Modeling the spread of Hemlock Woolly Adelgid

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ABSTRACT
In this paper, a mathematical model is proposed to explain the interaction between Eastern Hemlock Trees and the invasive species Hemlock Woolly Adelgid. A system of reaction diffusion equations is used for this modeling exercise. There are at most three (3) steady states for the system of which the coexistent state is the only stable steady states for some parameter values. The model dynamics show that the solutions exhibit traveling wave solutions. In addition, a sensitivity analysis is conducted to determine the impact of model parameters. Sensitivity analysis suggests that the mortality rate of Eastern Hemlock Trees and the predation intensity of Hemlock Woolly Adelgid drive the dynamics of the interaction. Since Eastern Hemlock trees are foundation trees that provide shelter for several species, they need to be protected for as long as possible. Based on the model dynamics and sensitivity analysis, it is postulated that selective and strategic removal of these trees will help curtail their destruction.

Keywords: Invasive Species Modeling, Hemlock Woolly Adelgid, Eastern Hemlock Tree, Reaction Diffusion Equations.

1 INTRODUCTION

The eastern hemlock tree (EHT) (*Tsuga Canadensis* (L.) Carr.), a foundation species (Ellison et al., 2010) in North America, ranges from as far north as Canada to as far south as Alabama, and from as far west as Minnesota to the east coast of the United States of America. The trees provide habitat for white-tailed deer and other wildlife species, such as turkey and ruffed grouse (Nesom, 2012; Pezet et al.,
and influence the vegetation and soil processes of aquatic environments (Birt, 2014). Moreover, EHT is a slow growing tree that may take almost 300 years to fully mature (Nesom, 2012). Therefore, any major decrease in its population will have a severe impact on the survival of other species which will lead to a loss of biodiversity causing an imbalance in the ecosystem (Birt et al., 2014; Brantley; Ford; Vose, 2013). There is therefore a need to prevent any decline of EHTs not due to natural causes. One way by which the EHT has declined is through the biological invasion of the Hemlock Woolly Adelgid (Birt, 2014; Brantley; Ford; Vose, 2013; Domec et al., 2013).

The Hemlock Woolly Adelgid (HWA) (Adelges tsugaek) is an insect that has been found to invade EHTs and causes a rapid decrease in the health and survival of infected trees (Nesom, 2012; Pezet et al., 2013; Birt et al., 2014). HWA is native to both Japan and China (Nesom, 2012). It feeds on Hemlock trees in its native environment; however, these trees have immunity to HWA. There are also many natural predators of HWA that are found in both Japan and China; the combination of host immunity and natural predators keep the population of HWA in China and Japan below epidemic levels. In the 1920s, HWA was transported to North America by boat and since then the EHTs of North America have been declining. EHT do not have host immunity over HWA in North America, and the natural predators of the HWA do not live in North America. Due to these circumstances, HWA invaded the Eastern United States successfully. The first reported sighting of HWA in North America was in British Colombia in 1920, and within 30 years the population of HWA had spread all the way down into Virginia (McClure; Salom; Shields, 2001). Since then, the range of HWA has been spreading quite quickly. (Figure 1). The average rate of spread is about 25 km/year (Domec et al., 2013) and its population levels have increased dramatically (McClure; Salom; Shields, 2001).

Figure 1: Spread of HWA and range of EHT in 2009 [7]

Source: McClure; Salom; Shields, 2001
HWA spread by numerous agents such as “wind, birds, deer, and humans” (McClure; Salom; Shields, 2001) and the species has adapted and survived in temperatures as low as -63°F. Due to its ability to survive in such extreme temperatures HWA will likely spread throughout the entire range of EHTs unless something is done to curtail the expansion.

After HWA infects a region of EHTs it takes anywhere from as little as 4 years to as many as 10 years to see a decline in tree health and population. The result of this is that the effect of HWA is detrimental to any trees that are affected. HWAs cause the needles of EHTs to die and fall off, also killing all the buds of the branches (Figure 2) which in turn cause the tree to decline in new growth.

Major destruction of branches can occur in as little as two years after first infection by HWA and there is no evidence of recovery after a tree has been infected by HWA (McClure; Salom; Shields, 2001). Once EHTs are infected, the trees do not recover and for that reason the populations of HWA must be controlled as much as possible.

