Fall 2009 Math 636

Bifurcation Analysis - One Dimensional ODEs

Population Models

Earlier in the lecture, we noted that growth of populations tend to follow classic S-shaped curves. When there are abundant resources, a population will grow exponentially, satisfying the Malthusian growth law:

$$\frac{dP}{dt} = rP,$$

where r is the growth rate. As populations grow, their growth rate slows, and the next approximation to population grow satisfies the logistic growth equation given by:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{M}\right),$$

where M is the carrying capacity.

Harvesting

Now consider modeling the population and harvesting some of the population using various strategies. We examine in detail, using geometric techniques, two common harvesting strategies.

Constant Harvesting

One of the simplest methods is the idea of harvesting where a set limit is established for harvesting. We will assume that the dynamics of the population satisfies the logistic growth model above and that a constant harvesting, h, is added to account for removing a constant number of the animal over a given time interval. The mathematical model becomes:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{M}\right) - h = F(P), \qquad P(0) = p_0.$$

If this ODE is inserted this into Maple to solve, then one obtains an explicit solution, which is very messy:

$$\begin{aligned} P(t) &= 1/2\,(Mr + \\ &\quad \tanh\Bigg(1/2\,\sqrt{-4\,hMr + M^2r^2}\,\Bigg(t + M\ln\left(-\frac{Mr - \sqrt{-4\,hMr + M^2r^2} - 2\,p0\,r}{Mr + \sqrt{-4\,hMr + M^2r^2} - 2\,p0\,r}\right) \\ &\quad \frac{1}{\sqrt{-4\,hMr + M^2r^2}}\Bigg)M^{-1}\Bigg)\sqrt{-4\,hMr + M^2r^2}\Bigg)r^{-1}. \end{aligned}$$

Clearly, this solution is difficult to analyze, so we turn to a geometric analysis of the model.

We graph the right hand side of the differential equation, $F(P)$. Any point where the $F(P)$ crosses the P-axis is an equilibrium of the differential equation. Whenever the graph is above the P-axis, then the solution is increasing, while if the graph is below the P-axis, then the

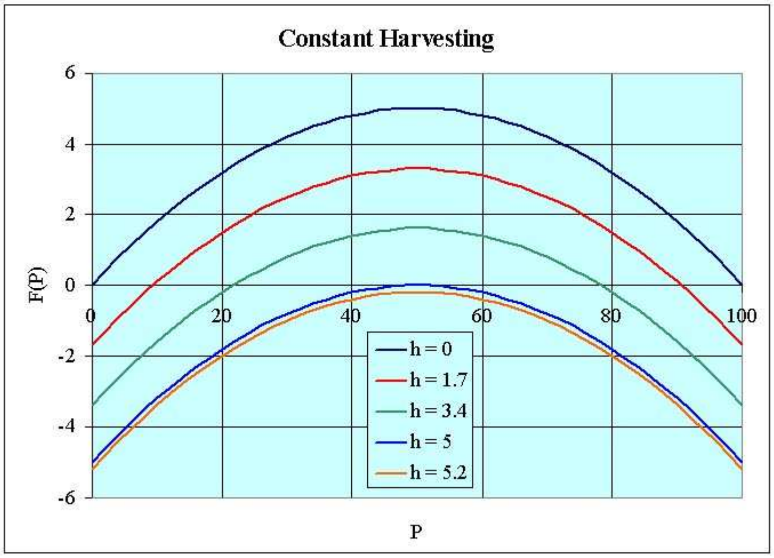


Figure 1: The phase portrait for different h values. The equilibria are on the P-axis with solutions moving right for $F(P) > 0$ and moving left for $F(P) < 0$.

solution of the ODE is decreasing. Above is a graph of the model with $r = 0.2$ and $M = 100$ for various harvesting values h.

