recovery cycle: Simulation output showing tree populations over two full periods.

The current number of *nonsusceptible* trees in the forest is given by $(T - S_{n+1})$. Hence, as MPB infest more and more trees each year, the number of nonsusceptible trees increases, causing the exponential term in (1) to approach 0. This significantly reduces the spread of infestation as MPB no longer have a sufficient number of susceptibles trees left to colonize. Eventually, this leads to a decrease in infested trees and an increase in susceptible trees. When the forest has recovered from an outbreak, it contains mostly susceptible trees. In this case, the exponential term approaches 1, reducing the infestation equation to $I_{n+1} = RI_n$. This yields exponential growth of infestation, triggering another outbreak. Thus, we see that MPB outbreaks are periodic in nature. Figure 4 illustrates this through simulation of the model.

3 Convert the Difference Equation to a Differential Equation Model

Here we move from a discrete-time to a continuous-time model by transforming the difference equation governing infested trees into an approximating differential equation. In order to get the difference equation into the appropriate form for this transformation, we must first perform some algebraic manipulations.

1. Take the natural logarithm of both sides of (1) and solve for βS_{n+1}. Label the result as (2).
2. Re-index the equation by subtracting 1 from all variable indices. Label the result as (3).
3. Subtract (3) from (2). Label the result as (4).
4. Since the number of juvenile trees is small during an outbreak, we may neglect the term containing $J_{NJ,n}$ in the equation governing susceptible trees, $S_{n+1} = S_n - I_n + sJ_{NJ,n}$. This results in $S_{n+1} = S_n - I_n$. Substitute the right side of this equation in for S_{n+1} in (4). Label the result as (5).
5. We are now ready to make the transition from a discrete-time to a continuous-time model. Let $y(t) = \ln I_n$ be some continuous function of time t years where $t = n$ for whole number values of t. Note that t is a real variable, as opposed to n which is an integer variable. Write (5) in terms of y. Label the result as (6).
6. Use the second finite difference approximation for a second derivative, $y'' \approx y(t+1) - 2y(t) + y(t-1)$, to convert the difference (6) to a second order differential equation (solved for y''). Label the result as (7).

4 Solve the Differential Equation

1. Multiply both sides of the second order differential equation (7) by $y'(t)$.
   (a) Integrate the left side of the equation with respect to time (omit the constant of integration).
   Hint: Integration by parts!
   (b) Integrate the right side of the resulting equation with respect to time (label the constant of integration C).
   Hint: u-substitution!
2. Solve for y' (take only the positive square-root). Label the result as (8). Note that the result is a *first order* differential equation.

Year	Infested tree density (trees/hectare)
1995	3.1
1996	3.2
1997	2.9
1998	3.0
1999	4.5
2000	5.5
2001	7.4
2002	39.1
2003	27.0
2004	11.8
2005	6.5
2006	4.6
2007	5.7
2008	5.2

Table 1. Infestation data taken from a MPB outbreak in the Sawtooth National Recreation Area, Idaho.

3. We can solve for the constant of integration, C, in (8) using the fact that $t = 0$ corresponds to the peak of the outbreak. That is, $y'(0) = 0$ and $y(0) = \ln I_{max}$ where I_{max} represents the maximum infestation (the value of which will be determined later). Solve for C and substitute it back into (8). Factor out any common factors. Label the result as (9).
4. Using the change of variables, $\hat{I}(t) = e^{y(t)}$, write (9) in terms of $\hat{I}(t)$ (solved for $\hat{I}'(t)$). Note that $\hat{I}(t)$ is our continuous function approximation for the discrete function I_n. Label the result as (10).
5. Solve the first order (10) using the separation of variables method. First, separate the variables. Then integrate both sides. You will need the integral formula

$$\int \frac{1}{x\sqrt{k-x}}dx = \frac{-2}{\sqrt{k}} \tanh^{-1}\left(\frac{\sqrt{k-x}}{\sqrt{k}}\right)$$

   where k is a positive constant. Do not solve for $\hat{I}(t)$ yet.
6. Find the value of the constant of integration using the fact that $\hat{I}(0) = I_{max}$.
7. Now solve for $\hat{I}(t)$. You will need the identities $\tanh^2(x) + \text{sech}^2(x) = 1$ and $\text{sech}(-x) = \text{sech}(x)$. Label the result as (11). (This is the *main result* of the project.)

   Note that this model (11) has t as the *independent variable* and $\hat{I}(t)$ as the *dependent variable*. The *parameters* of the model are β and I_{max}.

5 Model Parameterization

We now fit (11) to data taken from a recent outbreak in central Idaho given in Table 5 (data from [6]). This will entail adjusting the parameter values of the model (β and I_{max}) until the graph of the solution, (11), best fits a scatter plot of the data.

Note: A *hectare* (ha) is equal to 10,000 square meters (approximately 2.47 acres).

1. Plot the data in *Desmos* [4] (or similar graphing software).
   Desmos can be found at https://www.desmos.com/calculator. Create sliders for the parameters β and I_{max}.
2. Since the peak of the graph of (11) is centered around zero, and the peak in the data is centered somewhere in the early 2000s, we must horizontally shift the graph of (11) to align the peaks. Replace the time variable with $(t - t_{peak})$ and create a slider for t_{peak} (the time at which the outbreak peaks).
3. Adjust the sliders until the graph of (11) fits the data best by visual inspection of the graph.
4. Now calculate (in *Desmos* or similar) the sum of the squared errors (SSE) between the model and the data:
$$\begin{aligned} SSE &= \sum (\text{observed infestation} - \text{predicted infestation})^2 \\ &= \sum_{n=1995}^{2008} \left(I(n) - \hat{I}(n) \right)^2 . \end{aligned}$$
5. Adjust the sliders so that the SSE is minimized (as small as possible)..
6. Write down the parameter values that minimize the SSE as well as the value of the SSE.

6 Effect of Global Warming on Outbreak Severity

One measure of the severity of an outbreak is the *outbreak footprint* – the total number of trees (per hectare of forest) killed over the course of an outbreak. A formula for approximating the outbreak footprint derived in [5] is given by
$$F = \frac{2 \ln R}{\beta}.$$
This approximation is in terms of the MPB search efficiency β, and population growth rate R. Since R depends heavily on temperature, F can be used to assess the effect of climate change on the severity of outbreaks.

1. At the onset of an ongoing outbreak, it was determined that the MPB population growth rate was approximately 4.6. Predict the total number of trees killed in this outbreak (total infestation). (Use the fitted value of β from the previous section.)

2. Graph the footprint formula in *Desmos* using the fitted value of β, keeping R as the independent variable.

3. Given that increasing temperatures lead to higher MPB population growth rates, assess the impact of climate change on the severity of MPB outbreaks using the graph of F.

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