When HWAs invade an area, the population of HWA increases rapidly during the first year while EHTs are still of good health and creating new growth (McClure; Salom; Shields, 2001). The extent of infestation of HWA in a certain area depends directly on the quality of nutrition from the trees. The higher the quality of nutrition, the more the population of HWA will increase; but if the quality is poor then the population of HWA will decrease (McClure; Salom; Shields, 2001). After the first year, when HWA populations are at their highest, EHTs do not have much new growth if any. The populations of HWA decrease due to lower quality of tree health. During the third year EHTs tend to have slight growth, which

Figure 2: A figure that illustrates the effects of the invasion on HWA on EHT. The tree to the right is uninfected (healthy) and the tree at the center is infected. Picture taken from [8].

Source: USDA, 2005
sparks another increase in the population of HWA (McClure; Salom; Shields, 2001). During the fourth year, HWA populations crash again due to lower quality of food, because of tree decline and death (McClure; Salom; Shields, 2001). Seasonal variations may therefore influence the dynamics of both HWA and EHT. Moreover, the interaction between the HWA and EHT may mimic a predator prey system.

Several native insect species in the Eastern United States feed on HWA occasionally, but no native species has a significant effect on the overall population of HWA (McClure; Salom; Shields, 2001). To stop or at least slow the spread of HWA, scientists have been testing different predators of the HWA that are native to China or Japan to see if a release of this predator would have a limiting effect on HWA populations. The coccinellid lady beetle has shown the most promise as a nonnative species to the United States. The lady beetle favors HWA over any other prey, and they eat HWA right off the Hemlock Branches, saving a tree from destruction. The results from small test trials have been encouraging, but more data is needed before any widespread release can be made (McClure; Salom; Shields, 2001). Also, an introduction of another nonnative species such as the lady beetle could create another invasion by the introduced species. As a result, other techniques to control this menace must be sought. This reason motivates the use of mathematical models to determine the dynamics of the spread, to advise ecosystem managers on how to manage or eliminate the invasion.

The spread of biological invasions has been mathematically modeled by different types of equations. More recently reaction diffusion and integrodifference equations models have emerged as the most widely used in the used to predict the spread of biological invasions (Lubina; Levin, 1988; Okubo et al., 1989; Kot; Lewis; Van Den Driessche, 1996). Lubina and Levin (1988) modeled the spread of the California Sea Otter successfully using a reaction diffusion equation. In this study, they developed a model that accurately described the spread of the California Sea Otter and found the speed of expansion to be 4.8 km/yr., which was consistent to the spread expansion rate found in the field. They were able to show which parameters (mortality differences) significantly affected the spread of two separate sea otter populations. They also were able to show that some parameters play minor roles in the two populations.

The spread of the grey squirrel in Britain has also been successfully modeled using a reaction diffusion equation (Okubo et al., 1989). It was shown that the observed rate of spread was about 7.7 km a year. The reaction diffusion equation predicted the same rate of spread as what was measured in the field. Integrodifference equations have also been used to predict the spread of biological invasions (Kot; Lewis; Van Den Driessche, 1996). Although both integrodifference equations and reaction diffusion equations have been able to predict the spread of invasion, in this paper we will limit ourselves to the use of reaction diffusion equations. A reaction diffusion system will be used to determine the dynamics of the interaction between HWA and EHT.
2 METHODOLOGY

A system of reaction-diffusion equations is proposed to model the interactions between the HWA and EHT and in determining the dynamics of the spread of HWA and EHT. This system is based on the model of (Petrovskii; Morozov; Li, 2005) with suitable changes to mimic our modeling situation. The only change from Allee effect to Logistic growth in equation (1) is because HWA and EHT do not exhibit Allee effect. The system of reaction diffusion equations that is used for this modeling activity is

\[
\frac{\partial H}{\partial t} = D_1 \frac{\partial^2 H}{\partial x^2} + rH \left(1 - \frac{H}{K}\right) - \frac{AHP}{H+B}
\]  

\[
\frac{\partial P}{\partial t} = D_2 \frac{\partial^2 P}{\partial x^2} + \kappa AHP \frac{H}{H+B} - MP
\]