From the graph, we recall that for the logistic growth model (no harvesting), all solutions with small initial conditions grow away from the extinction or $P_e = 0$ equilibrium, and all positive solutions grow toward the carrying capacity, $P_e = M$. This is easily seen in the graph above. As the harvesting increases, the two equilibria move closer to each other with the lower equilibrium remaining unstable and the upper equilibrium remaining stable. The equilibria, P_e, are simply the solution of the quadratic equation

$$rP_e\left(1 - \frac{P_e}{M}\right) - h.$$

For our specific example, we see that as $h \to 5$ (which matches the maximum growth rate of the logistic growth equation), the two equilibria coalesce at $P_e = 50$, which becomes an equilibrium that is approached for initial conditions greater than 50, but repels solutions with initial conditions less than 50. When $h > 5$, there are no equilibria, and the model shows that the population always goes extinct. This model shows a classic example of a *saddle node* or *blue sky bifurcation*.

Saddle Node Bifurcation

The classic form of the saddle node bifurcation is the differential equation:

$$\dot{y} = \mu - y^2,$$

where μ is the bifurcation parameter. As the parameter, μ, varies, the behavior of the system changes or bifurcates at $\mu = 0$, where equilibria either appear or disappear, depending on the change of the parameter, μ. It is often called a *blue sky bifurcation* because the appearance of equilibria appear out of nowhere.

Below we show a bifurcation diagram for the classic differential equation above of the saddle node bifurcation. The horizontal axis shows the parameter, μ, as it varies. The vertical axis shows the value of the equilibria for a particular value of μ. The solid line indicates a stable equilibrium, and the dotted line indicates an unstable equilibrium.

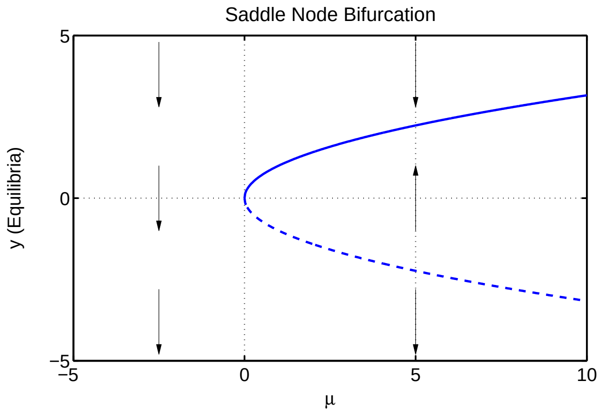


Figure 2: **Saddle Node or Blue Sky Bifurcation:**The solid lines indicate stable equilibria and the dotted lines indicate unstable equilibria.

Proportional Harvesting

Another common form of harvesting, such as netting fish, is when one puts in a constant effort to harvest. In this case, the quantity harvested is proportional to the population. Thus, the mathematical model can be written:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{M}\right) - hP = G(P), \qquad P(0) = p_0,$$

where again r is the growth rate, M is the carrying capacity with no harvesting, and h is the proportional rate of harvesting.

Once again, Maple can readily solve this differential equation, yielding the following result:

$$P\left(t\right) = M\left(r-h\right)\left(r + \frac{e^{-(r-h)t}\left(Mr - \mathit{p0}\,r - hM\right)r}{\mathit{p0}\ \left(r-h\right)} - \frac{e^{-(r-h)t}\left(Mr - \mathit{p0}\,r - hM\right)h}{\mathit{p0}\ \left(r-h\right)}\right)^{-1}$$

Again, we see that this algebraic solution is rather complex and hard to interpret. Thus, we again examine the right hand side of the differential equation geometrically.

We graph the right hand side of the differential equation, $G(P)$. The equilibria are found by the P-intercepts of $G(P)$,

$$G(P_e) = P_e\left(r - h - \frac{rPe}{M}\right) = 0$$

or

$$P_e = 0 \qquad \text{or} \qquad P_e = \frac{r-h}{rM}.$$

Whenever the graph is above the P-axis, then the solution is increasing, while if the graph is below the P-axis, then the solution of the ODE is decreasing. Below is a graph of the model with $r = 0.2$ and $M = 100$ for various harvesting values h.

