

# Qualitative Analysis of Spruce Budworm Outbreaks and Declines

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May 17, 2000

## Abstract

This paper shadows the qualitative analysis of spruce budworm outbreak and decline phenomena in the balsam fir forests of the Northeastern United States and Canada by [Ludwig et. al., (1978)]. Qualitative theory of differential equations and catastrophe theory is employed to model one complete cycle. This paper does not attempt to justify the analysis through replacing parameter values with real values. For a treatment of this subject see [Ludwig et. al., (1978)].

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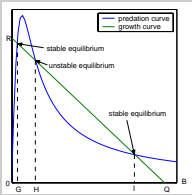
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## 1. Introduction

In quantitative sciences, mathematics is used as a tool to describe data, convey information and make predictions about future occurrences of systems. Population ecology is one such field. Models of specifics are created by identifying and separating variables, establishing formulas, and comparing the model with data obtained from the field. These models aid practioners in making informed management decisions without changing the system they model.

A classic application of the modeling of natural systems is found in "Qualitative Analysis of Insect Outbreak Systems: The Spruce Budworm and Forest" by Ludwig et. al. [Ludwig et. al., (1978)]. The paper seeks to model the outbreak of the Spruce Budworm in the Northeastern United States and Canada by using the Qualitative theory of Differential Equations and Catastrophe Theory. Then in an effort to justify the model, the authors replace the parameters with values provided by an informed entomologist.

The purpose of this paper is to explore the methodologies of the model; specifically as it relates to the qualitative theory of differential equations. This paper will shadow the step by step analysis of the qualitative section in the original paper by [Ludwig et. al., (1978)]. The following analysis will not consider the final testing of the model through replacement of the parameters with real values. For a treatment of this subject, see [Ludwig et. al., (1978)].

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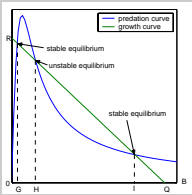
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## 2. Divide variables into fast and slow categories

Each variable in the following analysis has an associated time interval over which change will occur. Some variables, such as budworm density, can change dramatically in a few years. Therefore, an appropriate time interval for budworm density is the order of months. A major influence on budworm density is predation—particularly by birds (warblers, etc.). Due to reproductive strategies avian predators cannot alter their own numbers at a rate comparable to budworms. However, avian predators can rapidly alter their feeding behavior. Consequently, avian predation is assigned a fast variable.

Forests are assigned a slow variable since they cannot alter their numbers in a short amount of time. An appropriate time scale is on the order of tens of years. The forest will further be divided into two variables; one variable describing the energy reserve of the forest and the other the total surface area of branches.

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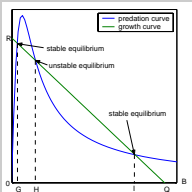
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### 3. Decide on the form of the fast variables

In the case of the budworm the main limiting features are the food supply and predation. Therefore, [Ludwig et. al., (1978)] chose the Logistic form,

$$\frac{dB}{dt} = r_B B \left( 1 - \frac{B}{K_B} \right), \quad (1)$$

where  $B$  represents the budworm density and  $K_B$  is the carrying capacity which is dependent upon the amount and quality of foliage available.

The effect of predation is given by the function  $g(B)$ ; which must possess several characteristics. There is an upper limit to the rate of budworm mortality due to predation. This upper limit is a function of variables such as predator search strategies, territorial behavior, and other habitat characters. In other words, predators can only eat so many budworms even when budworm populations are high. This effect is termed saturation. Conversely, there is a decrease in the effect of predation at low budworm densities. This is a common effect when predators have many alternative food sources. When budworm densities are low, avian predators encounter them only incidentally. In contrast, as their density increases, predators encounter them more often, develop a search image, and will seek them out. Therefore,  $g(B)$  should approach an upper limit  $\beta$  as  $B \rightarrow \infty$  and vanish quadratically as  $B \rightarrow 0$ .  $\beta$  may depend on slow variables and will be considered later. A form for  $g(B)$  that meets the criteria above is,

$$g(B) = \beta \frac{B^2}{\alpha^2 + B^2}, \quad (2)$$

where  $\alpha$  determines the scale at which saturation begins to take affect.

