MATH 227A: Mathematical Biology
Homework 5

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Problem 1

Consider the system $x' = -x + yx^3$, $y' = y - y^3x$.

a) Find the steady states of this system

To find the steady states, we set the rates to zero a solve for x and y. Solving strictly within the first quadrant, we have,

$$\begin{aligned}
x' &= -x + yx^3 \\
0 &= -x + yx^3 \\
x &= yx^3 \\
y &= \frac{1}{x^2} && (1) \\
y' &= y - y^3x \\
0 &= y - y^3x \\
y &= y^3x \\
y &= \frac{1}{\sqrt{x}} && (2) \\
x^4 &= x && \text{[from (1) and (2)]} \\
x(x^3 - 1) &= 0
\end{aligned}$$

Solving (1) and (2), we see that the system has steady states at (0, 0) and (1, 1). Note that we obtain the solution (0, 0) by simply plugging in zeros in the original equations as this point is not strictly in the first quadrant like we assume for solving the system.

b) Linearize around each steady state to determine the qualitative local behavior around it.

The Jacobian of the given system is,

$$J = \begin{pmatrix} -1 + 3x^2y & x^3 \\ -y^3 & 1 - 3xy^2 \end{pmatrix} \tag{3}$$

Computing the Jacobian at (0, 0),

$$J_{(0,\ 0)} = \begin{pmatrix} -1 & 0 \\ 0 & 1 \end{pmatrix}$$

So, the eigenvalues of the system are $\lambda = -1, 1$ since $J_{(0,\ 0)}$ is a diagonal matrix. Since we have one positive and one negative eigenvalue, the system converges to the steady state along the eigenvector for positive λ and diverges along the other eigenvector. This makes a **saddle node at (0, 0)**. Now computing the Jacobian at (1, 1),

$$J_{(1,\ 1)} = \begin{pmatrix} 2 & 1 \\ -1 & -2 \end{pmatrix}$$

We now compute the eigenvalues of the system,

$$\begin{aligned} det \begin{pmatrix} 2 - \lambda & 1 \\ -1 & -2 - \lambda \end{pmatrix} &= 0 \\ \lambda^2 - 4 + 1 &= 0 \\ \lambda^2 - 3 &= 0 \\ \lambda &= \pm\sqrt{3} \end{aligned}$$

The eigenvalues of the system are $\lambda = \pm\sqrt{3}$. Once again, since we have one positive and one negative eigenvalue, the system converges to the steady state along the eigenvector for positive λ and diverges along the other eigenvector. This makes a **saddle node at (1, 1)**.

c) Use Hartman Grobman's Theorem to justify whether this information can be transferred to the original system, and draw an estimated phase portrait of the original nonlinear system.

All partial derivatives that constitute the Jacobian of the system as shown in (4) exist and are continuous in the real number space. At both steady states, (0, 0) and (1, 1), all eigenvalues of $J_{(\mathrm{i,j})}$ have a non-zero real part. Thus, the qualitative observations about stability made by linearizing around (0, 0) and (1, 1) can be transferred back to the original system as these **steady states hyperbolic**. The nullcline analysis and the estimated phase portrait of the original nonlinear system are shown in Figure 1.

