Budworm Forest Model - Analysis of forest parameters

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We consider the Budworm forest model to simulate the impact of a spruce Budworm outbreak on the balsam fir tree forests. This model is a general model and can be applied for any parasite attack on a forest. The forest dynamics depend on a number of parameters like the growth rate of foliage, the Budworm population, the energy reserves available to the forest, etc. The Budworm population is a fast variable (with respect to time) and was discussed extensively in class lectures. In this report, we focus on the slow variables which are related to the health of the forest assuming the fast variables have reached their respective equilibrium states. We are interested in figuring out how do the slow variables behave given the values of fast variables and how the bifurcations occur on changing the fast variables. Additionally, we found some insights into the problem which were not directly described in the paper. Wherever possible we have tried to get biological insights from the mathematical results obtained.

INTRODUCTION

For the analysis of the slow variables which describe the forest health, we have referred to the paper titled : "Qualitative Analysis of Insect Outbreak Systems: The Spruce Budworm and Forest" written by Ludwig et al[1]. We use Matlab to plot our own figures and verify the ones given in the paper.

BACKGROUND, IMPORTANCE AND RELEVANCE

In the past few decades, computer technology has grown at a rapid pace. While modelling complex natural phenomena like rainfall, natural calamities, forest growth, we often encounter non linear equations which might be cumbersome to solve analytically. Hence we instead use graphical techniques relying on fixed point analysis, linearization etc. for analyzing such equations. These allow us to gain better insights, make predictions and take policy decisions. The predictions can be compared with the actual data and if there is a mismatch, the model can be tweaked accordingly. Today, when ecological conservation and economic optimization are key concerns, such analysis can be immensely helpful to both political leaders and scientists.

MODEL

The slow variables under consideration are the variables which capture the health and size of the forests. It is important to understand how these behave if we want to make predictions of how the forest is able to cope with the insect outbreak.

We consider two variables-

- S: the average size of the trees in the forest(which is an indicator of their age)
- E: The level of energy reserves (this includes the condition of the foliage and health of the trees).

Since we expect S and E to be bounded, we choose logistic equations to model their growth. Notice that these parameters are likely to affect each others' growth. For example, the budworm infestation can lead to a decrease in the trees' foliage which means that E will decrease. One would expect that with less E, the S would be smaller. This means that the logistic equations will have to be modified to include such couplings. This also means that these equations will have to be analyzed as a 2D system. Our theory thus points to the use of techniques like null-cline analysis and linearization.

Equations :

$$\frac{d(S)}{dt} = r_S S(1 - \frac{S}{K_S}\frac{K_E}{E})$$
$$\frac{d(E)}{dt} = r_E E(1 - \frac{E}{k_E}) - P\frac{B}{S}$$

Justification for these equations based on some biological considerations:

- The rate of change of E is modelled as a logistic with K_E and r_E being the carrying capacity and the rate of the logistic respectively. The impact of the budworm infestations will be to 'eat away' E i.e the energy reserve of the forest. This is captured by putting in a negative term which is proportional to the density of Budworms $\frac{B}{S}$ where B is the budworm population. The density term is used simply to normalize the effect of the budworm population. For Ex- a larger B in a large forest may be less devastating than a much smaller B in a small fledgling forest.
- Note that E plays a part in the S' equation. We assume that even in complete infestation free forest there is an upper limit on the size of the forest (a

reasonable assumption). However, if the E reserves go down then the upper limit should correspondingly go down. This is captured elegantly by the $\frac{K_S E}{K_E}$ term. P can be thought of as impact of the budworm infestation on E'.

- The equations have a lot a parameters. Therefore non-dimensionalize the equations so as to make it convenient to apply the techniques we have learn to deal with 2D systems.

NON-DIMENSIONALIZE THE PROBLEM

Let $S_1 = \frac{S}{K_S}$ and $E_1 = \frac{E}{K_E}$. Hence,

$$\frac{d(S_1)}{dt} = r_S(S_1)(1 - \frac{S_1}{E_1})$$
$$\frac{d(E_1)}{dt} = r_E(E_1)(1 - E_1) - \frac{PB}{S_1 K_S K_E}$$

Let $\tau = t\frac{P}{K_S K_E}$, $r_{E_1} = r_E \frac{K_S K_E}{P}$ and $r_{S_1} = r_S \frac{K_S K_E}{P}$ Thus,

$$\frac{d(S_1)}{d\tau} = r_{S_1}(S_1)(1 - \frac{S_1}{E_1})$$
$$\frac{d(E_1)}{d\tau} = r_{E_1}(E_1)(1 - E_1) - \frac{B}{S_1}$$

RESULTS

In here we present the results of our numerical and analytical analysis on the model of the previous section.

