Ordinary Differential Equations and Introduction to Dynamical Systems

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Overview

- Single Species Systems
  - Solving for Equilibria
  - Evaluating Stability of Equilibria Graphically
- Two Species Systems
  - Lotka-Volterra Predator-Prey
  - Evaluating Stability of Equilibria
- Examples from Epidemiology

Single Species Systems

- Exponential Growth
- Logistic Growth
- Other Equations

Exponential Growth

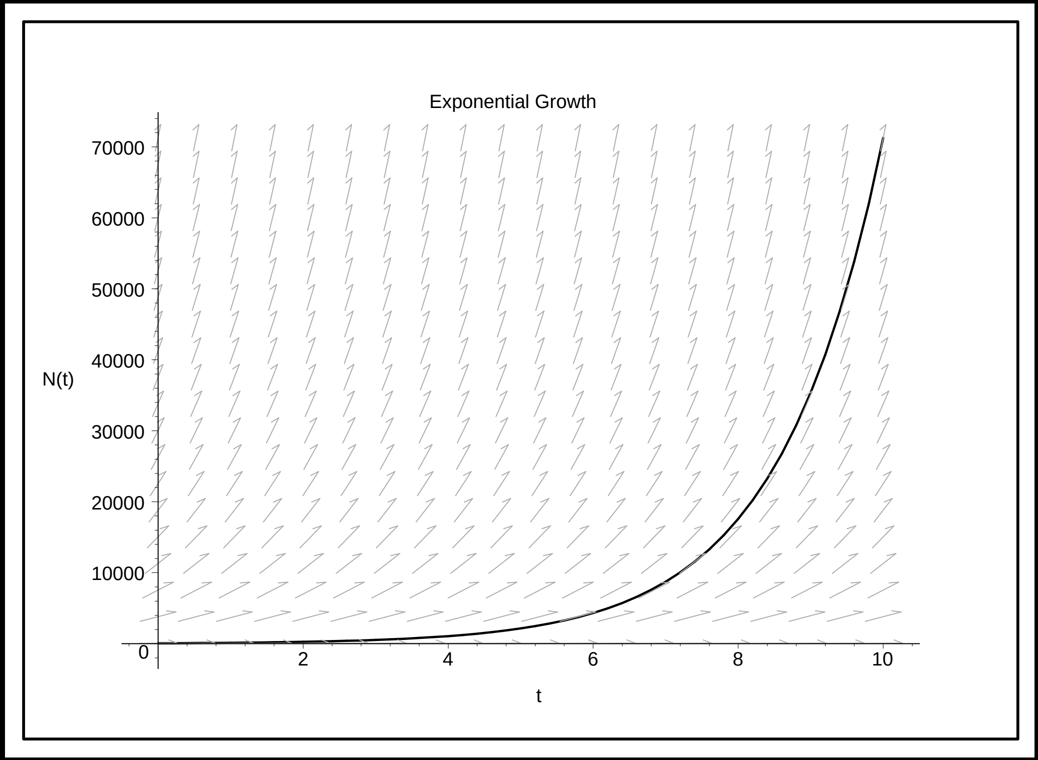
$$\frac{dN}{dt} = rN$$

Solution:

$$N(t) = N_0 e^{rt}$$

What happens to this population?

Exponential Growth



Logistic Growth

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

What do you think the solutions of this will look like?
Recall exponential growth was

$$\frac{dN}{dt} = rN$$

Equilibria

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

$$\frac{dN}{dt} = 0$$

$$rN^*\left(1 - \frac{N^*}{K}\right) = 0$$

$$N^* = 0 \quad or \quad N^* = K$$

Stability of Equilibria

First evaluate the stability of $N^* = 0$.
Near $N^* = 0$,

$$\frac{dN}{dt} \approx rN$$

So as N increase, $\frac{dN}{dt}$ grows exponentially.
Therefore, $N^* = 0$ is an unstable equilibrium.

Stability of Equilibria

What do you think will happen near $N^* = K$?