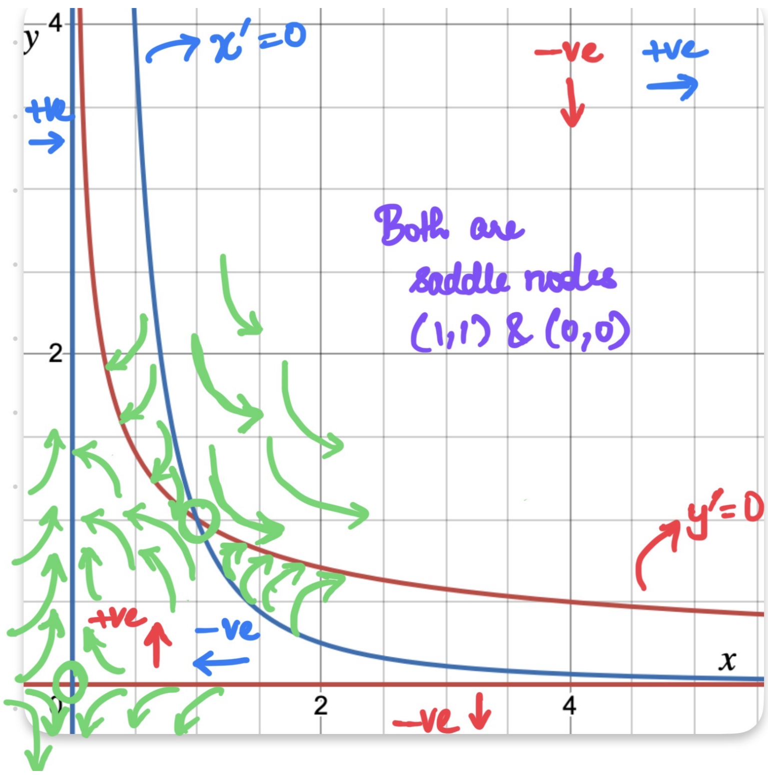

Figure 1: Phase portrait of the system in problem 1. The system has saddle nodes at both (0, 0) and (1, 1).

d) Now consider the system $x' = -x + yx$, $y' = y - yx$, which is identical to the first one but with different exponents. Linearize around the positive steady state $(1, 1)$. What can you conclude about the original system around the equilibrium based on the linearization alone?

The Jacobian of the given system is,

$$J = \begin{pmatrix} -1+y & x \\ -y & 1-x \end{pmatrix} \tag{4}$$

Computing the Jacobian at (1, 1),

$$J_{(1,\,1)} = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix}$$

We now compute the eigenvalues of the system,

$$\begin{aligned} det\begin{pmatrix} 0-\lambda & 1 \\ -1 & 0-\lambda \end{pmatrix} &= 0 \\ \lambda^2 + 1 &= 0 \\ \lambda &= \pm i \end{aligned}$$

The eigenvalues of the system are $\lambda = \pm i$. In contrast to the original system, this system has a **Lyapunov stable state** at (1, 1). Furthermore, since the eigenvalues have real parts that are zero, the steady state is not hyperbolic and the Hartman Grobman theorem is not applicable. Therefore, the complete nonlinear system might not exactly behave as stable center but might have qualitative behavior that is somewhat close to that.

Analyzing the two system around (1, 1) tells us two things: (1) The latter system has lesser nonlinearity than the original system and has a state that is approximately close to a stable center at (1, 1), but not exactly like so since the Hartman Grobman theorem was not applicable here. Increasing the nonlinearity by introducing cubic terms "magnified" the qualitative behavior of the system and showed that it has an unstable saddle node at (1, 1) rather than a stable one, suggesting that the latter system might be similarly unstable; (2) Relatedly, the observation also implicates the importance of the Hartman Grobman theorem. Although the linearization of the latter system suggested that it might have a stable center at (1, 1), the theorem did not allow this to be generalized back to the system—and rightly so, since upon "enhancing" the nonlinearity of the system, we see that there was "unstability" at (1, 1) and not stability as observed initially with the simpler system.

Problem 2

Consider a transcription factor that promotes its own growth. Let x be the messenger RNA, and y the protein itself. Assume that $x' = \sigma(y) - x$, $y' = x - y$, where $\sigma(x) = \dfrac{2x^2}{(1+x^2)}$. Notice this system is only defined for $x \geq 0$, $y \geq 0$.

a) Find the steady states of the system.

Setting the rates to zero to find the steady states,

$$\begin{aligned} x' &= \sigma(y) - x \\ 0 &= \sigma(y) - x \\ x &= \sigma(y) \qquad (5) \\ y' &= x - y \\ 0 &= x - y \\ x &= y \qquad (6) \end{aligned}$$

Solving (5) and (6) we get,

$$\begin{aligned} \sigma(y) &= y \\ \frac{2y^2}{1+y^2} &= y \\ 2y^2 &= y + y^3 \\ y \cdot (y^2 - 2y + 1) &= 0 \\ y \cdot (y-1)^2 &= 0 \end{aligned}$$

So, we get steady states at (0, 0) and (1, 1).

b) Linearize around each steady state to determine the qualitative local behavior around it.