Null-cline analysis

A simple way to better understand 2D systems is to identify curves along which one of the parameters is constant known as iso-clines. A special case of that is null clines on which the parameter value is 0 and it is as if the system is 1D. Note that null clines are important because they split the space into regions where the rates are positive and negative. Further the intersection of the null clines are the fixed points of the system. One can easily understand and guess the general trajectories of the system using them.

The equation of the null clines can be obtained by setting the derivative of S_1 and E_1 to 0.

$$r_{S_1}(S_1)(1 - \frac{S_1}{E_1}) = 0$$

This gives two null clines : $S_1 = 0$ and $S_1 = E_1$. But we assume S_1 is trivial and hence neglect it. Therefore, $S_1 = E_1$ is one null-cline.

$$r_{E_1}(E_1)(1 - E_1) - \frac{B}{S_1} = 0$$
$$S_1 = \frac{B}{r_{E_1}(E_1)(1 - E_1)}$$

If other parameters are kept constant, the value of B determines whether the two null clines intersect or not. If B is below some critical value, then the two null clines intersect. Thus we have two fixed points at the points of intersection. If B is above the critical value, there are no fixed points. The null clines for different values of B are shown below :

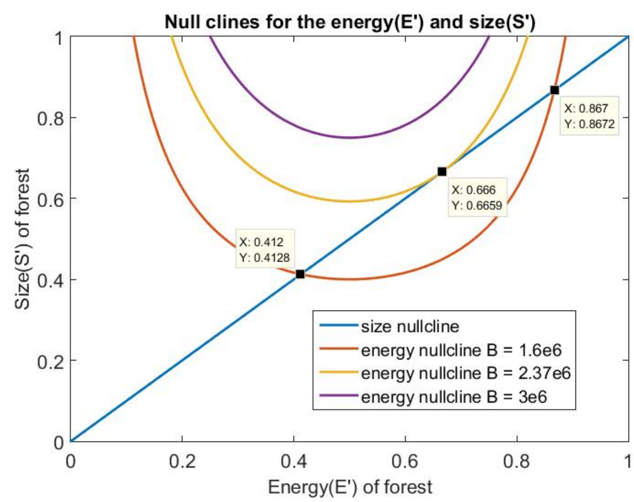

FIG. 1. All possible cases of null-clines

Note that in the above FIG.1, the values taken by the parameters are given in the table below (FIG.2). These other parameters are the characteristics of a particular forest. So, essentially we are trying to find the critical value of B beyond which the forest will not be able to survive. Understanding this will allow us to design policies and targets about controlling the budworm population to ensure the survival of these forests. For every forest depending on its strength parameters, the critical value will be different.

By equating the null-clines we can analytically find the fixed points which are determined by solving the following cubic equation:

Symbol	Description	Units	Value
r_E	Intrinsic Budworm growth rate	/year	1.0
K_E	maximum E level	-	1.0
r_S	Intrinsic Branch growth rate	/year	0.15
K_S	Maximum Branch density	branches/acre	24000
P	Consumption rate of E	branches/(larvae-year)	0.0015

FIG. 2. Estimated values - [1]

$$F(E) = E_1^3 r_{E_1} - E_1^2 r_{E_1} + B = 0$$

We used an online solver to obtain three fixed points by taking $r_{E_1} = 16 * 10^6$ and $B = 1.6 * 10^6$. Only two of them are of interest which occur at (0.412,0.412) and (0.867,0.867). The third fixed point is negative which doesn't make sense in this scenario as negative Energy and Surface Area is not possible.
On solving for derivative of F(E) = 0, we obtain $E = 0$ and $E = 2/3$. The cubic has three distinct real roots if and only if F(0) and F(2/3) are non-zero and have opposite sign. F(0) = B which is greater than zero and F(2/3) has to be less than zero for three distinct real roots. So we obtain the condition

$$B < \frac{4 r_{E_1}}{27}$$

. On substituting the value of r_{E_1} we get the critical value of B as $2.36 * 10^6$. We will see that this is where a saddle-node bifurcation occurs.

Bifurcation Diagram

The diagram in Fig. 3 is the conversion of bifurcation diagram in 1D. In 2D system, fixed points are in x-y plane and hence bifurcation diagram needs a 3rd dimension. But since fixed point (S_1*, E_1*) lies on line $S_1* = E_1*$, the first null cline, we can analyze the bifurcation diagram by plotting only one variable out of the two. This gives us FIG.3 which indicates a saddle-node bifurcation. Observe that we don't exactly get $B_{crit} = 2.36 * 10^6$ because in MATLAB, we cannot equate equations to exact 0 and hence there are some approximations.

