Assignment Solutions

Consider the following model for the interactions between the populations N and M,

$$\begin{aligned}\frac{dN}{dt} &= rN\left(1-\frac{N}{K}\right)-\alpha NM,\\ \frac{dM}{dt} &= sM\left(1-\frac{M}{L}\right)-\beta NM,\end{aligned} \tag{1}$$

where r, s, K, L, α, and β are all positive parameters.

(i) Is the interaction predator-prey, competitive, or mutualistic? Explain your reasoning. **[2 MARKS]**
Competition: the interaction is detrimental to both N and M. That is, the interaction terms (i.e., the $-\alpha NM$ and $-\beta NM$ terms) decrease the growth rates of N and M.

(ii) Briefly explain what each parameter represents. **[3 MARKS]**

- r ... Logistic growth rate of N (in the absence of M)
- s ... Logistic growth rate of M (in the absence of N)
- K ... Carrying capacity of N (in the absence of competition)
- L ... Carrying capacity of M (in the absence of competition)
- α ... Rate of removal of N per unit of M
- β ... Rate of removal of M per unit of N

(iii) Non-dimensionalize system (1) so that the dimensionless dynamics are given by

$$\begin{aligned}\frac{dx}{d\tau} &= x(1-x)-\mu_1 xy,\\ \frac{dy}{d\tau} &= \sigma y(1-y)-\mu_2 xy.\end{aligned}$$

What are the expressions for μ_1, μ_2, and σ in terms of the original parameters? **[2 MARKS]**
Choose the rescaling

$$N = Kx, \quad M = Ly, \quad t = \frac{1}{r}\tau.$$

The dimensionless parameters are given by

$$\mu_1 = \frac{\alpha L}{r}, \quad \mu_2 = \frac{\beta K}{r}, \quad \sigma = \frac{s}{r}.$$

(iv) Determine the coordinates of all four equilibria. **[3 MARKS]**
There are four equilibria: $(x_1, y_1) = (0,0)$, $(x_2, y_2) = (0,1)$, $(x_3, y_3) = (1,0)$, and

$$(x_4, y_4) = \left(\frac{\sigma(1-\mu_1)}{\sigma-\mu_1\mu_2}, \frac{\sigma-\mu_2}{\sigma-\mu_1\mu_2}\right).$$

Note that (x_4, y_4) is obtained as the solution of the algebraic system

$$\begin{aligned}1-x_4-\mu_1 y_4 &= 0,\\ \sigma(1-y_4)-\mu_2 x_4 &= 0.\end{aligned} \tag{2}$$

Let (x_1, y_1), (x_2, y_2), and (x_3, y_3) denote the equilibria in which at least one of the coordinates is zero and let (x_4, y_4) be the equilibrium in which $x_4 \neq 0$ and $y_4 \neq 0$. This assignment is primarily concerned with how the model behaves under changes in the interaction rates, i.e., changes in μ_1 and μ_2.

(v) State the conditions on μ_1 and μ_2 such that (x_4, y_4) is in the biologically relevant domain. **[2 MARKS]**

The equilibrium (x_4, y_4) is only biologically relevant if $x_4 > 0$ and $y_4 > 0$. This implies

$$\mu_1 < 1 \quad \text{and} \quad \mu_2 < \sigma,$$

or

$$\mu_1 > 1 \quad \text{and} \quad \mu_2 > \sigma.$$

(vi) Use linear stability analysis to classify (x_1, y_1), (x_2, y_2), and (x_3, y_3). **[5 MARKS]**

The Jacobian is

$$Df(x, y) = \begin{pmatrix} 1 - x - \mu_1 y - x & -\mu_1 x \\ -\mu_2 y & \sigma(1 - y) - \mu_2 x - \sigma y \end{pmatrix}.$$

Evaluating at each equilibrium and computing the associated eigenvalues, we find

- $(x_1, y_1) = (0, 0)$ is an UNSTABLE NODE (with eigendirections along the axes) for all μ_1 and μ_2.
- $(x_2, y_2) = (0, 1)$ is a $\begin{cases} \text{SADDLE} & \text{for } \mu_1 < 1 \\ \text{STABLE NODE} & \text{for } \mu_1 > 1 \end{cases}$
- $(x_3, y_3) = (1, 0)$ is a $\begin{cases} \text{SADDLE} & \text{for } \mu_2 < \sigma \\ \text{STABLE NODE} & \text{for } \mu_2 > \sigma \end{cases}$

For parts (vii) – (ix) below, suppose that $\mu_1 < 1$ and $\mu_2 < \sigma$.