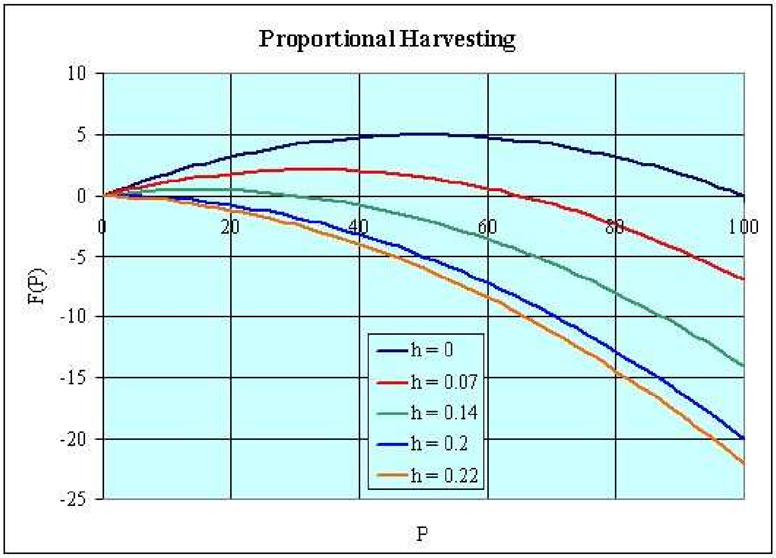


Figure 3: The phase portrait for different h values. The equilibria are on the P-axis with solutions moving right for $F(P) > 0$ and moving left for $G(P) < 0$.

The extinction equilibrium, $P_e = 0$, is unstable for $h < r$. As h increases, we see the larger equilibrium (carrying capacity) shrink, but it remains stable for $h < r$. For our specific example, we see that as $h \to 0.2$ (which matches the growth rate), the upper equilibrium fades to zero, which implies there is extinction. This is easy to understand because the harvesting rate approaches the growth rate. When $h > 0.2$, the the rate of harvesting exceeds the reproduction rate and extinction necessarily follows. This model shows a classic example of a *transcritical bifurcation.*

Transcritical Bifurcation

The classic form of the transcritical bifurcation is the differential equation:

$$\dot{y} = \mu y - y^2,$$

where μ is the bifurcation parameter. As the parameter, μ, varies, the behavior of the system changes or bifurcates at $\mu = 0$. In this case, there are equilibria at 0 and μ. When $\mu > 0$, then $y_e = \mu$ is stable and 0 is unstable. However, if $\mu < 0$, then $y_e = \mu$ is unstable and 0 is stable. In this case, the upper equilibrium remains stable, but there is a shift in stability of the equilibrium at 0, as it changes from being the upper equilibrium for $\mu < 0$ to the lower equilibrium with $\mu > 0$.

Below we show a bifurcation diagram for the classic differential equation above of the transcritical bifurcation. The horizontal axis shows the parameter, μ, as it varies. The vertical axis shows the value of the equilibria for a particular value of μ. The solid lines indicate stable equilibria, and the dotted lines indicate unstable equilibria.

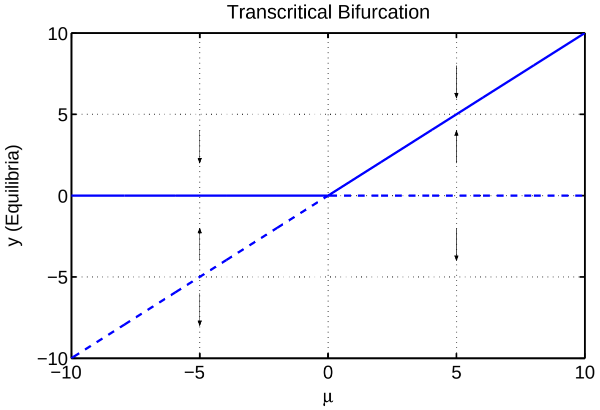


Figure 4: **Transcritical Bifurcation:** The solid lines indicate stable equilibria and the dotted lines indicate unstable equilibria.

Fluxgate Magnetometer

A number of models that have a switching mechanism use the hyperbolic tangent function. A one dimensional model that has been used for fluxgate magnetometer (and nerve impulse models) is given by the equation:

$$\dot{y} = -y + \tanh(cy) = H(y),$$

where c is a temperature dependent parameter that controls the behavior of the potential function from which this differential equation is derived. The equilibria are found by solving:

$$y_e = \tanh(cy_e),$$

which always has the solution $y_e = 0$. If $c < 1$, then $y_e = 0$ is the only solution. However, when $c > 1$, then there are always three equilibria. We can see this graphically by the figure below.

