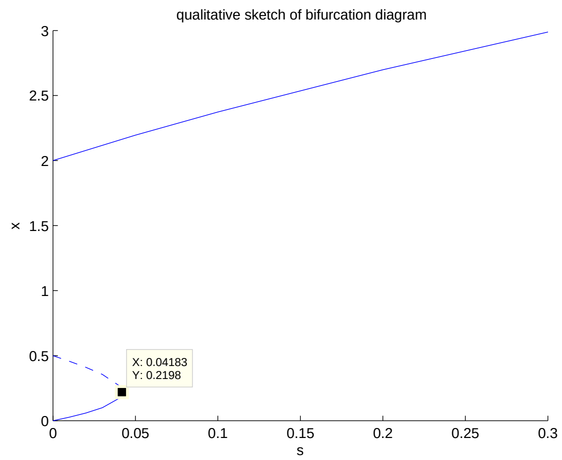


Exercise 3.9.7: Linear systems

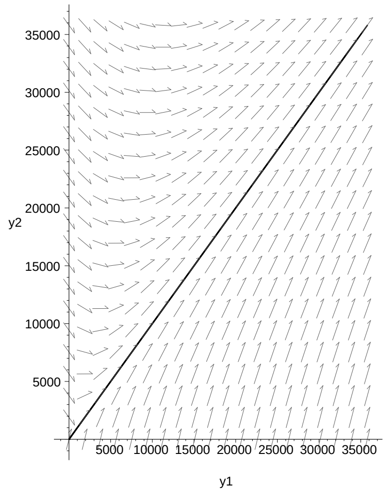
Thanks to Pandora Lam, University of Alberta, for providing this solution.

(a)

$$A = \begin{bmatrix} 1 & 1 \\ 3 & -1 \end{bmatrix}$$

$$\begin{aligned} \text{tr } A &= a + d = 1 + (-1) = 0 \\ \det A &= ad - bc = 1 * (-1) - 1 * 3 = -4 < 0 \\ \lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = 0 \pm \frac{1}{2}\sqrt{0 - 4 * (-4)} = \pm\frac{1}{2} * 4 = \pm 2 \end{aligned}$$

Hence, (0, 0) is a saddle point.

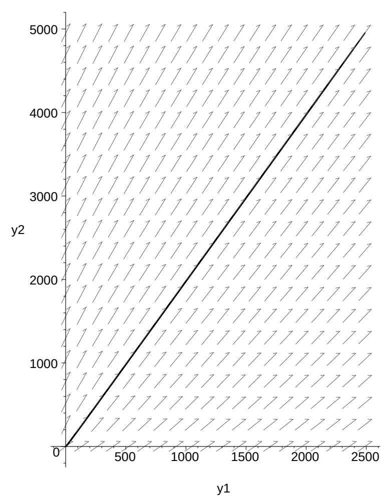


(b)

$$A = \begin{bmatrix} 2 & 1 \\ 2 & 3 \end{bmatrix}$$

$$\begin{aligned} \text{tr } A &= 2 + 3 = 5 > 0 \\ \det A &= ad - bc = 2 * (3) - 1 * 2 = 4 > 0 \\ \lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = \frac{5}{2} \pm \frac{1}{2}\sqrt{25 - 4 * (4)} = \frac{5}{2} \pm \frac{3}{2} = 4, 1 \end{aligned}$$

Hence, (0, 0) is an unstable node.

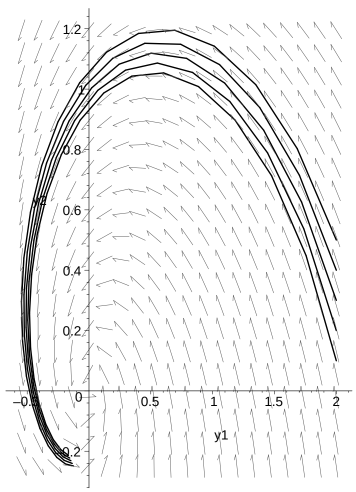


(c)

$$A = \begin{bmatrix} -1 & -2 \\ 2 & -1 \end{bmatrix}$$

$$\begin{aligned}
\text{tr } A &= -1 + (-1) = -2 < 0 \\
\det A &= ad - bc = -1 * (-1) - (-2) * 2 = 5 > 0 \\
\lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = \frac{-2}{2} \pm \frac{1}{2}\sqrt{4 - 4 * (5)} = -1 \pm \frac{1}{2}\sqrt{-16} = -1 \pm 2i
\end{aligned}$$

Hence, $(0, 0)$ is a stable spiral.

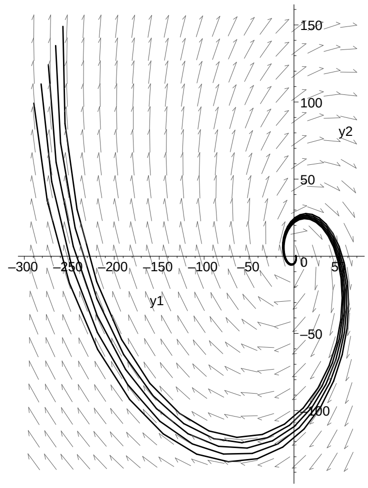


(d)

$$A = \begin{bmatrix} 1 & 2 \\ -2 & 1 \end{bmatrix}$$

$$\begin{aligned}
\text{tr } A &= 1 + 1 = 2 > 0 \\
\det A &= ad - bc = 1 * 1 - 2 * (-2) = 5 > 0 \\
\lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = \frac{2}{2} \pm \frac{1}{2}\sqrt{4 - 4 * (5)} = 1 \pm \frac{1}{2}\sqrt{-16} = 1 \pm 2i
\end{aligned}$$

Hence, $(0,\ 0)$ is an unstable spiral.