(vii) Prove that (x_4, y_4) is a stable node. **[3 MARKS]**

The linearization at (x_4, y_4) has the coefficient matrix

$$Df(x_4, y_4) = \begin{pmatrix} -x_4 & -\mu_1 x_4 \\ -\mu_2 y_4 & -\sigma y_4 \end{pmatrix},$$

where we have used (2) to simplify the Jacobian. So, we have

$$\begin{aligned} \operatorname{tr} Df(x_4, y_4) &= -(x_4 + \sigma y_4) < 0, \\ \det Df(x_4, y_4) &= (\sigma - \mu_1 \mu_2) x_4 y_4 > 0, \end{aligned}$$

where the second inequality comes from the fact that x_4 and y_4 are both positive (since they are in the biologically meaningful domain), and $\sigma - \mu_1 \mu_2 > 0$. It remains to show that the quantity $(\operatorname{tr} Df(x_4, y_4))^2 - 4 \det Df(x_4, y_4)$ is positive. We find that

$$\begin{aligned} (\operatorname{tr} Df(x_4, y_4))^2 - 4 \det Df(x_4, y_4) &= (x_4 + \sigma y_4)^2 - 4(\sigma - \mu_1 \mu_2) x_4 y_4, \\ &= (x_4 - \sigma y_4)^2 + 4 \mu_1 \mu_2 x_4 y_4, \\ &> 0. \end{aligned}$$

Hence, (x_4, y_4) is a STABLE NODE.

(viii) Determine the vector field along the x- and y-nullclines. **[2 MARKS]**

See Figure 1.

(ix) Carefully sketch the phase plane in the first quadrant $\{x \geq 0, y \geq 0\}$. **[7 MARKS]**

See Figure 1.

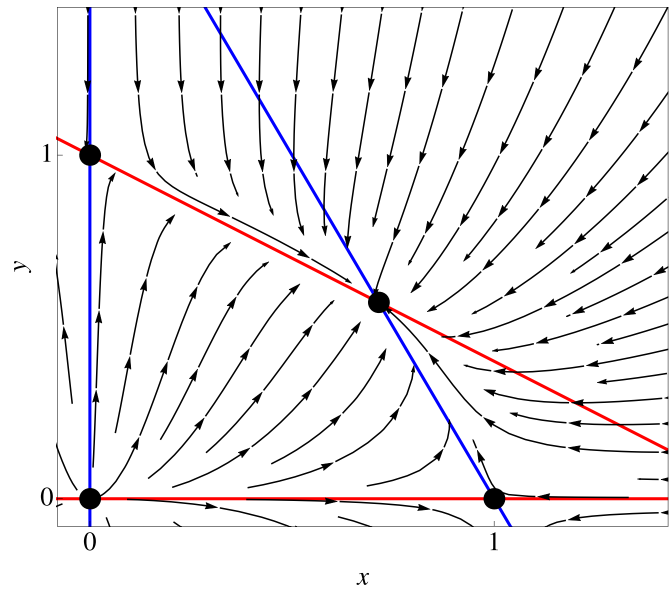

Figure 1: Representative phase plane for $\mu_1 < 1$ and $\mu_2 < \sigma$.

For part (x) below, suppose that $\mu_1 > 1$ and $\mu_2 < \sigma$.