The Jacobian of the given system is,

$$J = \begin{pmatrix} -1 & \sigma'(y) \\ 1 & -1 \end{pmatrix} \qquad (7)$$

$$\begin{aligned} \text{where} \qquad \sigma'(y) &= \frac{\mathrm{d}}{\mathrm{d}y}\left(\frac{2y^2}{1+y^2}\right) \\ &= \frac{(1+y^2)\,4y - 2y^2\,(2y)}{(1+y^2)^2} \\ &= \frac{4y}{(1+y^2)^2} \end{aligned}$$

Computing the Jacobian at the steady state (0, 0),

$$J_{(0,\ 0)} = \begin{pmatrix} -1 & 0 \\ 1 & -1 \end{pmatrix}$$

For $J_{(0,\ 0)}$, the trace $\tau = -2$ and determinant $\Delta = 1$. This lies on the curve $\tau^2 - 4\Delta = 0$ and is therefore an edge case for stability analysis. We now compute the eigenvalues.

$$\begin{aligned} det \begin{pmatrix} -1-\lambda & 0 \\ 1 & -1-\lambda \end{pmatrix} &= 0 \\ (\lambda+1)^2 &= 0 \\ \lambda_1 = \lambda_2 &= -1 \end{aligned}$$

The system has only one unique eigenvalue. We now compute the eigenvectors.

$$\begin{aligned} \begin{pmatrix} -1-\lambda & 0 \\ 1 & -1-\lambda \end{pmatrix} \cdot v &= 0 \\ \begin{pmatrix} 0 & 0 \\ 1 & 0 \end{pmatrix} \cdot v &= 0 \\ v = s \cdot \begin{pmatrix} 0 \\ 1 \end{pmatrix} \end{aligned}$$

where s is a scalar. So, any eigenvector is a scalar multiple of $(0, 1)^T$ and thus there is only one independent eigenvector. $J_{(0,\ 0)}$ is not diagonalizable. Since the eigenvalue is negative and the matrix is non-diagonalizable, (0, 0) is a **stable attractor degenerate node**. As $t \to \infty$, all trajectories align with eigenvector v, which is simply the y-axis.

Now computing the Jacobian at (1, 1),

$$J_{(1,\ 1)} = \begin{pmatrix} -1 & 1 \\ 1 & -1 \end{pmatrix}$$

For $J_{(1,\ 1)}$, the trace $\tau = -2$ and determinant $\Delta = 0$. This lies on the τ axis and is therefore an edge case for stability analysis. We now compute the eigenvalues.

$$\begin{aligned} det \begin{pmatrix} -1-\lambda & 1 \\ 1 & -1-\lambda \end{pmatrix} &= 0 \\ (\lambda+1)^2 &= 1 \end{aligned}$$

So, the system has eigenvalues $\lambda_1 = 0$ and $\lambda_2 = -2$. Now computing the eigenvector for $\lambda_1 = 0$,

$$\begin{aligned} \begin{pmatrix} -1-\lambda_1 & 1 \\ 1 & -1-\lambda_1 \end{pmatrix} \cdot v_1 &= 0 \\ \begin{pmatrix} -1 & 1 \\ 1 & -1 \end{pmatrix} \cdot v_1 &= 0 \\ v_1 &= \begin{pmatrix} 1 \\ 1 \end{pmatrix} \end{aligned}$$

Similarly for $\lambda_2 = -2$, we have,

$$\begin{pmatrix} -1-\lambda_2 & 1 \\ 1 & -1-\lambda_2 \end{pmatrix} \cdot v_2 = 0$$

$$\begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix} \cdot v_2 = 0$$

$$v_2 = \begin{pmatrix} -1 \\ 1 \end{pmatrix}$$

So, at $(1, 1)$ there is a line of equilibrium along the eigenvector corresponding to $\lambda_1 = 0$, which is $v_1 = (1, 1)^T$. Since λ_2 is negative, the steady state is a stable attractor. Ergo, the trajectories move toward the line of equilibrium. Thus, at (1, 1) the system has a **stable attractor line of equilibrium**.

c) Use Hartman Grobman's Theorem to justify whether this information can be transferred to the original system, and draw an estimated phase portrait of the original nonlinear system.