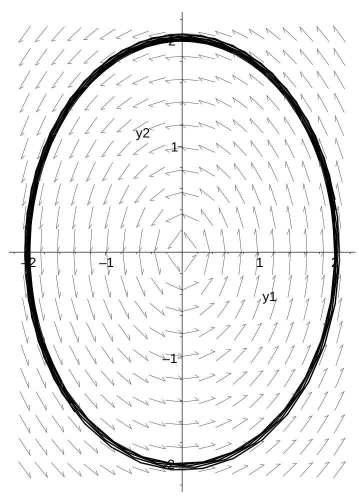


(e)

$$A = \begin{bmatrix} 0 & -2 \\ 2 & 0 \end{bmatrix}$$

$$\begin{aligned}
\text{tr } A &= 0 + 0 = 0 \\
\det A &= ad - bc = 0 * 0 - (-2) * 2 = 4 > 0 \\
\lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = 0 \pm \frac{1}{2}\sqrt{0 - 4 * (4)} = \pm\frac{1}{2}\sqrt{-16} = \pm 2i
\end{aligned}$$

Hence, (0, 0) is a center.



Exercise 3.9.8: A linear system with complex eigenvalues

Thanks to Pandora Lam, University of Alberta, for providing this solution.

We need to show that both $x^{(1)}(t)$ and $x^{(2)}(t)$ satisfy the differential equation

$$\frac{d}{dt}\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} \alpha & \beta \\ -\beta & \alpha \end{bmatrix}\begin{bmatrix} x_1 \\ x_2 \end{bmatrix}.$$

If we let

$$\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = x^{(1)}(t) = \begin{bmatrix} e^{\alpha t}\cos\beta t \\ -e^{\alpha t}\sin\beta t \end{bmatrix},$$

then

$$\begin{aligned}
\frac{d}{dt}\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} &= \begin{bmatrix} \alpha e^{\alpha t}\cos\beta t - \beta e^{\alpha t}\sin\beta t \\ -\alpha e^{\alpha t}\sin\beta t - \beta e^{\alpha t}\cos\beta t \end{bmatrix} \\
&= \begin{bmatrix} \alpha(e^{\alpha t}\cos\beta t) + \beta(-e^{\alpha t}\sin\beta t) \\ -\beta(e^{\alpha t}\cos\beta t) + \alpha(-e^{\alpha t}\sin\beta t) \end{bmatrix} \\
&= \begin{bmatrix} \alpha & \beta \\ -\beta & \alpha \end{bmatrix}\begin{bmatrix} e^{\alpha t}\cos\beta t \\ -e^{\alpha t}\sin\beta t \end{bmatrix} \\
&= \begin{bmatrix} \alpha & \beta \\ -\beta & \alpha \end{bmatrix}\begin{bmatrix} x_1 \\ x_2 \end{bmatrix},
\end{aligned}$$

as required.

Similarly, if we let

$$\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = x^{(2)}(t) = \begin{bmatrix} e^{\alpha t}\sin\beta t \\ e^{\alpha t}\cos\beta t \end{bmatrix},$$

then

$$\begin{aligned}
\frac{d}{dt}\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} &= \begin{bmatrix} \alpha e^{\alpha t}\sin\beta t + \beta e^{\alpha t}\cos\beta t \\ \alpha e^{\alpha t}\cos\beta t - \beta e^{\alpha t}\sin\beta t \end{bmatrix} \\
&= \begin{bmatrix} \alpha(e^{\alpha t}\sin\beta t) + \beta(e^{\alpha t}\cos\beta t) \\ -\beta(e^{\alpha t}\sin\beta t) + \alpha(e^{\alpha t}\cos\beta t) \end{bmatrix} \\
&= \begin{bmatrix} \alpha & \beta \\ -\beta & \alpha \end{bmatrix}\begin{bmatrix} e^{\alpha t}\sin\beta t \\ e^{\alpha t}\cos\beta t \end{bmatrix} \\
&= \begin{bmatrix} \alpha & \beta \\ -\beta & \alpha \end{bmatrix}\begin{bmatrix} x_1 \\ x_2 \end{bmatrix},
\end{aligned}$$

as required.

We now let $x(t) = c_1 x^{(1)}(t) + c_2 x^{(2)}(t)$, and rewrite $x(t)$ in the required form as follows:

$$\begin{aligned} x(t) &= c_1 x^{(1)}(t) + c_2 x^{(2)}(t) \\ &= c_1 \begin{bmatrix} e^{\alpha t}\cos\beta t \\ -e^{\alpha t}\sin\beta t \end{bmatrix} + c_2 \begin{bmatrix} e^{\alpha t}\sin\beta t \\ e^{\alpha t}\cos\beta t \end{bmatrix} \\ &= e^{\alpha t} \begin{bmatrix} c_1\cos\beta t + c_2\sin\beta t \\ -c_1\sin\beta t + c_2\cos\beta t \end{bmatrix}. \end{aligned}$$

Introducing a and ϕ such that $c_1 = a\cos(-\phi)$ and $c_2 = a\sin(-\phi)$, we get

$$\begin{aligned} x(t) &= ae^{\alpha t} \begin{bmatrix} \cos\beta t\cos(-\phi) + \sin\beta t\sin(-\phi) \\ -(\sin\beta t\cos(-\phi) - \cos\beta t\sin(-\phi)) \end{bmatrix} \\ &= ae^{\alpha t} \begin{bmatrix} \cos(\beta t + \phi) \\ -\sin(\beta t + \phi) \end{bmatrix}. \end{aligned}$$

Note that $c_1 = a\cos(-\phi)$ and $c_2 = a\sin(-\phi)$ imply

$$c_1^2 + c_2^2 = a^2\cos^2(-\phi) + a^2\sin^2(-\phi) = a^2,$$

or

$$a = \sqrt{c_1^2 + c_2^2}$$

and

$$\frac{a\sin(-\phi)}{a\cos(-\phi)} = \tan(-\phi) = -\tan(\phi) = \frac{c_2}{c_1},$$

or

$$\phi = \arctan(-\frac{c_2}{c_1}).$$

Exercise 3.9.9: The trace-determinant formula

Given a matrix,

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix},$$

The eigenvalues of A are the λ satisfying $|\lambda I - A| = 0$, where I is the 2×2 identity matrix. Notice that $\mathrm{tr}(A) = a + d$, and $\det(A) = ad - bc$. Hence,

$$\begin{aligned} 0 &= |\lambda I - A| \\ &= (\lambda - a)(\lambda - d) - bc \\ &= \lambda^2 + \lambda(-a - d) + ad - bc \\ &= \lambda^2 - \mathrm{tr}(A)\lambda + \det(A). \end{aligned}$$

From the quadratic formula, we find

$$\lambda_{1/2} = \frac{\mathrm{tr}(A) \pm \sqrt{(\mathrm{tr}(A))^2 - 4\det(A)}}{2}.$$

Q.E.D.