(x) Carefully sketch the phase plane in the first quadrant $\{x \geq 0, y \geq 0\}$. **[3 MARKS]**

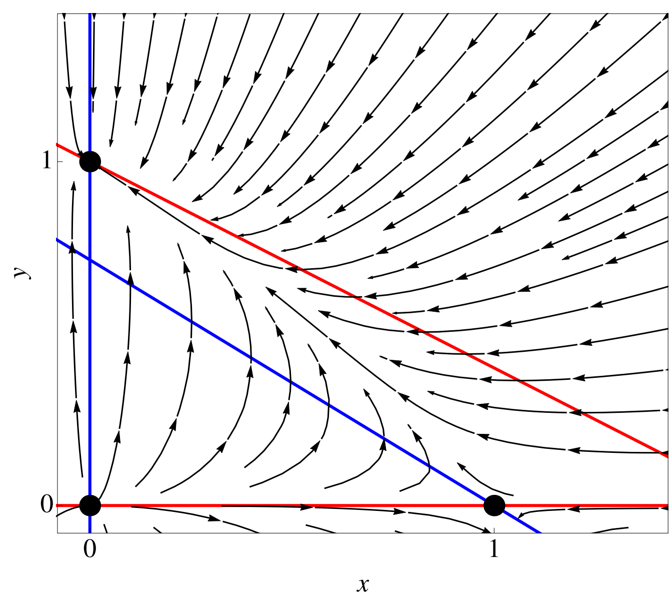

Figure 2: Representative phase plane for $\mu_1 > 1$ and $\mu_2 < \sigma$.

For part (xi) below, suppose that $\mu_1 < 1$ and $\mu_2 > \sigma$.

(xi) Carefully sketch the phase plane in the first quadrant $\{x \geq 0, y \geq 0\}$. **[3 MARKS]**

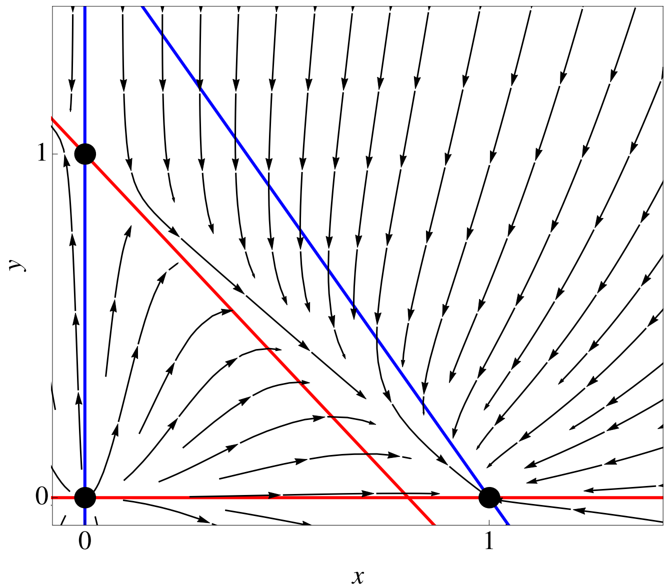

Figure 3: Representative phase plane for $\mu_1 < 1$ and $\mu_2 > \sigma$.

For parts (xii) – (xiii) below, suppose that $\mu_1 > 1$ and $\mu_2 > \sigma$.

(xii) Prove that (x_4, y_4) is a saddle. **[2 MARKS]**

The Jacobian evaluated at the non-trivial equilibrium is

$$Df(x_4, y_4) = \begin{pmatrix} -x_4 & -\mu_1 x_4 \\ -\mu_2 y_4 & -\sigma y_4 \end{pmatrix}.$$

Note that we have again used (2) to simplify the Jacobian. So, the determinant is

$$\det Df(x_4, y_4) = (\sigma - \mu_1\mu_2)x_4 y_4 < 0,$$

since x_4 and y_4 are both positive (they are in the biologically meaningful domain), and $\sigma - \mu_1\mu_2 < 0$, which follows from the fact that $\mu_1 > 1$ and $\mu_2 > \sigma$. Hence, (x_4, y_4) is a SADDLE.

(xiii) Carefully sketch the phase plane in the first quadrant $\{x \geq 0, y \geq 0\}$. **[3 MARKS]**

See Figure 4.