All partial derivatives that constitute the Jacobian of the system as shown in (7) exist and are continuous in the real number space. At steady state (0, 0), all eigenvalues of $J_{(0,0)}$ have a non-zero real part. Thus, the observations about stability made by linearizing around (0, 0) can be transferred back to the original system as this steady state **is hyperbolic**. However, at (1, 1), one of the eigenvalues has a zero real part and (1, 1) is **not hyperbolic**. Therefore, the observations made here cannot be directly translated to the original system. However, a nullcline analysis around (1, 1) can provide an estimate of what the phase portrait would look like at this steady state. The nullcline analysis and the estimated phase portrait are shown in Figure 2.

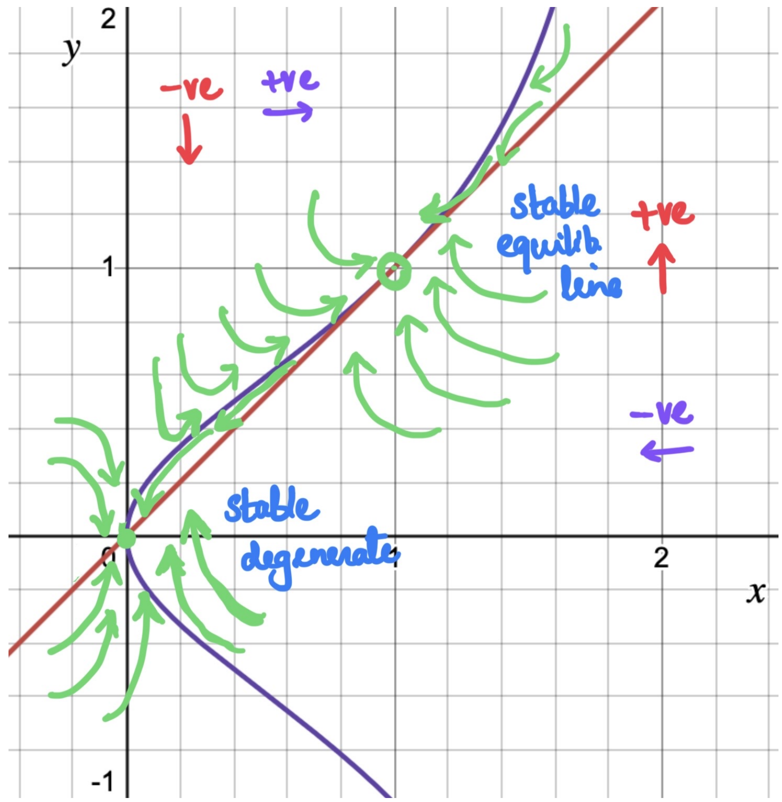

Figure 2: Phase portrait of the system in problem 2. At (0, 0), the system has a degenerate attractor where trajectories eventually align with the y-axis, the only eigenvector of the linearized system in this neighborhood. At (1, 1), the system has a stable equilibrium line that trajectories merge into. However, this is based on local linearization and may not exactly hold up in this neighborhood as the steady state (1, 1) is not hyperbolic. Nonetheless, the nullcline analysis shows a similar trend of approaching the equilibrium line along $x = y$.

Problem 3

Consider the system $x' = y - 2x$, $y' = \mu + x^2 - y$

a) Sketch the nullclines.

To obtain the nullcline equations, we set the rates to zero below,

$$x' = y - 2x$$
$$0 = y - 2x$$
$$y = 2x \tag{8}$$
$$y' = \mu + x^2 - y$$
$$y = x^2 + \mu \tag{9}$$

The nullcline equations, (8) and (9), are plotted for $\mu > 1$, $\mu < 1$, and $\mu = 1$ in Figure 3A. 3B shows the stability of the two steady states when the system is in the two steady state regime.

b) Find and classify the bifurcations that occurs as μ varies.

To compute the critical value of μ where bifurcation occurs, we solve the nullcline equation to find where they intersect to form steady states.

$$y = 2x \qquad \text{[from (8)]}$$
$$2x = x^2 + \mu \qquad \text{[subst. in (9)]}$$
$$x^2 - 2x + \mu = 0$$

which has exactly one solution when $\mu = 1$ since its discriminant $D = 4 - 4\mu = 0$, no real solutions when $\mu > 1$ since $D < 0$, and two solutions when $\mu < 1$ since $D > 0$. So, the critical value of μ is 1. Figure 3B confirms these analytical deductions. The system transitions from having two steady states to one, then zero as μ increases. By analyzing the trajectories around the nullclines and steady states, we see that in the regime of two steady states, the state associated with higher x and y values is a saddle node while that with lower x and y values is stable. Since the system transitions from having one stable and one saddle node to having no steady states, this is a **saddle node bifurcation**.

c) Sketch the phase portrait as a function of μ.