Exercise 3.9.10: Using the trace-determinant formula

Thanks to Pandora Lam, University of Alberta, for providing this solution.

(a)

$$A = \begin{bmatrix} 1 & 5 \\ 3 & 2 \end{bmatrix}$$

$$\begin{aligned} \text{tr } A &= a + d = 1 + 2 = 3 \\ \det A &= ad - bc = 1 * 2 - 5 * 3 = -13 < 0 \\ \lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = \frac{3}{2} \pm \frac{1}{2}\sqrt{9 - 4 * (-13)} = \frac{3}{2} \pm \frac{1}{2}\sqrt{61} \approx 5.41, -2.41 \end{aligned}$$

Hence, (0, 0) is a saddle point.

(b)

$$A = \begin{bmatrix} 0 & -2 \\ 1 & -3 \end{bmatrix}$$

$$\begin{aligned} \text{tr } A &= a + d = 0 + (-3) = -3 < 0 \\ \det A &= ad - bc = 0 * (-3) - 1 * (-2) = 2 > 0 \\ \lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = \frac{-3}{2} \pm \frac{1}{2}\sqrt{9 - 4 * (2)} = \frac{-3}{2} \pm \frac{1}{2} = -1, -2 \end{aligned}$$

Hence, (0, 0) is a stable node.

(c)

$$A = \begin{bmatrix} -2 & 4 \\ -3 & 4 \end{bmatrix}$$

$$\begin{aligned} \text{tr } A &= a + d = -2 + 4 = 2 > 0 \\ \det A &= ad - bc = -2 * 4 - 4 * (-3) = 4 > 0 \\ \lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = \frac{2}{2} \pm \frac{1}{2}\sqrt{4 - 4 * (4)} = 1 \pm \frac{1}{2}\sqrt{-12} = 1 \pm \sqrt{3}i \end{aligned}$$

Hence, (0, 0) is an unstable spiral.

(d)

$$A = \begin{bmatrix} 2 & 1 \\ 1 & 3 \end{bmatrix}$$

$$\begin{aligned} \text{tr } A &= a + d = 2 + 3 = 5 > 0 \\ \det A &= ad - bc = 2 * 3 - 1 * 1 = 5 > 0 \\ \lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = \frac{5}{2} \pm \frac{1}{2}\sqrt{25 - 4 * (5)} = \frac{5}{2} \pm \frac{1}{2}\sqrt{5} \approx 3.62, 1.38 \end{aligned}$$

Hence, (0, 0) is an unstable node.

(e)

$$A = \begin{bmatrix} -2 & -1 \\ 1 & 2 \end{bmatrix}$$

$$\begin{aligned} \text{tr } A &= a + d = -2 + 2 = 0 \\ \det A &= ad - bc = -2 * 2 - (-1) * 1 = -3 < 0 \\ \lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = 0 \pm \frac{1}{2}\sqrt{0 - 4 * (-3)} = \pm\frac{1}{2}\sqrt{12} = \pm\sqrt{3} \end{aligned}$$

Hence, (0, 0) is a saddle point.

(f)

$$A = \begin{bmatrix} -1 & -2 \\ 2 & 1 \end{bmatrix}$$

$$\begin{aligned} \text{tr } A &= a + d = -1 + 1 = 0 \\ \det A &= ad - bc = -1 * 1 - (-2) * 2 = 3 > 0 \\ \lambda_1, \lambda_2 &= \frac{\text{tr } A}{2} \pm \frac{1}{2}\sqrt{(\text{tr } A)^2 - 4 * \det A} = 0 \pm \frac{1}{2}\sqrt{0 - 4 * (3)} = \pm\frac{1}{2}\sqrt{-12} = \pm\sqrt{3}i \end{aligned}$$

Hence, (0, 0) is a center.

Exercise 3.9.11: Two-population model

Thanks to Pandora Lam, University of Alberta, for providing the outline of this solution.

The two-population model, (3.8), is

$$\begin{aligned} \dot{x} &= \alpha x + \beta xy, \\ \dot{y} &= \gamma y + \delta xy. \end{aligned}$$

There are two steady states, namely $P_1 = (0, 0)$ and $P_2 = (-\frac{\gamma}{\delta}, -\frac{\alpha}{\beta})$.

In the solutions shown below, we determine the stability of any biologically relevant steady states. Note that P_1 always is biologically relevant. However, P_2 only is biologically relevant if α and β as well as γ and δ have opposite signs.

Knowing the stability of the steady states will be helpful in sketching the phase portraits, not (yet) provided here.

The Jacobian matrix for the system is

$$J = \begin{bmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} \end{bmatrix} = \begin{bmatrix} \alpha + \beta y & \beta x \\ \delta y & \gamma + \delta x \end{bmatrix}.$$

In general then, the stability of $P_1 = (0,0)$ is determined by

$$J(0,0) = \begin{bmatrix} \alpha & 0 \\ 0 & \gamma \end{bmatrix},$$

with eigenvalues $\lambda_1 = \alpha$ and $\lambda_2 = \gamma$.

Similarly, the stability of $P_2 = (\frac{-\gamma}{\delta}, \frac{-\alpha}{\beta})$ is determined by

$$J(\frac{-\gamma}{\delta}, \frac{-\alpha}{\beta}) = \begin{bmatrix} 0 & \frac{-\beta\gamma}{\delta} \\ \frac{-\alpha\delta}{\beta} & 0 \end{bmatrix},$$

with $\operatorname{tr} J = 0$ and $\det J = -\alpha\gamma$.

(a) Case $\alpha > 0,\ \beta > 0,\ \gamma > 0,\ \delta < 0$

For $P_1 = (0,0)$:
The eigenvalues are $\lambda_{1,2} > 0$, therefore $P_1 = (0,0)$ is an unstable node.

For $P_2 = (\frac{-\gamma}{\delta}, \frac{-\alpha}{\beta})$:
Since α and β have the same sign, P_2 is not biologically relevant.

INSERT PHASE PORTRAIT HERE

Biological interpretation: We have a predator-prey model ...

(b) Case $\alpha > 0,\ \beta > 0,\ \gamma < 0,\ \delta < 0$

For $P_1 = (0,0)$:
The eigenvalues are $\lambda_1 = \alpha > 0$ and $\lambda_2 = \gamma < 0$, therefore $P_1 = (0,0)$ is a saddle point.