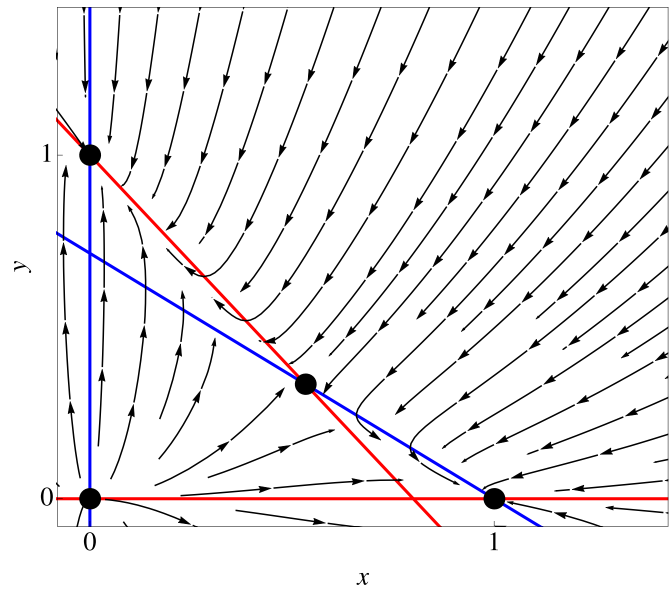

Figure 4: Representative phase plane for $\mu_1 > 1$ and $\mu_2 > \sigma$.

Finally, it is important to be able to explain what you have calculated. The explanation is as important as the calculation itself, since it indicates your understanding of your analysis.

(xiii) Interpret the phase planes from parts (ix) – (xiii) with respect to the original variables and parameters. At minimum, you should address the following points:

- Under what conditions do N and M stably coexist?
- When N and M do not stably coexist, what is the long-term behaviour of the system?
- Explain, in terms of the original parameters, why these different behaviours are observed.

[5 MARKS]

Stable coexistence only occurs for $\mu_1 < 1$ and $\mu_2 < \sigma$. In terms of the original variables and parameters, stable coexistence of N and M can only occur if

$$\alpha L < r, \quad \text{and} \quad \beta K < s.$$

Note that αL is the maximal rate of predation of M on N and r is the intrinsic growth rate of N in the absence of M. Similarly, βK is the maximal rate of predation of N on M and s is the intrinsic growth rate of M in the absence of N. Thus, stable coexistence can only occur if

- the intrinsic growth rate of N exceeds the maximal predation rate due to competition with M, and
- the intrinsic growth rate of M exceeds the maximal predation rate due to competition with N.

In the case of stable coexistence, the system settles to a steady state where both N and M survive, but at levels below their respective carrying capacities (because of the competition).

For all other cases ($\alpha L > r$ and $\beta K < s$, $\alpha L < r$ and $\beta K > s$, and $\alpha L > r$ and $\beta K > s$), at least one of N or M becomes extinct because the predation due to competition overwhelms the intrinsic growth. In ecology, this is known as the *principle of competitive exclusion.* I leave it to you to check which cases correspond to extinction of N or M.

The remainder of the assignment is **bonus** material.

(xiv) Fix $\mu_2 < \sigma$. Explain what happens as μ_1 increases through 1. **[1 MARK]**
Transcritical bifurcation of the equilibria $(0, 1)$ and (x_4, y_4).

(xv) Fix $\mu_1 < 1$. Explain what happens as μ_2 increases through σ. **[1 MARK]**
Transcritical bifurcation of the equilibria $(1, 0)$ and (x_4, y_4).

(xvi) Sketch the *two-parameter plane* (i.e., plot μ_1 against μ_2) and show all bifurcation boundaries in the (μ_1, μ_2) plane. Give explicit formulae for the bifurcation boundaries. For this part, you may assume that $\sigma > 1$. You are not required to identify the types of bifurcations. **[3 MARKS]**
One set of bifurcation boundaries is found by solving the algebraic equation

$$\det Df(x_4, y_4) = 0,$$

corresponding to a zero eigenvalue of (x_4, y_4) (node to saddle transition or vice versa). The other set of bifurcation boundaries is obtained as the solution of the system

$$\begin{aligned} \operatorname{tr} Df(x_4, y_4) &= 0, \\ \det Df(x_4, y_4) &> 0, \end{aligned}$$

corresponding to the transition from stable focus to unstable focus (or vice versa).