The phase portrait of the system for different values of μ and the bifurcation plot with x at steady state as a function of μ is shown in Figure 4.

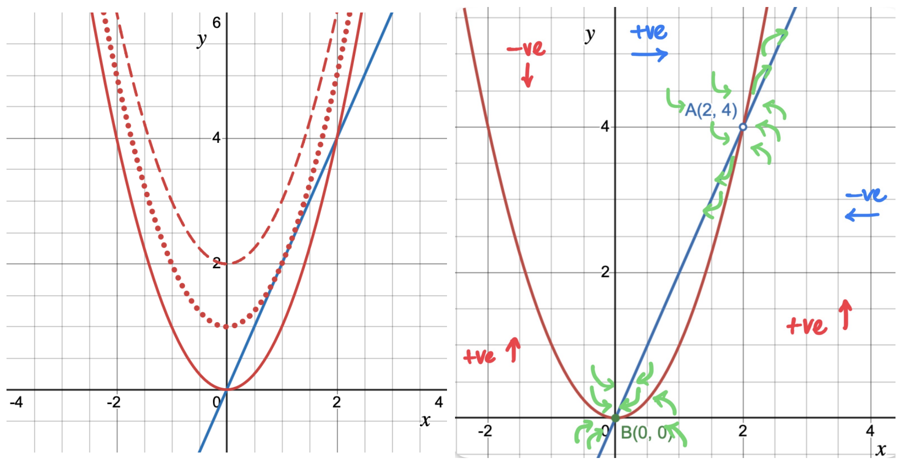

Figure 3: *On the left* are nullclines of the system in problem 3 for different values of μ: $\mu = 0$ as a solid line, $\mu = 1$ as dotted line, and $\mu = 2$ as dashed line. The system transitions from two steady states to one, then zero as μ increases. *On the right* are the nullclines with trajectories showing the stability of the two steady states when $\mu = 0$ — one saddle node and one stable steady state.

Problem 4

(Budworms vs. the forest) Ludwig et al. (1978) proposed a model for the effects of spruce budworm on the balsam fir forest. In Section 3.7, we considered the dynamics of the budworm population; now we turn to the dynamics of the forest. The condition of the forest is assumed to be characterized by S (t), the average size of the trees, and $E(t)$, the "energy reserve" (a generalized measure of the forest's health). In the presence of a constant budworm population B, the forest dynamics are given by the ODE system.

a) Interpret the terms in the model biologically.

The given ODE system is,

$$\frac{\mathrm{d}S}{\mathrm{d}t} = r_S S\left(1 - \frac{SK_E}{K_S E}\right) \tag{10}$$

$$\frac{\mathrm{d}E}{\mathrm{d}t} = r_E E\left(1 - \frac{E}{K_E}\right) - P \cdot \frac{B}{S} \tag{11}$$

The rate equation for average tree size, (10), is a slight variation of the classical growth equation with a carrying capacity. The first term represents how the presence of large trees can contribute to grow the size of the trees even further, in the absence of predation—essentially, intrinsic growth at rate r_S.