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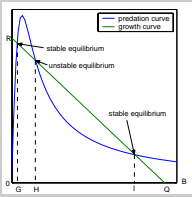
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Equation 2 is subtracted from the right-hand side of Equation 1 since the interaction has a negative effect on Budworm populations.

$$\frac{dB}{dt} = r_B B \left( 1 - \frac{B}{K_B} \right) - \beta \frac{B^2}{\alpha^2 + B^2}, \quad (3)$$

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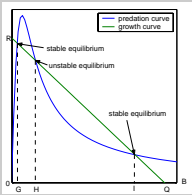
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#### 4. Analyze the behavior of the fast variables with the slow variables held constant.

The first step in analyzing the model is to identify the equilibria and determine their stability. Equilibria occur where  $dB/dt = 0$ ; therefore they must satisfy,

$$r_B B \left( 1 - \frac{B}{K_B} \right) - \beta \frac{B^2}{\alpha^2 + B^2} = 0, \quad (4)$$

Obviously  $B = 0$  is an equilibrium. The derivative is positive for  $B$  slightly greater than zero; therefore it is an unstable equilibrium point. The remaining roots of **Equation 4** satisfy

$$r_B \left( 1 - \frac{B}{K_B} \right) - \beta \frac{B}{\alpha^2 + B^2} = 0, \quad (5)$$

and depend on the four variables:  $r_B, K_B, \beta, \alpha$ .

#### Scale equation to reduce the number of parameters and create a dimensionless model

In an effort to ease the analysis of the model the parameters are scaled in such a way to make the model dimensionless. For example,  $B$  and  $\alpha$  have the same dimension. Therefore, [Ludwig et. al., (1978)] propose setting  $\mu = B/\alpha$ , which is dimensionless. Substituting this scaled variable into **Equation 5** yields **Equation 6**

$$r_B \left( 1 - \frac{\alpha \mu}{K_B} \right) - \frac{\mu}{1 + \mu^2} = 0, \quad (6)$$

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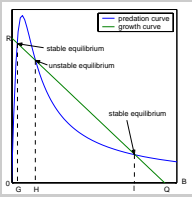
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Multiply through by  $\frac{\alpha}{\beta}$

$$\frac{\alpha r_B}{\beta} \left( 1 - \frac{\alpha \mu}{K_B} \right) - \frac{\mu}{1 + \mu^2} = 0, \quad (7)$$

In order to further ease analysis [[Ludwig et. al., \(1978\)](#)] set the two combinations of the four variables equal to  $R$  and  $Q$ .

$$R = \frac{\alpha r_B}{\beta} Q = \frac{K_B}{\alpha}, \quad (8)$$

In keeping with the dimensionless format the time must also be adjusted. They introduce

$$\tau = \frac{\beta t}{\alpha}, \quad (9)$$

The final dimensionless form becomes

$$\frac{dB}{d\tau} = R \left( 1 - \frac{\mu}{Q} \right) - \frac{\mu}{1 + \mu^2}, \quad (10)$$

Remember the purpose of the dimensionless form is to ease the analysis and at the present moment the goal is to determine the remaining equilibria of the equation. Once again, setting the right hand side of [Equation 8](#) equal to zero gives us the remaining roots. Therefore the remaining roots of the system will be given by

$$R \left( 1 - \frac{\mu}{Q} \right) = \frac{\mu}{1 + \mu^2}, \quad (11)$$

where the left-hand side is the per capita growth rate and the right-hand side is the per capita death rate, both in terms of the scaled variables. Notice that the

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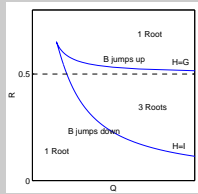
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per capita death rate is not a function of the scaled variables  $R$  and  $Q$ . This is a consequence of the form and will ease the analysis in latter sections.

The right and left hand sides of the equation can be graphed vs.  $\mu$  to obtain **Figure 1**. The per capita growth rate is the straight line with intercepts at  $R$  and  $Q$ . The per capita death rate is the curve that begins at the origin and is asymptotic to the  $\mu$  axis at large values. Remember that  $\mu$  is directly proportional to  $B$ ; accordingly, the  $\mu$  axis will be referred to as  $B$ . The roots of the equation are where the lines cross—the death rate equals the growth rate. The derivative is positive when the growth rate is larger than the death rate and it is negative when the death rate is greater than the growth rate. Therefore,  $G$  and  $I$  will be stable equilibria while  $H$  will be unstable.