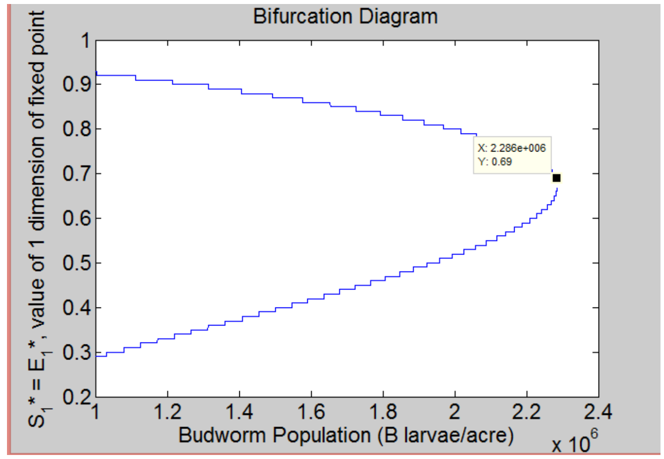

FIG. 3. Bifurcation Diagram

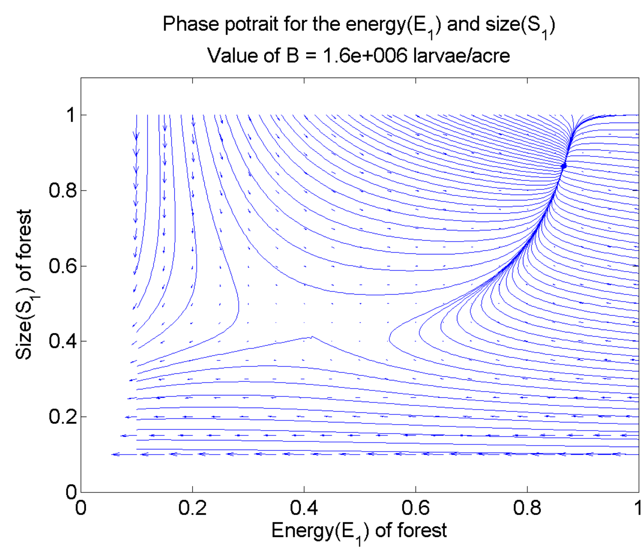

FIG. 4. Phase potrait having two fixed points

Phase Portrait

Classification of fixed points under linearization assumption

We have learnt how linearization assumption can be used to analyze the nature of fixed points of 2D systems. If the fixed points are not of a borderline type, then the predictions under the assumption holds for the actual non-linear system as well.

We assume that our 2D non linear system can be analyzed in such a way. The Jacobian with respect to variables S and E is as follows

$$J = \begin{bmatrix} r_1(1 - \frac{2s}{e}) & \frac{r_1 s^2}{e^2} \\ \frac{B}{s^2} & r_2(1 - 2e) \end{bmatrix}$$

For the chosen parameters, we have obtained a B_{crit} value of $2.36 * 10^6$. Let us consider 3 cases with B values