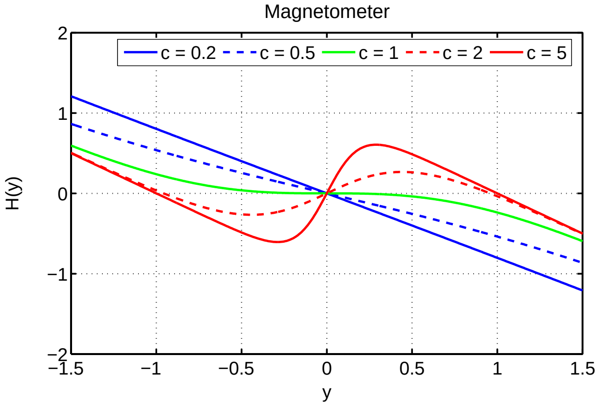


Figure 5: The phase portrait for different c values. The equilibria are on the y-axis with solutions moving right for $H(y) > 0$ and moving left for $H(y) < 0$.

For this model, the equilibrium, $y_e = 0$, is stable for $c < 1$ and becomes unstable for $c > 1$. The two new equilibria that appear after a *pitchfork bifurcation* at $c = 1$ are stable equilibria.

Pitchfork Bifurcation

The a classic example of a *pitchfork bifurcation* is given by the differential equation:

$$\dot{y} = \mu y - y^3,$$

where μ is the bifurcation parameter. Again we take μ as the bifurcation parameter. In this case, there are equilibria at $y_e = 0$ (unstable) and $y_e = \pm\mu$ (stable), when $\mu > 0$, and $y_e = 0$ (stable) is the only equilibrium, when $\mu < 0$.

Below we show a bifurcation diagram for the classic differential equation above of the pitchfork bifurcation. The horizontal axis shows the parameter, μ, as it varies. The vertical axis shows the value of the equilibria for a particular value of μ. The solid lines indicate stable equilibria and the dotted lines indicate unstable equilibria. From the diagram, it is fairly clear how this type of bifurcation gets its name.

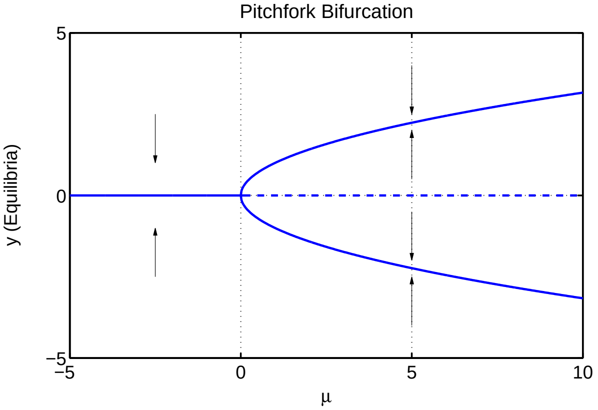


Figure 6: **Pitchfork Bifurcation:** The solid lines indicate stable equilibria and the dotted lines indicate unstable equilibria.

Modeling the Spruce Budworm

Most species of spruce budworms are serious pests that destroy coniferous forests. There are about a dozen species of the genus Choristoneura that range through the boreal forests of United States and Canada. The species, Choristoneura fumiferana or eastern spruce budworm, is amongst the most destructive native insect species in the northern spruce and fir forests, particularly affecting balsam fir trees in Eastern United States and Canada. There are periodic outbreaks of this pest with the first recorded outbreak occurring in Maine around 1807, which was followed by another outbreak in 1878. Using tree ring studies, scientists have determined that outbreaks of the spruce budworm have occurred every 40-60 years, since at least the 16th century. In the 20th century, Eastern Canada has seen three major outbreaks between 1910-1920, 1940-1950, and 1970-1980.

Mathematicians and ecologists have developed models for the periodicity of these outbreaks. One theory uses cusp-catastrophe theory with populations jumping between endemic and epidemic levels. Another theory considers spatially synchronized population oscillations caused by delayed density-dependent feedback that has high amplitude oscillations from entrainment.

Juvenile

Adult

Our study examines the cusp-catastrophe theory model, which combines a one-dimensional nonlinear ordinary differential equation with a slow varying parameter.