Here \(t\) represents time and \(x\) represents a spatial coordinate. Additional parameters of equations (1) and (2) are defined in Table 1 below.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>HWA</strong></td>
<td></td>
</tr>
<tr>
<td>(H)</td>
<td>HWA</td>
</tr>
<tr>
<td>(D_1)</td>
<td>Diffusion of HWA</td>
</tr>
<tr>
<td>(r)</td>
<td>Growth Rate of HWA</td>
</tr>
<tr>
<td>(K)</td>
<td>Carrying Capacity of HWA</td>
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<tr>
<td><strong>EHT</strong></td>
<td></td>
</tr>
<tr>
<td>(P)</td>
<td>EHT</td>
</tr>
<tr>
<td>(D_2)</td>
<td>Diffusion of EHT</td>
</tr>
<tr>
<td>(\kappa)</td>
<td>Food utilization coefficient</td>
</tr>
<tr>
<td>(A)</td>
<td>Predation Intensity</td>
</tr>
<tr>
<td>(B)</td>
<td>Half-saturation EHT density</td>
</tr>
<tr>
<td>(M)</td>
<td>Mortality of EHT</td>
</tr>
</tbody>
</table>

Source: Authors

We develop the theory and analyze the models in the next section.
3 MODEL ANALYSIS

The model equations are nondimensionalized and stability analysis is carried out by determining the eigenvalues for the model system. A traveling wave solution is also determined in this section.

3.1 NONDIMENSIONALISATION

By multiplying equation (1) by $1/\alpha K$ and equation (2) by $1/\alpha\kappa K$ and setting $u = \frac{H}{K}, t = aT$, $x = \sqrt{\frac{\alpha}{D_1}} x$, $\gamma = \frac{\tau K}{\alpha}$, $\nu = \frac{p}{\kappa K}$, $\alpha = \frac{K}{B}$, $\epsilon = \frac{D_2}{D_1}$, $\delta = \frac{M}{a}$ and $a = \frac{A}{kKB}$ the non-dimensional version of equations (1) and (2) are given by

\[
\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \gamma u(1 - u) - \frac{uv}{\alpha u + 1} \tag{3}
\]

\[
\frac{\partial v}{\partial t} = \epsilon \frac{\partial^2 v}{\partial x^2} + \frac{uv}{\alpha u + 1} - \delta v \tag{4}
\]

The number of parameters has been reduced from 8 to 5. We now determine if the system will produce travelling wave solutions.

3.2 EIGENVALUES AND TRAVELING WAVE SOLUTIONS

To determine whether the model system (3) – (4) exhibit a traveling wave solution, we let $z = x - ct$, then

\[
u(x, t) = U(z) \tag{5}
\]

and

\[
u(x, t) = V(z) \tag{6}
\]

Substituting (5) and (6) into the model equations (3) and (4) gives

\[-cu'(z) = U''(z) + \gamma U(1 - U) - \frac{uv}{\alpha u + 1} \tag{7}\]
\[-cV'(z) = \varepsilon V''(z) + \frac{uv}{\alpha u + 1} - \delta V \quad (8)\]

Without the loss of generality assume that \(D_1 \gg D_2\), i.e., the diffusion of the predator is significantly larger than the diffusion of the prey, then \(\varepsilon\) will be almost zero (0). Setting \(\varepsilon = 0\) and \(U' = W\) we obtain the ordinary differential equation (ODE) system,

\[U' = W \quad (9)\]

\[V' = -\frac{1}{c} \frac{uv}{\alpha u + 1} + \frac{\delta}{c} V \quad (10)\]

\[W' = -cW - \gamma U(1 - U) + \frac{uv}{\alpha u + 1} \quad (11)\]

The steady states for (9), (10), and (11) are \((U, V, W) = (0, 0, 0)\) \((1, 0, 0)\) and \((-\frac{\delta}{-1 + \delta \alpha}, \frac{1}{(-1 + \delta \alpha)^2}, 0)\).

The general Jacobian matrix for the steady states is given by

\[
J(U^*, V^*, W^*) = \begin{bmatrix}
0 & \frac{V^*}{(\alpha u^* + 1)^2} & -\frac{u^*}{c(au^* + 1)} + \frac{\delta}{c} \\
-\frac{1}{c} \frac{v^*}{(\alpha u^* + 1)^2} & \frac{u^*}{c(au^* + 1)} & \frac{1}{(\alpha u^* + 1)^2} \\
yU^* + \frac{V^*}{(\alpha u^* + 1)^2} & \frac{1}{(\alpha u^* + 1)^2} & -c
\end{bmatrix} \quad (12)
\]