## Examine the equilibria of the fast variables as a function of $R$ and $Q$

From **Figure 1** it is easy to see that the number and value of the equilibrium points depend upon the values of  $R$  and  $Q$ . At most there will be three equilibria and at least there will be one. To illustrate the dynamic of the system, imagine  $B=G$  initially. Imagine  $R$  increasing slowly while  $Q$  is held fixed. As this happens, the stable equilibrium  $G$  and the unstable equilibrium  $H$  approach each other while  $I$  increases only slightly. At some value of  $R$  and  $Q$ ,  $G$  and  $H$  coalesce, the unstable equilibrium disappears and  $B$  remains at  $G$ . If  $R$  continues to increase the growth rate curve will surpass the death rate curve completely. The budworm population will be sent to the only remaining equilibrium point at  $I$ . This behavior coincides with an outbreak of budworms.

Now, when  $R$  is decreased, the equilibria  $H$  and  $I$  are reformed; however, the budworm population remains at  $I$ . It is only when  $R$  decreases to the point in

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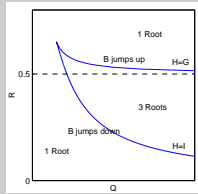
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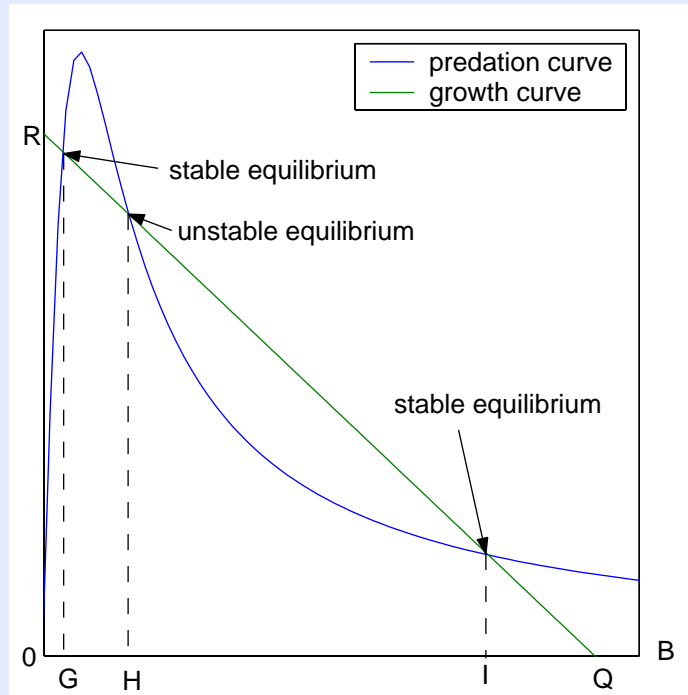
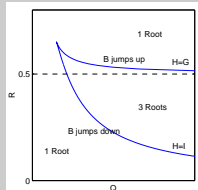


Figure 1: Graph of per capita growth rate and percapita death rate. Intersections are equilibrium points where G and I are stable and H is unstable.



which H and I coalesce and disappear that the population suddenly jumps down to G.

The question of the significance of G and I remains. They are the budworm limitations by predators and food, respectively. If the forest conditions improve past the point where predation controls growth an outbreak will occur. Consequently, if the forest is destroyed far enough, the predators can again regain control of budworm density.

It is very important to recognize that the conditions in which jumps occur will be different due to the wide variation of the combinations of  $R$  and  $Q$ . The values of  $R$  and  $Q$  where two roots coalesce are known as bifurcation values. Bifurcation curves occur at the points where the left hand side of **Equation 9** is tangent to the predation term on the right. The following conditions need to be met.

$$R \left( 1 - \frac{\mu}{Q} \right) = \frac{\mu}{1 + \mu^2}, \quad (12)$$

and

$$\frac{d}{d\mu} R \left( 1 - \frac{\mu}{Q} \right) = \frac{d}{d\mu} \frac{\mu}{1 + \mu^2}, \quad (13)$$