The spruce budworm is always present, but it is usually controlled by birds predating on the insect. However, every 30-60 years there is a serious outbreak of the pest that results in devastation of a forest in about four years. The spruce budworm is particularly destruction to the balsam fir trees in Eastern Canada.

We want to model this complicated interaction of the spruce budworm population with its host, the coniferous trees, and its primary predator, birds. The model is complicated by the significant differences in time scales between these particular species. The spruce budworms reproduce very rapidly with the ability to increase 5-fold in a single year. The balsam fir can replace its foliage in about 7 years and can live for about 100 years. To simplify the model we will assume that the birds are smart opportunistic predators with plenty of different sources of food and that they maintain a relatively constant population. We assume that the needles of the balsam fir are the primary source of food for the spruce budworms, and these leaves provide both nourishment and hiding for the spruce budworms.

The mathematical model for the Spruce Budworm is based on a paper by Ludwig, Jones, and Hollings (1978), which became important through a *Nature* article of Robert May (1977). This is a simple one-dimensional differential equation that tracks the population of the spruce budworm with several parameters that account for their interactions with their food source, the balsam firs, and their predators, the birds. As noted above, the bird population will be treated as being constant, and it is assumed that it is most limited by territorial factors and not food sources. Its predatory behavior is considered a learned behavior, which has been shown to satisfy a Holling's Type III interaction and will be discussed later. The foliage coverage of the trees is a slow dynamic when compared to the spruce budworm generation time, so it is considered to have a slow dynamic in the model. This is often referred to as a slow moving parameter. Our study will use some of the bifurcation principles that we have discussed above.

The model of Ludwig, Jones, and Holling (1978) has the following form:

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

where r_B is the intrinsic growth rate of the spruce budworm and K_B is the carrying capacity, which is assumed to depend on the availability of the foliage of the balsam firs.

The rate of predation, $g(B)$, is from avian predators, which associate reward with prey, a learned behavior. Thus, they focus on their best sources of prey. This allows a low density prey to escape notice, and the functional form of this type of predation has been shown to follow the Holling's Type III S-shaped response given by:

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

where β represents the saturation level of the predator (constant population, which can only eat so much prey) and α, which determines the densities of spruce budworm that cause avian predators to switch to them as a primary source of food. The resulting model for the population of the spruce budworm is given by:

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

Introduction of Dimensionless Variables

The model above has 4 parameters, and we want to analyze the behavior of this equation when the slow varying parameters are held constant. It is convenient to scale out two of the parameters and analyze the model depending on only these two scaled parameters. We can readily scale out two parameters by changing the population scale and the time scale. That is, we introduce a new scaled population and time given by:

$$\mu = sB \qquad \text{and} \qquad \tau = qt.$$

A scaled differential equation is written:

$$\begin{aligned} \frac{d\mu}{d\tau} &= \frac{s}{q}\frac{dB}{dt} = \frac{s}{q}\left(r_B B\left(1 - \frac{B}{K_B}\right) - \beta\frac{B^2}{\alpha^2 + B^2}\right) \\ &= \frac{s}{q}\left(r_B \frac{\mu}{s}\left(1 - \frac{\mu}{sK_B}\right) - \beta\frac{(\mu/s)^2}{\alpha^2 + (\mu/s)^2}\right) \end{aligned}$$

Let $s = 1/\alpha$, then

$$\frac{d\mu}{d\tau} = \frac{r_B}{q}\mu\left(1 - \frac{\alpha\mu}{K_B}\right) - \frac{\beta}{\alpha q}\left(\frac{\mu^2}{1 + \mu^2}\right).$$

Take $q = \beta/\alpha$, then

$$\frac{d\mu}{d\tau} = \frac{\alpha r_B}{\beta}\mu\left(1 - \frac{\alpha\mu}{K_B}\right) - \frac{\mu^2}{1 + \mu^2}.$$

If we define the new scaled parameters,

$$R = \frac{\alpha r_B}{\beta} \qquad \text{and} \qquad Q = \frac{K_B}{\alpha},$$

then the scaled model is given by:

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

A simple linearization near the equilibrium, $\mu_e = 0$, gives

$$\frac{d\mu}{d\tau} = R\mu,$$

which is Malthusian growth and gives the natural result that at low densities the spruce budworm population grows exponentially. Thus, we want to find other equilibria and study their behavior. The other equilibria are found by solving the equation:

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

It is important to interpret the equation above, and its interpretation is relatively simple from an ecological perspective. The left hand side of the equation is the *per capita* growth rate of the scaled population variable, μ, (with respect to the scaled time, $\tau = \beta t/\alpha$). The scaled equation on the right hand side is the *per capita* death rate of the spruce budworms due to avian predation. Any points of intersection of the curves formed by the left and right hand sides of the equation above produce non-zero equilibria for the differential equation for μ. The equation on the left hand side is a straight line with intercepts at $\mu = Q$ and a y-intercept at R. The right hand side intersects the origin and has a horizontal asymptote of $y = 0$. Elementary techniques from Calculus show that this function has a maximum at $(1, \frac{1}{2})$.

Bifurcation Analysis

We want to perform a bifurcation analysis of the scaled differential equation for the spruce budworm population given by the model:

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

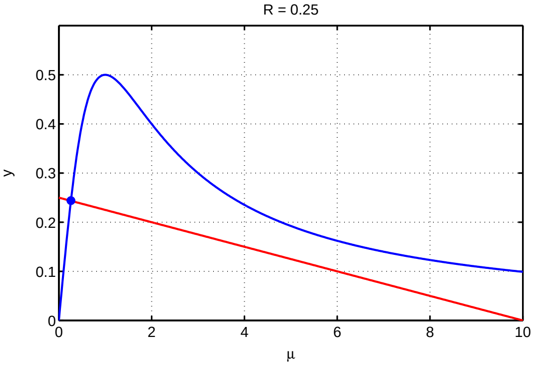
where we assume that the parameter Q is approximately constant, since the carrying capacity K_B scales with the parameter α, which measures the densities for predators to change prey sources. The parameter R is a more complex combination of parameters, which slowly increases at low densities and decreases when there is an outbreak of the spruce budworm that causes massive defoliation of the forests.

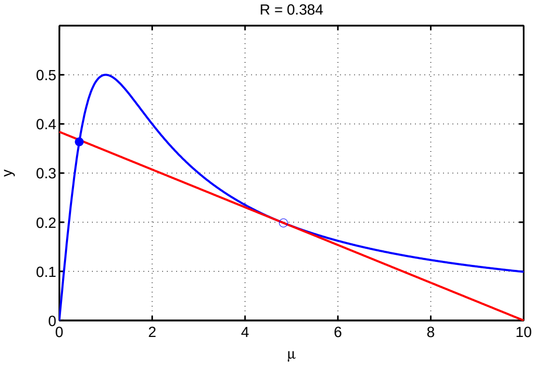
Clearly, there is the trivial or extinction equilibrium, $\mu_e = 0$, and linear analysis readily shows that this equilibrium is unstable. As noted above, the other equilibria are found by solving the equation:

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

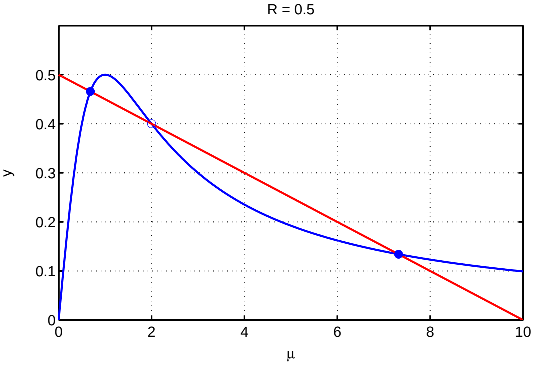
which has one to three solutions. The solutions to this equation are readily seen by graphing the right and left sides of the equation for different values of R (Q fixed). Suppose that we begin with a small value of R, say $R = 0.25$. The graph below (left) shows there is only one additional equilibrium at $\mu_e = 0.260$ and it is clear that this equilibrium is stable. Biologically, this scaled population represents an endemic population of spruce budworms in a healthy forest.