For $P_2 = (\frac{-\gamma}{\delta}, \frac{-\alpha}{\beta})$:
P_2 is not biologically relevant.

INSERT PHASE PORTRAIT HERE

Biological interpretation: We have a predator-prey model ...

(c) Case $\alpha < 0,\ \beta > 0,\ \gamma < 0,\ \delta < 0$

For $P_1 = (0,0)$:
The eigenvalues are $\lambda_1 = \alpha < 0$ and $\lambda_2 = \gamma < 0$, therefore $(0,0)$ is a stable node.

For $P_2 = (\frac{-\gamma}{\delta}, \frac{-\alpha}{\beta})$:
P_2 is not biologically relevant.

INSERT PHASE PORTRAIT HERE

Biological interpretation: We have a predator-prey model ...

(d) Case $\alpha > 0,\ \beta > 0,\ \gamma > 0,\ \delta > 0$

For $P_1 = (0,0)$:
The eigenvalues are $\lambda_1 = \alpha > 0$ and $\lambda_2 = \gamma > 0$, therefore $(0,0)$ is an unstable node.

For $P_2 = (\frac{-\gamma}{\delta}, \frac{-\alpha}{\beta})$:
P_2 is not biologically relevant.

INSERT PHASE PORTRAIT HERE

Biological interpretation: We have a mutualism or symbiosis model ...

(e) Case $\alpha > 0,\ \beta > 0,\ \gamma < 0,\ \delta > 0$

For $P_1 = (0,0)$:
The eigenvalues are $\lambda_1 = \alpha > 0$ and $\lambda_2 = \gamma < 0$, therefore $(0,0)$ is a saddle point.

For $P_2 = (\frac{-\gamma}{\delta}, \frac{-\alpha}{\beta})$:
P_2 is not biologically relevant.

INSERT PHASE PORTRAIT HERE

Biological interpretation: We have a mutualism or symbiosis model ...

(f) Case $\alpha > 0,\ \beta < 0,\ \gamma > 0,\ \delta < 0$

For $P_1 = (0,0)$:
The eigenvalues are $\lambda_1 = \alpha > 0$ and $\lambda_2 = \gamma > 0$, therefore $(0,0)$ is an unstable node.

For $P_2 = (\frac{-\gamma}{\delta}, \frac{-\alpha}{\beta})$:
P_2 IS biologically relevant! Since $\mathrm{tr}\ J = 0$ and $\det J = -\alpha\gamma < 0$, $P_2 = (\frac{-\gamma}{\delta}, \frac{-\alpha}{\beta})$ is a saddle point.

INSERT PHASE PORTRAIT HERE

Biological interpretation: We have a competition model ...

(g) Case $\alpha < 0,\ \beta < 0,\ \gamma < 0,\ \delta < 0$

For $P_1 = (0,0)$:
The eigenvalues are $\lambda_1 = \alpha < 0$ and $\lambda_2 = \gamma < 0$, therefore $(0,0)$ is a stable node.

For $P_2 = (\frac{-\gamma}{\delta}, \frac{-\alpha}{\beta})$:
P_2 is not biologically relevant.

INSERT PHASE PORTRAIT HERE

Biological interpretation: We have a competition model ...

Exercise 3.9.12: Predator-prey model

Thanks to Pandora Lam, University of Alberta, for providing this solution.

(a) Let $x(t)$ be the prey population, and $y(t)$ be the natural predator population.

Assuming exponential growth for the prey population in the absense of the predator, and exponential decay for the predator population in the absense of prey, the 2-species interaction model reads

$$\frac{dx}{dt} = \alpha x - \beta xy,$$
$$\frac{dy}{dt} = \gamma y + \delta xy.$$

(b) Let r_1 be the rate that the poison kills the prey population, and r_2 be the rate that the poison kills the predator population.

The new model then reads

$$\frac{dx}{dt} = \alpha x - \beta xy - r_1 x,$$
$$\frac{dy}{dt} = \gamma y + \delta xy - r_2 y.$$

Exercise 3.9.13: Inhibited enzymatic reaction

Let $s = [S]$, $e = [E]$, $b_1 = [B_1]$, $q = [Q]$, $b_2 = [B_2]$, and $i = [I]$.

The first reaction gives the following differential equations:

$$\frac{ds}{dt} = -k_1 se + K_{-1} b_1,$$
$$\frac{de}{dt} = -k_1 se + K_{-1} b_1 + k_2 b_1,$$
$$\frac{db_1}{dt} = k_1 se - K_{-1} b_1 - k_2 b_1,$$
$$\frac{dq}{dt} = k_2 b_1.$$

The second gives the following three equations:

$$\frac{db_2}{dt} = k_1 ei - k_{-1} b_2,$$
$$\frac{de}{dt} = -k_1 ei + k_{-1} b_2,$$
$$\frac{di}{dt} = -k_1 ei + k_{-1} b_2.$$

Exercise 3.9.14: A feedback mechanism for oscillatory reactions

Thanks to Pandora Lam, University of Alberta, for providing this solution.

We are given the following pathway:

$$A \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} B \underset{k_{-2}}{\overset{k_2}{\rightleftharpoons}} C \underset{k_{-3}}{\overset{k_3}{\rightleftharpoons}} A.$$

Let $a = [A],\ b = [B]$, and $c = [C]$.

A differential equation model for the above pathway then is

$$\frac{da}{dt} = k_{-1} b + k_3 c - k_1 a - k_{-3} a,$$
$$\frac{db}{dt} = k_1 a + k_{-2} c - k_{-1} b - k_2 b,$$
$$\frac{dc}{dt} = k_2 b + k_{-3} a - k_{-2} c - k_3 c.$$

Exercise 3.9.15: Enzymatic reaction with two intermediate steps

Thanks to Pandora Lam, University of Alberta, for providing this solution.

We are given the following reaction:

$$S + E \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} C_1 \underset{k_{-2}}{\overset{k_2}{\rightleftharpoons}} C_2 \underset{k_{-3}}{\overset{k_3}{\rightleftharpoons}} E + P.$$

Let $s = [S],\ e = [E],\ c_1 = [C_1],\ c_2 = [C_2]$, and $p = [P]$.