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

Stability near K

If N is just slightly above K,

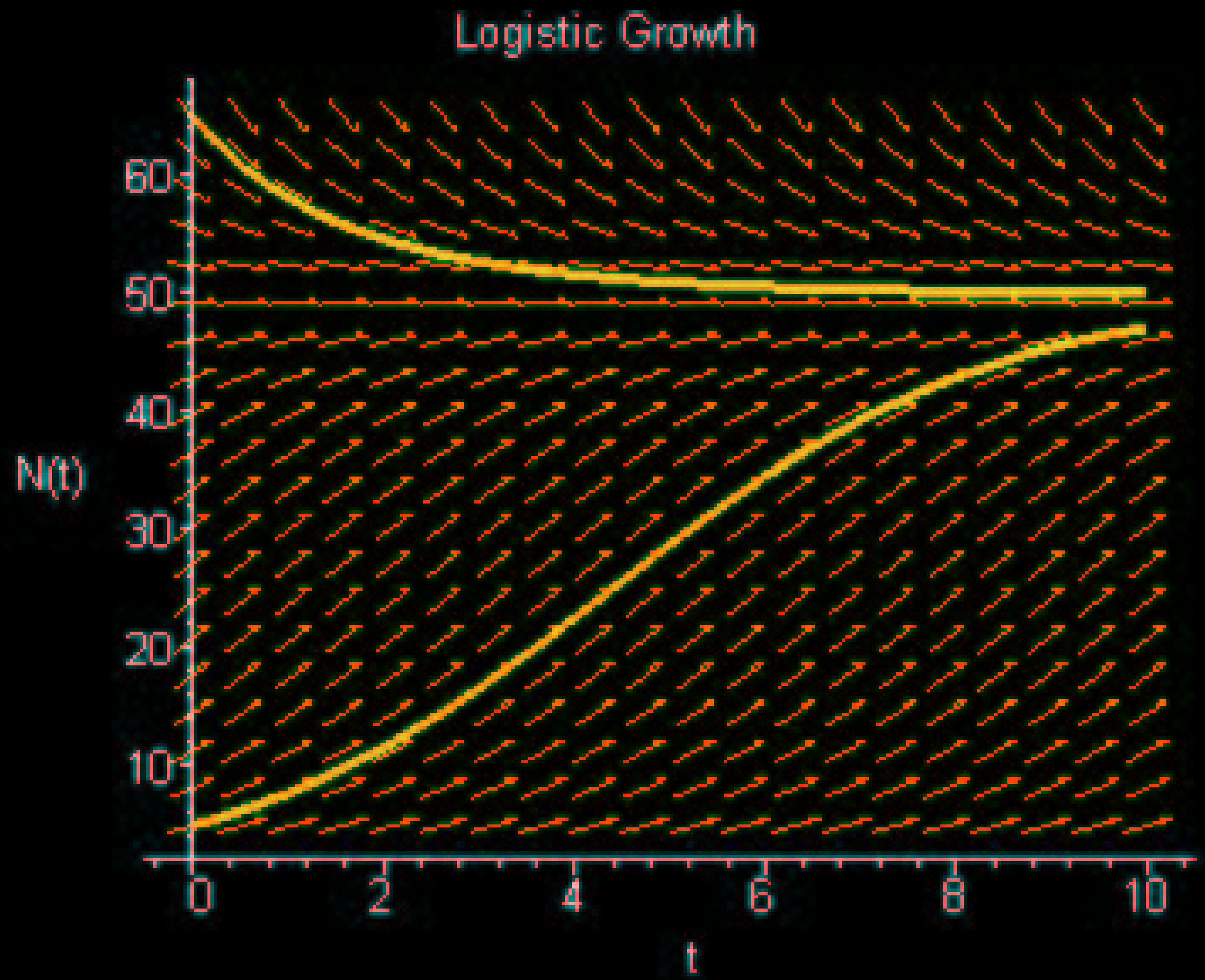
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) < 0$$

but if N is just slightly below K,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) > 0$$

Therefore, $N^* = K$ is stable.