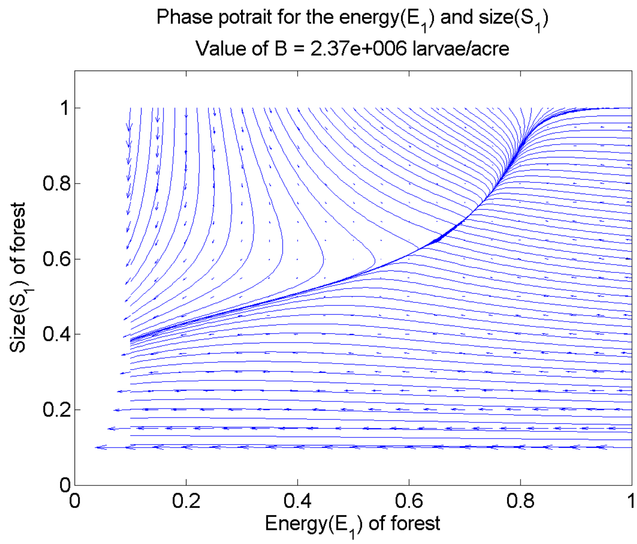

FIG. 5. Phase potrait having a hybrid fixed point limiting case

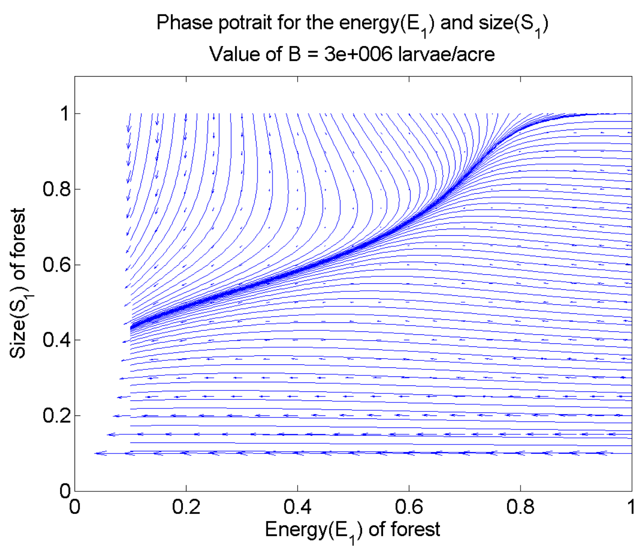

FIG. 6. Phase potrait having no fixed points

larger, smaller and equal to this critical value and check what the linearization theory can tell us.

For B $= 1.6 * 10^6$ (lesser than critical), it predicts a saddle at (0.413,0.413) and an attracting stable node at (0.867,0.867).

For B $= 3 * 10^6$ (larger than the critical), the Jacobian predicts complex eigen values which means there are no real fixed points. We then verified these predictions by plotting a phase portrait using streamline and quiver functions in MATLAB.

Note that the predictions seem to hold true from what we observe in figures 4, 5, 6. Depending on the initial conditions of (S,E) we get a particular trajectory in the phase portrait. For B $= 1.6 * 10^6$, we observe a stable node at (0.867,0.867) and a saddle node at (0.412,0.412). For B $< 2.37 * 10^6$, we get a stable node and a saddle node. For B $= 2.37 * 10^6$, we get a half stable node. For B $> 2.37 * 10^6$, we do not get any fixed points.

Biological significance of the above: If the Budworm population goes above B_{crit}, no matter what initial values of (S,E) are chosen eventually the forest will be destroyed. The Budworm infestation is too severe for the forest to survive. If we want to take control measures, we must ensure that the Budworm population stays below this value.

For values less than B_{crit}, we have a saddle-node pair of fixed points. The presence of the saddle has some interesting consequences.

- Notice that for a forest to survive we need a minimal contribution from both (S,E). This is so because even if S is maximum but if E does not back it up, the forest will not survive. A large forest with sparse energy resources will not be able to survive the infestation. On the other hand a small, relatively young forest will not survive even if it had plenty of reserves.

- It is only when both of these characteristics are present in a balanced amount is that the forest will survive in spite of the budworm onslaught. In fact in this case, the stable fp is (0.867,0.867) which means the forest is in a pretty good shape inspite of the attack.

- Thus, below the critical value, there is a certain danger zone which the forest needs to steer clear from. For lower B, the danger zone will be narrower and pushed down and leftwards in the phase portrait.

If we do the Budworm analysis in detail, we can infer that at equilibrium, the budworm population reaches a fixed point. The value of the fixed point is low if the initial budworm population was in a refuge zone. If the initial Budworm population lies in the outbreak zone, then the value of the Budworm population is relatively higher. However, even if the Budworm population stabilises to the higher fixed point, we cannot comment on the state of the forest without considering the forest parameters. If the forest is 'strong enough', it can sustain and reach the stable fixed point inspite of the value of B being large. Thus, in order to understand the Budworm and forest variables together, we can calculate the maximum Budworm population which the forest can sustain for a fixed set of forest parameters.

CONCLUSION

The problem was to analyze the behaviour of the measures of a forest's health (slow-changing) given that a Budworm infestation has lead to a stable population of the Budworms.

Using intuitions about the way forests grow and our knowledge of growth equations, equations for rate of change of the forest variables were obtained.

The following non linear techniques were used:

- Finding null clines
- calculating fixed points and their classification
- Linearization and eigen vector analysis

Using the above, we were able to get an idea of the behaviour of the 2D system without explicitly solving any differential equations.

Some of the key findings are listed below

- For the given parameters and a stable Budworm population we are able to predict if a forest will be able to survive the infestation or not.
- This is because the system shows a saddle node bifurcation. This implies that their is a critical population of Budworms beyond which the situation is hopeless, the forest will not be able to survive no matter how robust its energy reserves are or how big it is.
- But below this critical value, the forest will be able to withstand the attack provided it is resilient enough.

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[1] D. Ludwig; D. D. Jones; C. S. Holling, "Qualitative Analysis of Insect Outbreak Systems: The Spruce Budworm and Forest", The Journal of Animal Ecology, Vol. 47, No. 1. (Feb., 1978), pp. 315-332.
[2] Steven Strogatz, Nonlinear Dynamics and Chaos, Section 3.7, Exercise 8.1.10.