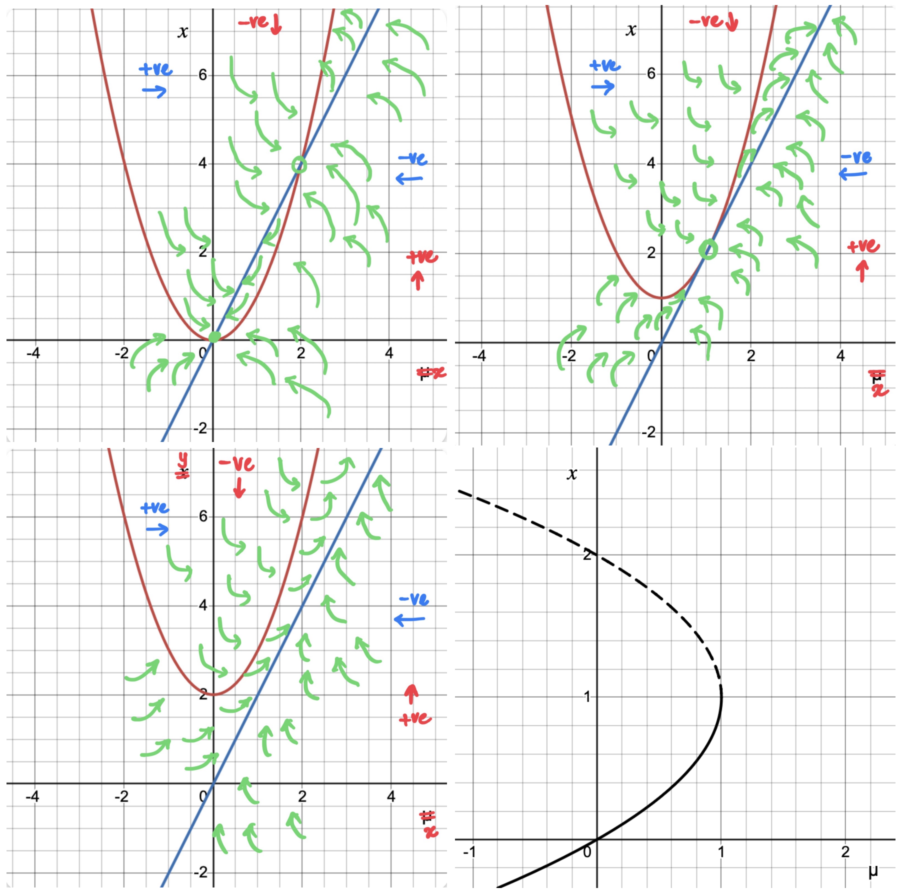

Figure 4: *Top and bottom-left* are phase portraits of the system in problem 3 for different values of μ: $\mu < 1$, $\mu = 1$, and $\mu > 1$ going top-bottom, left-right. When the system has no steady states, the trajectories tend to approach one of the nullclines but do not converge. *Bottom-right* is a bifurcation plot that shows x at steady state as a function of μ. The system has a **saddle node bifurcation** at $\mu = 1$.

The second term captures a couple of different phenomena that contribute to decreasing average tree size — (1) $\dfrac{S}{K_S}$: as trees grow bigger, they reach their carrying capacity K_S due to resource limit and to attain population stability; (2) $\dfrac{K_E}{E}$: as the energy reserve of the forest goes up, it reaches its carrying capacity K_E as well; however, the availability of a larger amount of energy reserve contributes positively to the carrying capacity K_S and negatively to reducing the average tree size. In essence, the second term can be interpreted as $S \cdot (\frac{K_E}{K_S\,E})$, wherein the fraction of energy reserve "adjusts" the set carrying capacity K_S to an effective tree size carrying capacity $\frac{K_E}{K_S\,E}$.

In the energy reserve rate equation, (11), the first two terms take together is again simply the growth curve under carrying capacity K_E. The last term represents depletion of the energy reserve caused by budworm feeding. The ratio $\frac{B}{S}$ represents the fact that if the trees are large, the relative effective damage caused is lesser than if the trees were smaller; P is simply a proportionality constant translating how strongly budworms affect the energy reserve.

b) Nondimensionalize the system.

To nondimensionalize the system we begin by defining the following:

$$S = \bar{s}\,s, \qquad E = \bar{e}\,e, \qquad t = \bar{\tau}\,\tau$$

where the quantities with a bar are new parameters, while s, e, and τ are non-dimensional versions of the system variables. Differentiating S with respect to t using the chain rule,

$$\frac{dS}{dt} = \frac{\mathrm{d}(\bar{s}s)}{\mathrm{d}\,(\bar{\tau}\tau)} = \frac{\bar{s}}{\bar{\tau}} \cdot \frac{\mathrm{d}s}{\mathrm{d}\tau} = r_S \bar{s}s\left(1 - \frac{\bar{s}s\,K_E}{K_S\,\bar{e}e}\right)$$

$$\frac{\mathrm{d}s}{\mathrm{d}\tau} = r_S\,\bar{\tau}s\left(1 - \frac{\bar{s}s\,K_E}{K_S\,\bar{e}e}\right)$$