A differential equation model for the above reaction then is

$$\begin{aligned}
\frac{ds}{dt} &= k_{-1}c_1 - k_1 se,\\
\frac{de}{dt} &= k_{-1}c_1 + k_3c_2 - k_1 se - k_{-3}ep,\\
\frac{dc_1}{dt} &= k_1 se + k_{-2}c_2 - k_{-1}c_1 - k_2c_1,\\
\frac{dc_2}{dt} &= k_2c_1 + k_{-3}ep - k_{-2}c_2 - k_3c_2,\\
\frac{dp}{dt} &= k_3c_2 - k_{-3}ep.
\end{aligned}$$

Exercise 3.9.16: Self-intoxicating population

Thanks to Pandora Lam, University of Alberta, for providing this solution.

We are working with the following system:

$$\begin{aligned}
\dot{n} &= (\alpha - \beta - Ky)n,\\
\dot{y} &= \gamma n - \delta y.
\end{aligned}$$

To avoid having to consider all sorts of special cases in the solution below, we assume $\alpha, \beta, \gamma, \delta, K > 0$ instead of $\alpha, \beta, \gamma, \delta, K \geq 0$.

(a) The term αn represents birth, increasing the population.
The term $-\beta n$ represents natural death, decreasing the population.
The term $-Kyn$ represents death due to a toxic environment, decreasing the population.

The term γn represents the production of waste products, proportional to the size of the population.
The term $-\delta y$ represents natural degradation of the waste products.

(b) We begin with the nullclines.

There are two n-nullclines, given by $\dot{n} = 0$, namely the vertical line

$$n = 0$$

and the horizontal line

$$y = \frac{\alpha - \beta}{K}.$$

Similarly, there is one y-nullcline, given by $\dot{y} = 0$, namely the straight line passing through the origin (with positive, finite slope γ/δ)

$$y = \frac{\gamma}{\delta} n.$$

We now find steady states by looking for all the intersections of an n-nullcline with a y-nullcline.

The intersection of the first n-nullcline, $n = 0$, and the y-nullcline is given by the solution of $n = 0$ and $y = \gamma n/\delta$, that is, at

$$P_1 := (n, y) = (0, 0).$$

The intersection of the second n-nullcline, $y = (\alpha - \beta)/K$, and the y-nullcline is given by the solution of $y = (\alpha - \beta)/K$ and $y = \gamma n/\delta$, that is, at

$$P_2 := (n, y) = \left(\frac{\delta}{\gamma}\frac{\alpha - \beta}{K}, \frac{\alpha - \beta}{K}\right).$$

We will refer to P_1 as the trivial steady state and P_2 as the nontrivial (coexistence) steady state. Note that P_2 is biologically relevant only provided $\alpha > \beta$.

We think it doesn't make sense to sketch a phase portrait here (since there are too many cases, and not all information has been determined yet). It should come later, in part (e).

(c) We think it doesn't make sense to sketch a vector field here (since there are too many cases, and not all information has been determined yet). It should come later, in part (e).

(d) The Jacobian matrix of the system is

$$J(n, y) = \begin{bmatrix} \frac{\partial f_1}{\partial n} & \frac{\partial f_1}{\partial y} \\ \frac{\partial f_2}{\partial n} & \frac{\partial f_2}{\partial y} \end{bmatrix} = \begin{bmatrix} \alpha - \beta - Ky & -Kn \\ \gamma & -\delta \end{bmatrix}$$

The stability of P_1 is determined by

$$J(0, 0) = \begin{bmatrix} \alpha - \beta & 0 \\ \gamma & -\delta \end{bmatrix}.$$

The eigenvalues of $J(0, 0)$ are $\lambda_1 = \alpha - \beta$ and $\lambda_2 = -\delta < 0$.

If $\alpha < \beta$, then P_1 is the only biologically relevant steady state. In this case, $\lambda_1 < 0$, and P_1 is a stable node.

If $\alpha > \beta$, then both steady states are relevant. In this case, $\lambda_1 > 0$, and P_1 is a saddle point.

Similarly, the stability of P_2 is determined by

$$J\left(\frac{\delta}{\gamma}\frac{\alpha - \beta}{K}, \frac{\alpha - \beta}{K}\right) = \begin{bmatrix} 0 & -\frac{\delta}{\gamma}(\alpha - \beta) \\ \gamma & -\delta \end{bmatrix}.$$

We have $\operatorname{tr} J = -\delta < 0$ and $\det J = \delta(\alpha - \beta)$.

If $\alpha < \beta$, then $\det J < 0$, and P_2 is a saddle point (but in this case, P_2 is not biologically relevant).

If $\alpha > \beta$, then $\det J > 0$, and P_2 is either a stable node or a stable spiral.

To summarize what we have so far:

If $\alpha < \beta$, then P_1 is the only relevant steady state, and it is a stable node.

If $\alpha > \beta$, then both P_1 and P_2 are biologically relevant. In this case, P_1 is a saddle point, and P_2 is a stable node or a stable spiral.

For P_2 to be a stable node, we need $(\text{tr } J)^2 - 4 \det J > 0$, that is $\delta^2 - 4\delta(\alpha - \beta) > 0$, or $\delta > 4(\alpha - \beta) > 0$.

Similarly, for P_2 to be a stable spiral, we need $(\text{tr } J)^2 - 4 \det J < 0$, or $\delta < 4(\alpha - \beta)$.

(e) Here we look at one of the cases determined above, namely when $\delta < 4(\alpha - \beta)$. In this case, P_1 is a saddle point, and P_2 is a stable spiral.

INSERT VECTOR FIELD AND PHASE PORTRAIT HERE

Interpretation in terms of the biology: Starting from any initial population (other than zero), the population and amount of toxicity eventually reach a steady state. That is, under ideal conditions (no stochasticity), the population persists, no matter how much waste it produces. The steady state is reached in a damped oscillatory fashion. However, depending on the initial conditions, trajectories may pass close to the first n-nullcline, $n = 0$. When this happens, n is very small. That is, in the presence of stochastic events, the population could become extinct.

(f) Solution not available.

Exercise 3.9.17: Fish populations in a pond

(a) Exponential growth:

$$\frac{dT}{dt} = r_T T$$

(b) Growth with competition:

$$\frac{dT}{dt} = (-mB + r_T)T$$

(c) Exponential growth:

$$\frac{dB}{dt} = r_B b$$

Growth with competition:

$$\frac{dB}{dt} = (-nT + r_B)B$$

(d) Solution not available.