For the eigenvalues at the steady state \((0, 0, 0)\) we have

\[
det \begin{bmatrix}
-\lambda & 0 & 1 \\
0 & \frac{\delta}{c} - \lambda & 0 \\
0 & 0 & -c - \lambda
\end{bmatrix} = 0, \quad (13)
\]

so that \(\lambda_1 = 0, \lambda_2 = -c, \lambda_3 = \frac{\delta}{c}\).
The steady state \((0,0,0)\) is an unstable steady state, since \(\delta, c > 0\). For the eigenvalues at the steady state \((1,0,0)\) we have

\[
det \begin{pmatrix}
-\lambda & 0 & 1 \\
0 & \frac{1}{c(\alpha+1)} + \delta - \lambda & 0 \\
-\gamma + 2\gamma & \frac{1}{\alpha+1} & -c - \lambda
\end{pmatrix} = 0, \quad (14)
\]

so that

\[
\lambda_1 = \frac{-1 + \delta(\alpha + 1)}{c(\alpha + 1)} \quad \text{and} \quad \lambda_2, \lambda_3 = -\frac{1}{2} c \pm \frac{1}{2} \sqrt{c^2 + 4\gamma}.
\]

This steady state is also unstable since \(\gamma > 0\) and \(\lambda = -\frac{1}{2} c + \frac{1}{2} \sqrt{c^2 + 4\gamma} > 0\).

The characteristic equation for the steady state \(\left(\frac{\delta}{1 - \delta \alpha}, \frac{\gamma(1 - \delta - \delta \alpha)}{(\alpha \delta - 1)^2}, 0\right)\) is given by

\[
p(\lambda) = \det \begin{pmatrix}
-\lambda & 0 & 1 \\
\gamma(\delta + \alpha \delta - 1) & -\lambda & 0 \\
\gamma(1 - 2\alpha \delta + \delta^2 \alpha + (\alpha \delta)^2) & \delta & -c - \lambda
\end{pmatrix}
\]

This reduces to

\[
p(\lambda) = \lambda^3 + c\lambda^2 + \frac{\gamma(1 - 2\alpha \delta + \delta^2 \alpha + (\alpha \delta)^2)}{1 - \alpha \delta} \lambda + \frac{\gamma \delta (\delta + \alpha \delta - 1)}{c} \quad (15)
\]

To determine the stability of this stable state we use the Routh-Hurwitz criteria, that is,

\[
c > 0, \quad \frac{\gamma \delta (\delta + \alpha \delta - 1)}{c} > 0 \quad \text{and} \quad \frac{c \gamma(1 - 2\alpha \delta + \delta^2 \alpha + (\alpha \delta)^2)}{1 - \alpha \delta} > \frac{\gamma \delta (\delta + \alpha \delta + (\alpha \delta)^2)}{c}
\]

Since all the parameters are positive a plot of the inequalities for \(\alpha\) and \(\delta\) yields a small region where choices of \(\alpha\) and \(\delta\) yields a stable steady state (see Figure 3 below).
Choices of $\alpha, \delta$ from this region and positive values for $c$ and $\gamma$ yield 3 negative eigenvalues for the steady state.

In addition, a travelling wave solution exist if $c \geq \sqrt{\frac{3\gamma(1-2\alpha\delta+\alpha\delta^2+|\alpha\delta|^2)}{1-\alpha\delta}}$.

4 RESULTS

In this section, a description of the results for the modeling is given. A confirmation of the results from the previous section is shown in section 4.1. A sensitivity analysis for the model parameters is also carried out to determine the most sensitive parameters that drive the models in section 4.2.

4.1 SIMULATIONS

Figure 4 shows a plot of $p(\lambda)$ vs. $\lambda$ for equation (15), for the choice of parameter values $\alpha, \gamma$ and $\delta$ from Figure 3.
Figure 4: A plot of \( p(\lambda) \) vrs \( \lambda \) showing only negative values of \( \lambda \). These values are -0.033, -0.203 and -4.76. Here \( c=5, \alpha=0.5, \gamma=1, c=5, \alpha=0.5, \gamma=1 \) and \( \delta=0.8 \).

For \( c = 5, \alpha = 0.5, \gamma = 1 \) and \( \delta = 0.8 \), all the 3 eigenvalues are negative (see Figure 4). Moreover, this stable steady state is between the steady states \((0,0,0)\) and \((1,0,0)\), so none of the 2 species will go extinct.