Defining $\bar{\tau} = \dfrac{1}{r_S}$, $\bar{s} = K_S$, and $\bar{e} = K_E$, we get,

$$\frac{\mathrm{d}s}{\mathrm{d}\tau} = s\left(1 - \frac{s}{e}\right)$$

Similarly, differentiating E with respect to t using the chain rule,

$$\frac{dE}{dt} = \frac{\mathrm{d}(\bar{e}e)}{\mathrm{d}\,(\bar{\tau}\tau)} = \frac{\bar{e}}{\bar{\tau}} \cdot \frac{\mathrm{d}e}{\mathrm{d}\tau} = r_E \bar{e}e\left(1 - \frac{\bar{e}\,e}{K_E}\right) - P\frac{B}{\bar{s}\,s}$$

$$\frac{\mathrm{d}e}{\mathrm{d}\tau} = r_E\,\bar{\tau}e\left(1 - \frac{\bar{e}\,e}{K_E}\right) - P\frac{B\,\bar{\tau}}{\bar{e}\,\bar{s}\,s}$$

Defining $r = \dfrac{r_E}{r_S}$ and $\rho = \dfrac{P\,B}{K_E\,K_S\,r_S}$, we get,

$$\frac{\mathrm{d}e}{\mathrm{d}\tau} = r\,e\,(1-e) - \frac{\rho}{s}$$

So, the equivalent nondimensional system is given by,

$$\frac{\mathrm{d}s}{\mathrm{d}\tau} = s\left(1 - \frac{s}{e}\right) \tag{12}$$

$$\frac{\mathrm{d}e}{\mathrm{d}\tau} = r\,e\,(1-e) - \frac{\rho}{s} \tag{13}$$

with the following definitions,

$$\bar{\tau} = \frac{1}{r_S}, \qquad \bar{s} = K_S, \qquad \bar{e} = K_E, \qquad r = \frac{r_E}{r_S}, \qquad \rho = \frac{P\,B}{K_E\,K_S\,r_S}$$

and nondimensional system variables,

$$S = \bar{s}\,s, \qquad E = \bar{e}\,e, \qquad t = \bar{\tau}\,\tau$$

c) Sketch the nullclines of the system. What type of bifurcation occurs at the critical value of B?

Defining $\bar{\rho} = \dfrac{\rho}{B}$ and solving the setting the rates to zero to find the nullclines, we have,

$$\begin{aligned}
\frac{\mathrm{d}s}{\mathrm{d}\tau} &= s\left(1 - \frac{s}{e}\right) \\
0 &= s^*\left(1 - \frac{s^*}{e^*}\right) \qquad (14) \\
\frac{\mathrm{d}e}{\mathrm{d}\tau} &= r\,e\,(1-e) - \frac{\bar{\rho}B}{s} \\
0 &= r^*\,e^*\,(1-e^*) - \frac{\bar{\rho}B}{s^*} \\
\bar{\rho}B &= r\,s^*\,e^*\,(1-e^*) \qquad (15)
\end{aligned}$$

Figure 5A shows the nullclines of the system at low and high values of B. The system transitions from having two steady state to none as B increases. In the regime of two steady states, one of them is stable and the other is a saddle node. Since The system exists in two regimes, one with no steady states and the other with one unstable saddle and one stable steady state, this is a **saddle node bifurcation** as shown in Figure 5B. To identify the critical value of B, we solve (14) and (15). From (14),

$$\begin{aligned}
s^* &= e^* && [\text{ assuming } s^* > 0\ ] \qquad (16) \\
\frac{\bar{\rho}B}{r} &= s^*\,e^*\,(1-e^*) && [\text{ from (15) }] \\
&= s^{*2}(1-s^*) && [\text{ using (16) }] \qquad (17)
\end{aligned}$$

Since we are only interested in positive steady state values and the cubic equation in (17) has a local maxima at the critical value of B, for which there is a unique positive s^*. From (16), $e^* = s^*$ at this point. Defining $\bar{B} = \dfrac{\bar{\rho}B}{r}$, differentiating (17) with respect to s^*, and setting the latter to zero,

$$\begin{aligned}
\frac{\mathrm{d}\bar{B}}{\mathrm{d}s^*} &= 2s^*(1-s^*) - s^{*2} \\
0 &= 2s^*(1-s^*) - s^{*2} \\
&= 2s^*(2-3s^*)
\end{aligned}$$