(e) We get the system

$$\frac{dT}{dt} = r_T T - mBT,$$
$$\frac{dB}{dt} = r_B B - nBT.$$

The steady states are determined by $dT/dt = dB/dt = 0$. This means that any steady state $(\tilde{T}, \tilde{B})$ must satisfy

$$r_T \tilde{T} = m\tilde{B}\tilde{T},$$
$$r_B \tilde{B} = n\tilde{B}\tilde{T}.$$

Therefore, we get the trivial steady state,

$$(\tilde{T}, \tilde{B}) = (0, 0),$$

and the nontrivial steady state,

$$(\tilde{T}, \tilde{B}) = (\frac{r_B}{n}, \frac{r_T}{m}).$$

The jacobian matrix of this system, evaluated at the nontrivial steady state, is

$$J\left(\frac{r_B}{n}, \frac{r_T}{m}\right) = \begin{pmatrix} r_T - m\tilde{B} & -m\tilde{T} \\ & \\ -n\tilde{B} & r_B - n\tilde{T} \end{pmatrix} = \begin{pmatrix} 0 & -\frac{mr_B}{n} \\ & \\ -\frac{nr_T}{m} & 0 \end{pmatrix}.$$

Exercise 3.9.18: Exact solution for the logistic equation

(a) We have

$$N' = \mu N\left(1 - \frac{N}{K}\right), \quad N(0) = N_0.$$

Solution method 1: We recognize the differential equation as a separable equation, so that we can write

$$\int_{N_0}^{N(t)} \frac{d\bar{N}}{\bar{N}\left(1 - \frac{\bar{N}}{K}\right)} = \int_0^t \mu \, d\bar{t}.$$

Using partial fractions, we can rewrite the left hand side:

$$\int_{N_0}^{N(t)} \left[\frac{1}{\bar{N}} + \frac{\frac{1}{K}}{1 - \frac{\bar{N}}{K}}\right] d\bar{N} = \int_0^t \mu \, d\bar{t}.$$

We integrate to obtain

$$\begin{aligned}
\left[\ln \bar{N} - \ln\left(1 - \frac{\bar{N}}{K}\right)\right]_{N_0}^{N(t)} &= \mu t \\
\ln\left(\frac{\bar{N}}{1-\frac{\bar{N}}{K}}\right)_{N_0}^{N(t)} &= \mu t \\
\ln\left(\frac{N(t)}{1-\frac{N(t)}{K}}\right) - \ln\left(\frac{N_0}{1-\frac{N_0}{K}}\right) &= \mu t \\
\ln\left(\frac{\left(1-\frac{N_0}{K}\right)N(t)}{\left(1-\frac{N(t)}{K}\right)N_0}\right) &= \mu t.
\end{aligned}$$

Exponentiating both sides and rearranging gives

$$\begin{aligned}
\frac{K-N_0}{K-N(t)}\,N(t) &= N_0 e^{\mu t} \\
(K-N_0)N(t) &= N_0 e^{\mu t}(K-N(t)) \\
(K-N_0+N_0e^{\mu t})N(t) &= N_0 K e^{\mu t} \\
N(t) &= \frac{N_0 K e^{\mu t}}{K-N_0+N_0 e^{\mu t}} \\
&= \frac{e^{\mu t} N_0}{1+\frac{N_0}{K}(e^{\mu t}-1)}.
\end{aligned}$$

Solution method 2: Let $u = \frac{1}{N}$. Then $N = \frac{1}{u}$ and

$$\frac{dN}{dt} = -\frac{1}{u^2}\frac{du}{dt}.$$

Substitution into the logistic equation gives

$$\begin{aligned}
-\frac{1}{u^2}\frac{du}{dt} &= \mu\frac{1}{u}\left(1-\frac{1}{K}\frac{1}{u}\right) \\
\frac{du}{dt} &= \mu\left(\frac{1}{K}-u\right).
\end{aligned}$$

We separate variables and integrate, as follows:

$$\begin{aligned}
\int_{u_0}^{u(t)} \frac{d\bar{u}}{\frac{1}{K}-\bar{u}} &= \int_0^t \mu\, d\bar{t} \\
-\ln\left(\frac{1}{K}-\bar{u}\right)\Big|_{u_0}^{u(t)} &= \mu t \\
-\ln\left(\frac{1}{K}-u(t)\right)+\ln\left(\frac{1}{K}-u_0\right) &= \mu t \\
\ln\left(\frac{\frac{1}{K}-u_0}{\frac{1}{K}-u(t)}\right) &= \mu t \\
\frac{1-Ku_0}{1-Ku(t)} &= e^{\mu t} \\
1-Ku(t) &= (1-Ku_0)e^{-\mu t} \\
u(t) &= \frac{1}{K}\left[1-(1-Ku_0)e^{-\mu t}\right].
\end{aligned}$$

Now we return to original variables, as follows:

$$\begin{aligned}
\frac{1}{N(t)} &= \frac{1}{K}\left[1-\left(1-K\frac{1}{N_0}\right)e^{-\mu t}\right] \\
N(t) &= \frac{K}{1-\left(1-\frac{K}{N_0}\right)e^{-\mu t}} \\
&= \frac{Ke^{\mu t}}{e^{\mu t}-1+\frac{K}{N_0}} \\
&= \frac{e^{\mu t}N_0}{\frac{N_0}{K}e^{\mu t}-\frac{N_0}{K}+1} \\
&= \frac{e^{\mu t}N_0}{1+\frac{N_0}{K}(e^{\mu t}-1)}.
\end{aligned}$$

(b) This solution is of the same form as that of the Beverton-Holt model, except we have $e^{\mu t}$ in place of r^{n+1}.