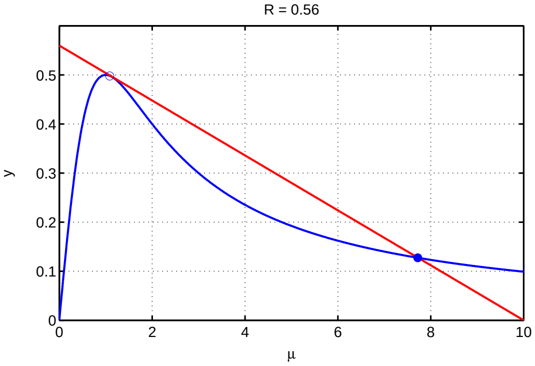
As the budworm population grows and R increases, the line from the left hand side of the equation becomes tangent to the curve from the right hand side of the equation at $R = 0.38397$. This is a saddle node (blue sky) bifurcation with a new equilibrium appearing at $\mu_e = 4.828$. As R increases more, this results in two new equilibria with the lower one being unstable and the upper one being stable. However, the solution of the differential equation remains trapped





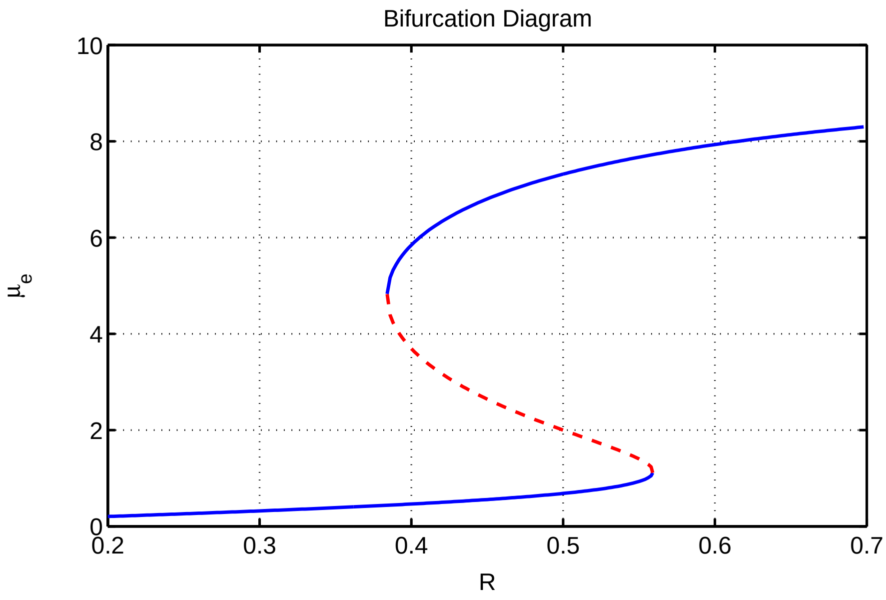
near the lower stable equilibrium. Thus, the spruce budworm population remains endemic, and the forest remains healthy and can grow with the bird population keeping the budworms sufficiently in check.





As R continues to increase to $R = 0.5595$, we see another saddle node (blue sky) bifurcation in the reverse direction and the lower two equilibrium points vanishing. This results in only having a single stable equilibrium with a high value. At this point there is an outbreak of the spruce budworms in large numbers as they saturate the ability of the predators to control their population and achieve very high numbers. The population goes to a carrying capacity, which causes massive defoliation of the forests. In the model this changes the slow dynamics of the parameter R, and it begins to decrease.

As defoliation continues, we again pass through the saddle node bifurcation at $R = 0.5595$, but now the solution remains at the larger equilibrium, so the health of the forest continues to decline. This continues until the budworms so severely damage the forest that their population collapses. The is shown in the model when the second saddle node bifurcation occurs at $R = 0.38397$, and the only remaining equilibrium is the stable endemic equilibrium. From this point we see that this cycle between the growth of the forest and the outbreak of spruce budworms continues in a cyclical manner.



This type of dynamical model where we model the fast dynamics for the population of the spruce budworm, μ, and include a slowly varying parameter, R, fits into some interesting modeling called *Catastrophe theory*. You can learn more about these systems in the Math 638 course. This particular model is shown on Ricardo Carretero's website:
http://www-rohan.sdsu.edu/ rcarrete/teaching/M-638/lectures/lectures.html.

References:

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[2] D. Ludwig, D. D. Jones and C. S. Holling, Qualitative analysis of insect outbreak systems: The spruce budworm and forest, *J. of Animal Ecology* (1978), 47, 315-332.

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