After differentiating both sides,

$$\frac{R}{Q} = \frac{\mu^2 - 1}{(1 + \mu^2)^2}, \quad (14)$$

Solving for R and Q parametrically yields the following:

$$R = \frac{2\mu^3}{(1 + \mu^2)^2}, Q = \frac{2\mu^3}{\mu^2 - 1}, \quad (15)$$

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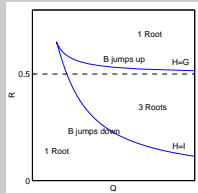
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Graphing  $R$  vs.  $Q$  yields [Figure 2](#). The upper curve is where  $H=G$  and the budworm density jumps up. The lower curve is where  $H=I$  and the density jumps down. This type of phenomena is modeled by Catastrophe theory [[Thom, \(1975\)](#)]. The particular type of catastrophe modeled here is classified as a cusp catastrophe because there are two parameter values ( $R$  and  $Q$ ) and one fast variable. [[Zeeman, \(1976\)](#)] provides practical application of catastrophe theory to biological systems. Basically, the critical region is thought of as a 3 dimensional pleated sheet. The inflection points of the upper and lower portions of the pleat define the bifurcation curves. The jump occurs when the system "falls" to the other surface. To jump the other way the system must pass completely through the bimodal region before it jumps again.

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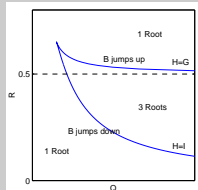
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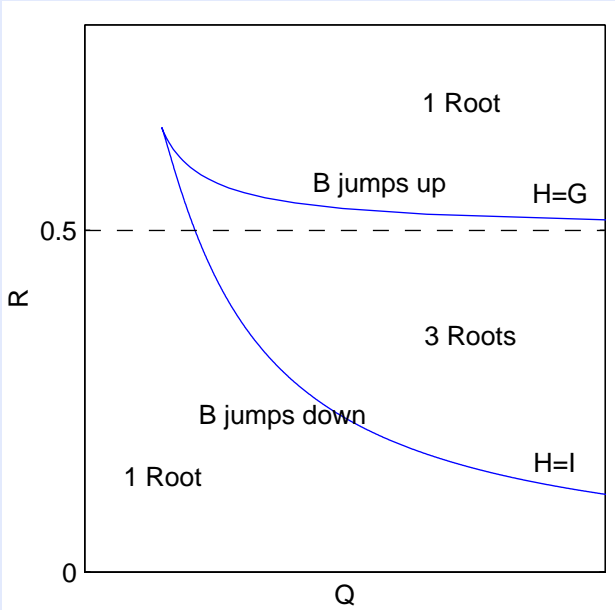
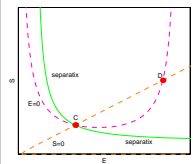


Figure 2: Bifurcation curves of Budworm density



## 5. Decide upon the form of the slow variables

The next step in the analysis employed by [Ludwig et. al., (1978)] is to analyze the slow variables while holding the fast variable fixed. They identify  $S$  as the total surface area of the branches in a stand of trees. The condition of the foliage and overall health of the trees will be given as  $E$ ; this is analogous to the trees energy reserve.

To describe  $S$  the authors chose the logistic form since it is bounded by the upper limit  $K_S$ —the maximum amount of surface area.

$$\frac{dS}{dt} = r_S S \left( 1 - \frac{S}{K_S} \frac{K_E}{E} \right), \quad (16)$$

The factor  $K_E/E$  reflects the fact that  $S$  does not increase under conditions of stress. During most times  $E$  will be close to its maximum  $K_E$  and  $S$  will approach its maximum  $K_S$ . The energy reserve is also given an equation of the logistic form since it is bounded by its maximum  $K_E$ ,

$$\frac{dE}{dt} = r_E E \left( 1 - \frac{E}{K_E} \right) - P \frac{B}{S}, \quad (17)$$

The second term on the right hand side of the equation describes the stress exerted by the budworm population.  $B/S$  is proportional to the stress with a constant  $P$ . Budworms have units of number of budworms per acre while  $S$  has units of branch surface area per acre; therefore,  $B/S$  is the number of budworms per branch.

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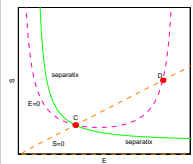
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## 6. Analyze the long-term behavior of the slow variables, with the fast variables held at the corresponding equilibria

The next logical step in the analysis is to analyze slow variables with the fast variables held fixed. To accomplish this, [Ludwig et. al., (1978)] obtain the isoclines for  $E$  and  $S$ . The isoclines are where  $dS/dt$  and  $dE/dt$  are zero. Therefore,  $dS/dt = 0$  if:

$$S = \frac{K_s}{K_E} E \quad \text{or} \quad S = 0, \quad (18)$$

and

$$dE/dt = 0, \quad (19)$$

if

$$S = \frac{PB}{r_E E \left(1 - \frac{E}{K_E}\right)} = \frac{PBK_E}{r_E} * \frac{1}{E(K_E - E)}, \quad (20)$$