4.5 Exercises for PDEs

Exercise 4.5.1: Diffusion through a membrane

$$u_t = Du_{xx}, \quad u_t = 0$$

(a) $u_{xx} = 0 \Rightarrow u_x = \text{const} = c \Rightarrow u(x) = cx + d$

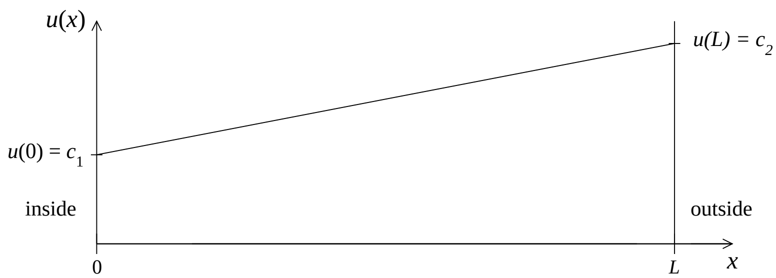
Boundary conditions:

$$u(0) = c_1 \Rightarrow d = c_1$$
$$u(L) = c_2 \Rightarrow cL + c_1 = c_2 \Rightarrow c = \frac{c_2 - c_1}{L}$$

Solution:

$$u(x) = \frac{c_2 - c_1}{L}x + c_1$$

For $c_2 > c_1$:



(b) $J(x) = -D\frac{\partial}{\partial x}u(x) = -D\frac{c_2-c_1}{L} = -\frac{D}{L}(c_2-c_1)$. The flux is proportional to the concentration difference. The proportionality factor $\frac{D}{L}$ is called *permeability.*

Exercise 4.5.2: Fundamental solution

Solution not available.

Exercise 4.5.3: Signalling in ant populations

$$u_t = Du_{xx}, \quad u(0) = \alpha\delta_0(x), \quad D = 1 \tag{4.10}$$

(a) Fundamental solution of $\{u_t = Du_{xx}, u(0) = \delta_0(x)\}$ is $g(x) = \frac{1}{\sqrt{2\pi t}}e^{-\frac{x^2}{4t}}$. Hence $u(x) = \alpha g(x)$ solves (4.10).

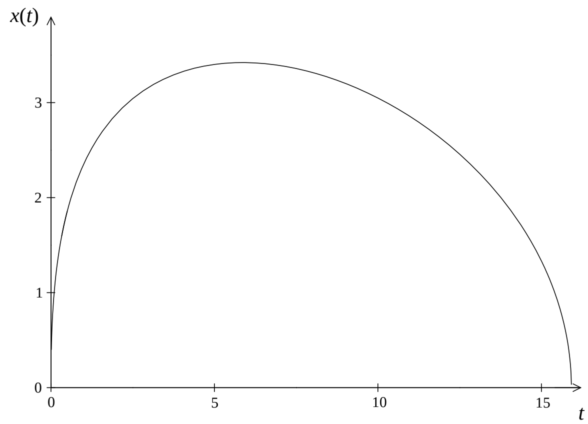
At $x(t)$: $u(x(t)) = 0.1 \cdot \alpha = \alpha g(x)$

$$\Rightarrow g(x) = \frac{1}{10},\ e^{-\frac{x^2}{4t}} = \frac{\sqrt{2\pi t}}{10},\ e^{\frac{x^2}{4t}} = \frac{10}{\sqrt{2\pi t}},\ x^2 = 4t\ln\left(\frac{10}{\sqrt{2\pi t}}\right)$$

$$\Rightarrow x(t) = \sqrt{4t\ln\left(\frac{10}{\sqrt{2\pi t}}\right)}$$

(b)

Range of Influence



(c) $x(t)$ defined only for $\ln\left(\frac{10}{\sqrt{2\pi t}}\right) > 0$, hence $\frac{10}{\sqrt{2\pi t}} > 1$. So

$$10 > \sqrt{2\pi t},\ 100 > 2\pi t,\ \frac{50}{\pi} > t$$

$$\Rightarrow t^* = \frac{50}{\pi} \approx 15.9$$

Exercise 4.5.4: Dingos in Australia

(Thanks to Dr. Markus Owen (Nottingham), who used this problem in one of his Math-bio classes).

$$u_t = Du_{xx} + ku(1-u), \qquad k = 1$$

(a) $D_1 = 100$, wave speed of a travelling wave,

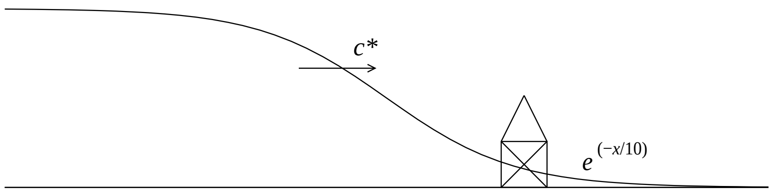
$$\begin{aligned} c^* &= 2\sqrt{D_1 f'(0)}, \quad f'(0) = k = 1 \\ &= 2\sqrt{D_1} = 20 \quad \left(\frac{\text{miles}}{\text{month}}\right) \end{aligned}$$

distance = 100 miles $\Rightarrow T = \frac{100 \text{ miles}}{c^*} = \frac{100}{20} = 5$ months.

The *decay rate* of this wave front is:

$$\lambda_1 = -\frac{c^*}{2D_1} = -\frac{10}{100} = -\frac{1}{10},$$

The wave looks like $e^{-\frac{1}{10}x}$ near farm A.

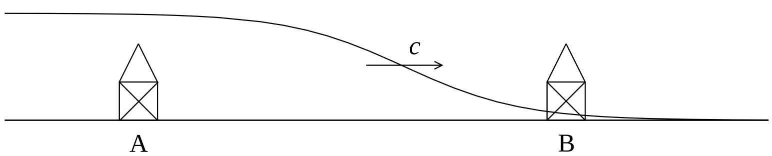


(b) Between A and B: $D_2 = 50$

Decay rate $\lambda_1 = -\frac{1}{10} = -\frac{c}{2D_2}$

$$\Rightarrow \text{ wave speed} = c = -\lambda_1 2D_2 = \frac{1}{10} \cdot 2 \cdot 50 = 10$$

$$\Rightarrow T_2 = 10 \text{ months from farm } A \text{ to } B.$$



Exercise 4.5.5: Signal transport in the axon

$$u_t = u_{xx} + u(1-u)(u-\frac{1}{2})$$
$$u_x(t,0) = 0, \quad u_x(t,l) = 0$$

(a) Steady states: $u_t = 0$. Introduce $v := u_x$.

$$u_x = v$$
$$v_x = -u(1-u)(u-\frac{1}{2}) = u^3 - \frac{3}{2}u^2 + \frac{1}{2}u$$

(b) equlibria of (a): $v = 0$, $u = 0$, 1, $\frac{1}{2}$.