4.2 SENSITIVITY ANALYSIS

A sensitivity analysis was carried out by first fitting a Gaussian process (GP) model to simulation output. GPs are surrogate statistical models that can accurately predict output from non-linear computer simulations (Sacks et al., 1989). A maximin Latin hypercube sampling (LHS) design was used to generate 80 combinations of values of \( \alpha \), \( \delta \) and \( \gamma \) from the ranges \((0.1, 10)\), \((0.001, 0.03)\), and \((-0.2, 5)\), respectively, using the R package LHS. The value of \( \varepsilon \) was fixed at 0.05. An LHS has the property that the values of each parameter are uniformly distributed over its range. A maximin LHS design is the LHS design with the maximum minimum Euclidian distance between design points, over a set of generated LHS designs. Such designs are space-filling and prevent confounding between model parameters. A 3-dimensional scatterplot of the maximin LHS design that was used is shown in Figure 5. Such a design achieved Pearson correlations of -0.014, 0.003, and -0.018 between \( \alpha \) and \( \delta \), \( \delta \) and \( \gamma \), and \( \alpha \) and \( \gamma \), respectively.
The R package mlegp (Dancik; Dorman, 2008) was used for the sensitivity analysis and to fit GPs to EHT and HWA output from the simulation and for subsequent sensitivity analysis. The GP approximations of the output were very accurate, as assessed by leave-one-out cross-validated diagnostic plots, where predictions at each design point are calculated after removing that design point from the GP training set. Specifically, the correlation between the GP-predicted output and observed simulation output was 0.999 for both EHT and HWA and 92.5% of standardized residuals fell within ±2 for both EHT and HWA output.

The sensitivity analysis is shown in Figure 6. Main effects plots show predicted simulation output as a function of a single model parameter while functional analysis of variance (FANOVA) decomposition quantifies parameter importance by measuring the percent in the total variability in simulation output that can be attributed to changes in values of one or more model parameters. The parameter $\gamma$ is the most important parameter for EHT and accounts for 99.29% of EHT’s total variability, while $\alpha$ is most important parameter for HWA and accounts for 73.81% of its variability. EHT values increase with increasing values of $\gamma$ but are not sensitive to changes in $\alpha$ or $\delta$. On the other hand, HWA values decrease with increasing values of $\alpha$, and to a lesser extent with increasing values of $\delta$. 

![Figure 5: Maximum LHS design for values of $\alpha$, $\gamma$ and $\delta$](source: Authors)
5 DISCUSSION AND CONCLUSION

In this paper we have used a reaction diffusion model to evaluate the spread and interaction between HWA and EHT. We have shown that there are at most 3 steady states for this model. Based on the model the system is always driven to a stable steady state where both species coexist. In other words, the 2 species will eventually coexist based on our model. In addition, the system traveling wave solution with a minimum wave speed given by

\[ c = \sqrt{\frac{3\gamma(1-2\alpha\delta+\alpha\delta^2+|a\delta|^2)}{1-\alpha\delta}}. \]
To calculate the exact minimum wave speed will require ecosystem managers experimentally determining the parameter values which can then be compared with spread rate of 25 km/yr. determine by (Domec et al., 2013).

The parameter region for coexistence is very narrow. This is supported by literature (Borer, 2006). This may be due to habitat heterogeneity and temporal reasons. The time scales for HWA and EHT are so different and may play a role in the coexistence of the 2 species. Growth rate of EHT is restricted by habitat heterogeneity.

The sensitivity analysis shows that \( \alpha = \frac{K}{B} \) and \( \delta = \frac{MkKB}{A} \) are the key parameters that drive HWA dynamics, while \( \gamma = \frac{rK^2B}{A} \) drives the dynamics of EHT. These same parameters drive the stability of the model system. The sensitivity analysis is therefore in agreement with the stability analysis on the spread of HWA. The parameters \( \alpha \) and \( \delta \) are related to the carrying capacity (\( K \)) of HWA, the predation intensity (\( A \)) and the mortality (\( M \)) of EHT. Since \( K \) stays fairly constant, the key dimensional parameter driving the spread are the predation intensity and mortality of EHT. Moreover, our results indicate that HWA spread can be controlled by decreasing its predation intensity though this may be difficult in practice (Courchamp; Woodroffe; Roemer, 2003; Lozano et al, 2013). Interestingly, however, our results also suggest that one could control the spread of HWA by increasing EHT mortality, for example by selective and strategic removal of EHT (Lozano et al, 2013). This will have a larger impact on HWA than on EHT. In the future, seasonality and habitat heterogeneity will be included in the model to determine its influence on the spread. Moreover, including time scales may change the dynamics and better mimic the ecological system.
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