When  $B$  is relatively small the two curves cross at two points: C and D (Figure 3). Point C is a saddle point and D is a sink. A single pair of solutions reach C. These solutions form a separatrix. If the initial values for  $E$  and  $S$  lie to the right of the separatrix, then  $(E, S)$  will approach D as  $t \rightarrow \infty$ . If  $E$  and  $S$  start out to the left of the separatrix,  $(E, S)$  will approach  $E = -\infty$ . [Ludwig et. al., (1978)] claim "while this is not realistic, it is a consequence of the form." To remedy the problem they limit  $E$  by zero; thereby creating a stable equilibrium at  $S = 0$  and  $E = 0$ .

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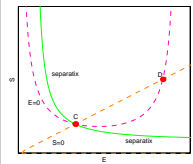
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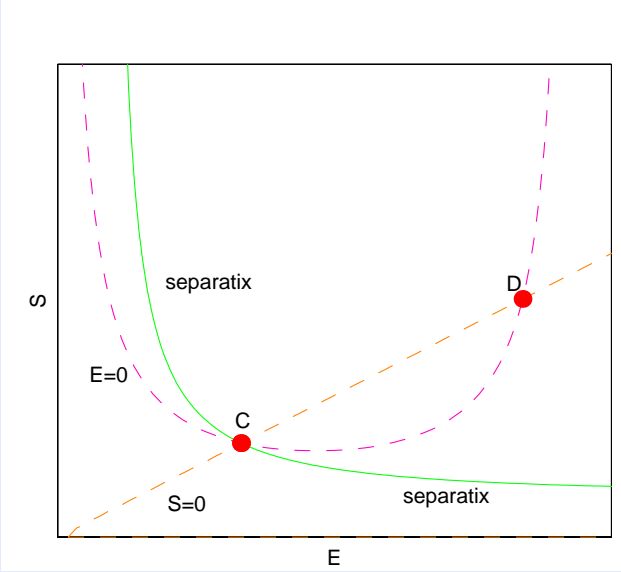
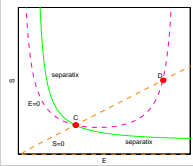


Figure 3: Equilibrium points of slow variables



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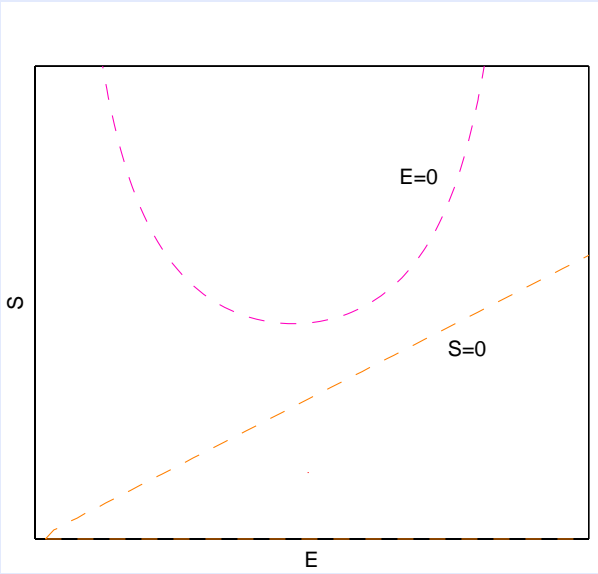
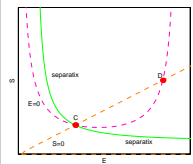


Figure 4: Case in which  $E$  nullcline surpasses  $S$  nullcline. All solution go to zero.

The dynamic of this system can be illustrated simply by noting that if budworm density increases it has the effect of raising the  $E$  nullcline. At some point the two equilibria coalesce and then disappear as the  $E = 0$  curve surpasses the  $S = 0$  line. This leaves the only remaining equilibria at  $(0,0)$ . This dynamic is shown in **Figure 4**. Remember that  $E$  represents the energy reserve of the forest and  $S$  represents the branch area. So the effect shown in **Figure 4** describes the destruction of the forest.