Jacobian:

$$Df(u,v) = \begin{pmatrix} 0 & 1 \\ 3u^2 - 3u + \frac{1}{2} & 0 \end{pmatrix}$$

$$Df(0,0) = \begin{pmatrix} 0 & 1 \\ \frac{1}{2} & 0 \end{pmatrix},\ \mathrm{tr}(Df(0,0)) = 0,\ \det(Df(0,0)) < 0 \Rightarrow \textit{saddle}$$

$$Df(\frac{1}{2},0) = \begin{pmatrix} 0 & 1 \\ \frac{3}{4} - \frac{3}{2} + \frac{1}{2} & 0 \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ -\frac{1}{4} & 0 \end{pmatrix}$$

$$\mathrm{tr}(Df(\frac{1}{2},0)) = 0, \quad \det(Df(\frac{1}{2},0)) > 0 \Rightarrow \textit{center}$$

$$Df(1,0) = \begin{pmatrix} 0 & 1 \\ \frac{1}{2} & 0 \end{pmatrix},\ \mathrm{tr}(Df(0,0)) = 0,\ \det(Df(0,0)) < 0 \Rightarrow \textit{saddle}$$

(c) Hamilton function if

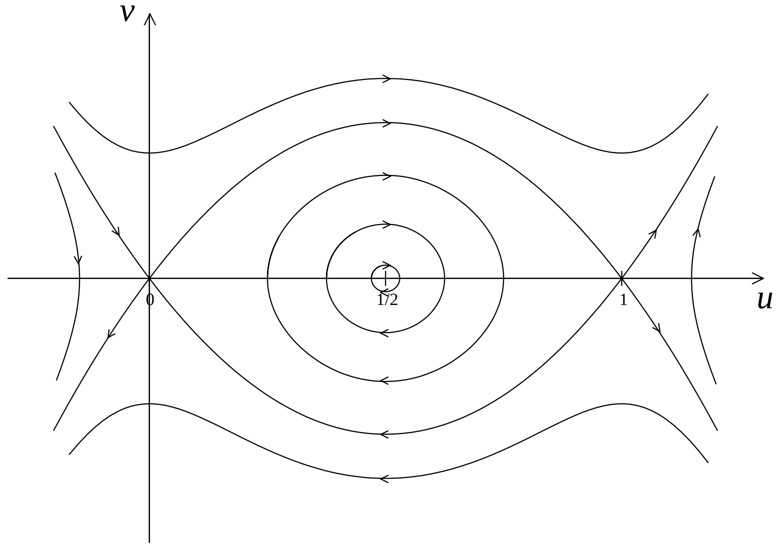
$$\frac{d}{dx}H(u,v) = 0 \qquad \text{and} \qquad u_x = \frac{\partial H}{\partial v},\ v_x = -\frac{\partial H}{\partial u},$$

Here $H(u,v) = \frac{1}{2}(v)^2 - \frac{1}{4}u^4 + \frac{1}{2}u^3 - \frac{1}{4}u^2$.

Let's check:

$$\begin{aligned} \frac{\partial H}{\partial v} &= v = u_x \checkmark \\ \frac{\partial H}{\partial u} &= -u^3 - \frac{3}{2}u^2 - \frac{1}{2}u = -v_x \checkmark \\ \frac{d}{dx}H(u,v) &= \frac{\partial H}{\partial u}\frac{du}{dx} + \frac{\partial H}{\partial v}\frac{dv}{dx} = -v_x u_x + u_x v_x = 0. \end{aligned}$$

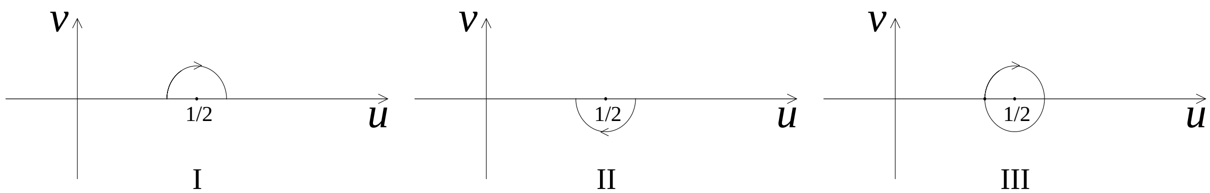
(d)



(e) Neumann boundary conditions:

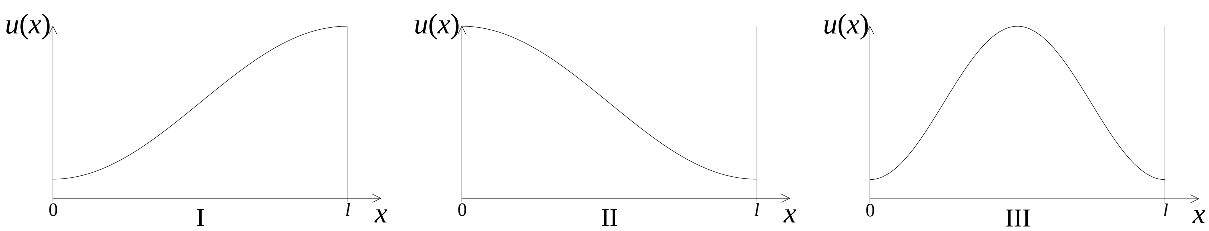
$$v(0) = 0 \qquad v(l) = 0$$

Following candidates in the phase-portrait of (d):

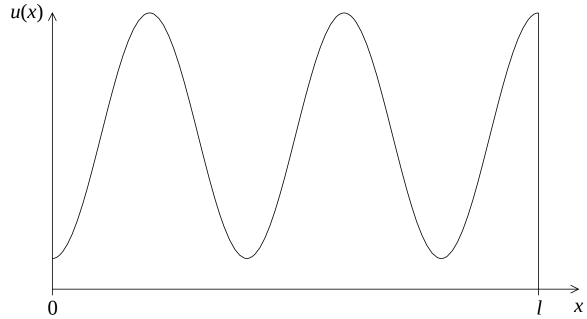


etc.

As functions of x:



etc.



$$a = 9$$
$$a = 8 + 1$$

(4.11)

(f) Solution not available.

Exercise 4.5.6: Separation

Solution not available.

Exercise 4.5.7: Linear transport

Solution not available.

Exercise 4.5.8: Correlated random walk

Solution not available.