So, we have $s^* = e^* = \frac{2}{3}$ at which the function has a local maxima. The corresponding critical value of B is

$$\begin{aligned}
B &= \bar{B} \cdot \frac{r}{\bar{\rho}} \\
&= s^{*2}(1-s^*) \cdot \frac{r}{\bar{\rho}} \\
&= \left(\frac{2}{3}\right)^2 \cdot \frac{1}{3} \cdot \frac{r}{\bar{\rho}} \\
&= \frac{4}{27} \cdot \frac{r}{\bar{\rho}}
\end{aligned}$$

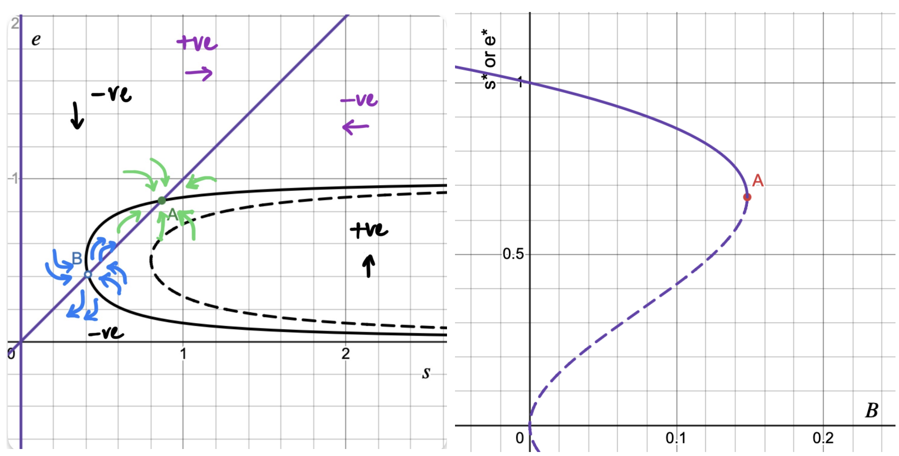

Figure 5: *On the left* are nullclines of the system in (10). The solid black line shows the system at low values of B, while the dashed line corresponds to high values of B. A is a stable steady state, where B is a saddle node. *On the right* is the bifurcation plot for parameter B. The system has two steady states (one saddle and one stable) for $B < \frac{4}{27}$ and no steady states for higher B—it has a **saddle node bifurcation**. *These plots were generated by setting* $\bar{\rho} = r = 1$.

d) Sketch the phase portrait for both large and small values of B.

The phase plot of the system is presented in Figure 6. The caption describes the system.

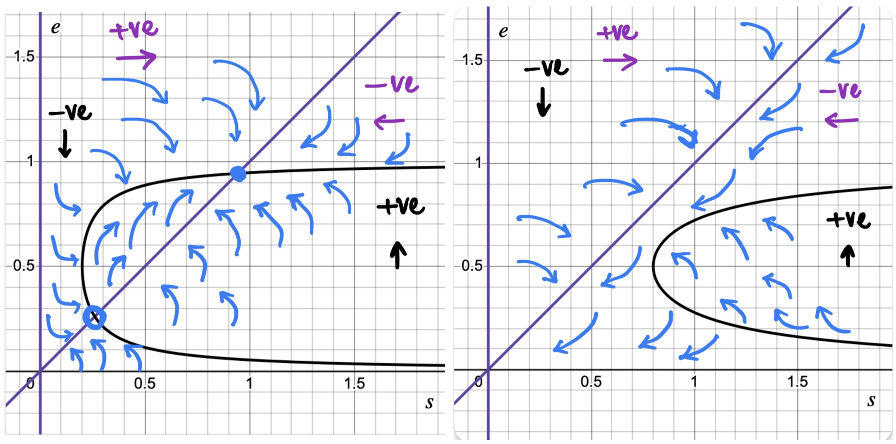

Figure 6: *On the left* is a phase plot of the system in (10) for low values of B. The system has two steady states—one saddle node and one stable. *On the right* is the phase plot of the system for high values of B. There are no steady states and the trajectories generally approach the nullclines.