## 7. Combine the preceeding results to describe the behavior of the complete system

[Ludwig et. al., (1978)] assert there is the possibility of periods in which budworm populations are controlled by predators and therefore low and stable (at G). In **Figure 2** this occurs when the system resides below the upper critical curve. In **Figure 3**,  $E$  and  $S$  will increase to the point D. Accordingly, if the system crosses the upper branch of the bifurcation curve in **Figure 2** the budworm population increases to I in **Figure 1**. This increase is relatively rapid and extreme enough to cause **Figure 3** to give way to **Figure 4**. Thereby causing a collapse of the forest since  $(E, S)$  will head towards the stable equilibrium  $(0, 0)$ . Note the effect of the  $E = 0$  isocline surpassing the  $S = 0$  isocline in **Figure 4** is to cause  $R$  in **Figure 1** to decrease past the point where G and H are reformed. However, the budworm density does not jump down until the system passes completely through the bimodal region in **Figure 2**. When  $R$  is sufficiently low enough the lower critical curve in **Figure 2** will be crossed and the budworm population jumps down.

This describes a complete outbreak/decline cycle of the budworm/balsam interaction as described by [Ludwig et. al., (1978)]. The authors note that factors that might cause  $R$  to increase significantly are external driving variables that change one of the parameters of  $R$ . For example, weather might change  $r_B$  the instantaneous rate of budworm density.

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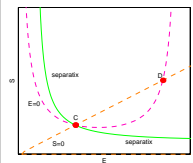
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## 8. Coupling of equations

In order to combine the equations into one system of equations, all the variables need to be expressed in a common way. First, consider [Equation 3](#).  $K_B$ , the carrying capacity of budworms, is proportional to  $S$  since this depends on food limitations, not predation. Therefore  $K_B$  can be written as,

$$K_B = K'S, \quad (21)$$

Where  $K_B$  measures larvae per unit acre and  $K'$  measures larvae per branch area.

Similarly, the predation term ([Equation 2](#)) is adjusted to reflect the fact that predators search units of foliage, not acres of forest. This means the relevant density must be larvae per branch area. To accomplish this, [[Ludwig et. al., \(1978\)](#)] made the half-saturation density of  $B$  proportional to  $S$ , thus yielding the following,

$$\alpha = \alpha'S, \quad (22)$$

where the new parameter

$$\alpha', \quad (23)$$

is measured in larvae per unit branch area. Substituting the new variables into  $R$  and  $Q$  yields:

$$R = \frac{\alpha' r_B}{\beta} S, \quad Q = \frac{K'}{\alpha'}, \quad (24)$$

The implications of the new form are important.  $R$  is proportional to  $S$  while  $Q$  is independent of  $S$ . Therefore, when the forest is young  $R$  will be small and  $Q$  can be large by comparison. Budworm densities will be low in budworms

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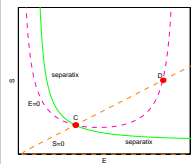
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per branch because predators will find it easy to search the small number of branches per acre. As the forest grows ( $S$  increases), so does  $R$  and control by predators begins to yield. At some point the upper bifurcation curve in **Figure 2** will be crossed and  $B$  jumps to the only remaining stable equilibrium at  $I$ . At this point budworms have escaped control by predators and are now limited by food. Once again, the effect of the jump in budworm density could cause **Figure 3** to give way to **Figure 4**; thereby causing the destruction of the forest. The final forms of the equations are given below:

$$\frac{dB}{dt} = r_B \left( 1 - \frac{B}{K'S} \right) - \beta \frac{B^2}{(\alpha'S)^2 + B^2}, \quad (25)$$

$$\frac{dS}{dt} = r_S \left( 1 - \frac{SK_E}{EK_S} \right), \quad (26)$$

$$\frac{dE}{dt} r_E E \left( 1 - \frac{E}{K_E} \right) - P \frac{B}{S}, \quad (27)$$

In conclusion, the approximation of parameter values has been omitted. For a discussion of the specific parameter values see [Ludwig et. al., (1978)].

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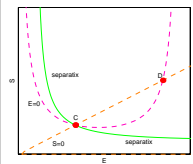
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## References

- [Holling, (1973)] **Holling, C.S. (1973)**. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, **4**, 1-23.
- [Ludwig et. al., (1978)] **Ludwig et. al. (1978)**. Qualitative analysis of insect outbreak systems: the Spruce Budworm and forest. *Journal of Animal Ecology*, **47**, 315-332.
- [Thom, (1975)] **Thom, R. (1975)**. *Structural Stability and Morphogenesis*.
- [Zeeman, (1976)] **Zeeman, E.C. (1976)**. Catastrophe theory. *Scientific American*, **234**, 65-83.

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