Graphical View of Stability



Other Alternatives

- Gompertz Equation

$$\frac{dN}{dt} = r_0 e^{-\alpha t} N$$

- Delay or lag time

$$\frac{dN}{dt} = F(N(t), N(t-T))$$

Other Alternatives

- Allee effect

$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right)\left(\frac{N}{K_0}-1\right)$$

- Discrete time

$$N(t+1) = F(N(t))$$

- Stochastic processes

Interacting Populations

- Predator-prey models
- Competition
- Mutualism

Classic Predator-Prey

Lotka-Volterra Predator-Prey Model

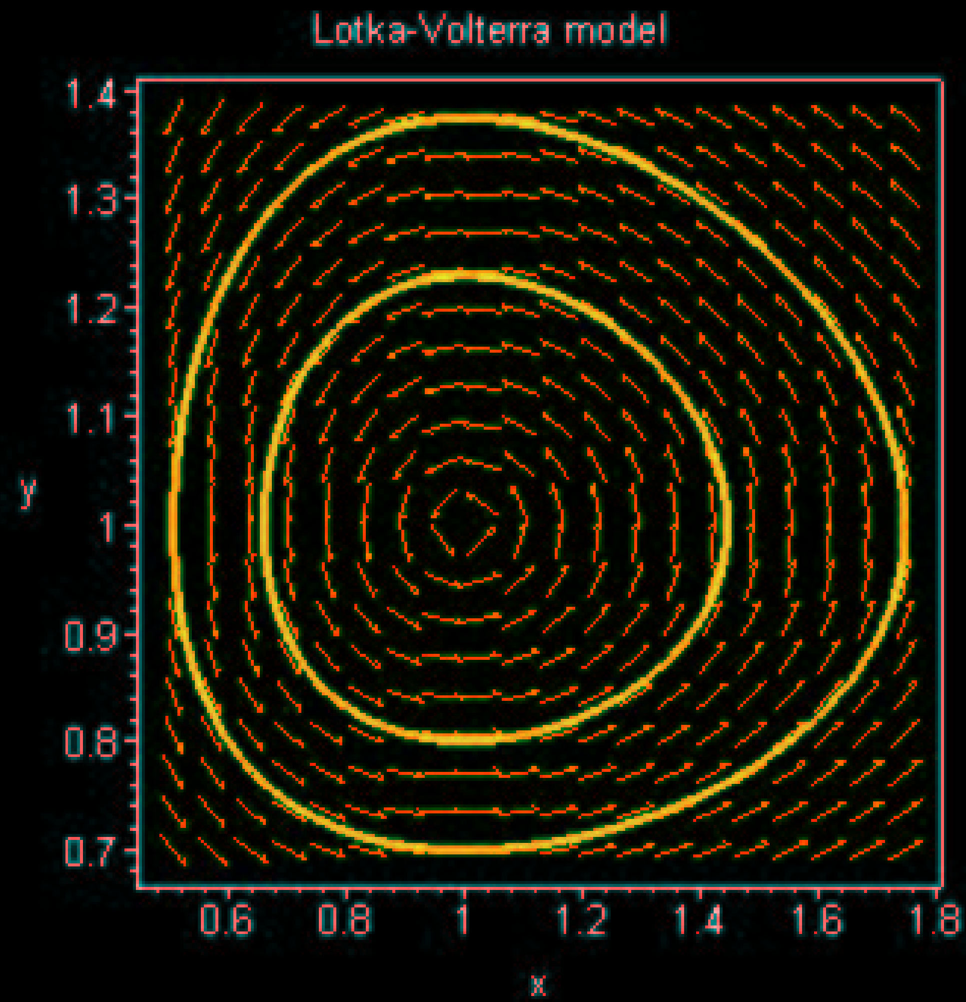
$$\frac{dN}{dt} = rN - cNP$$
$$\frac{dP}{dt} = bNP - mP$$

Classic Predator-Prey

Lotka-Volterra Predator-Prey Model

- Historical interest
- Mass-action term
- Bad mathematical model
- Structurally unstable

Lotka-Volterra Phase Plane



Interacting Populations

More Realistic Predator-prey models

$$\begin{aligned}\frac{dN}{dt} &= rN\left(1-\frac{N}{K}\right)-P\left(\frac{A}{N+B}\right)\\ \frac{dP}{dt} &= eP\left(\frac{A}{N+B}\right)-dP\end{aligned}$$

Interacting Populations

Another More Realistic Predator-prey models

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - P\left(\frac{AN}{N^2 + B^2}\right)$$

$$\frac{dP}{dt} = eP\left(\frac{AN}{N^2 + B^2}\right) - dP$$

Interacting Populations

Competition

$$
\begin{aligned}
\frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right) \\
\frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_2}\right)
\end{aligned}
$$

Interacting Populations

Mutualism

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1\left(1-\frac{N_1}{K_1}+b_{12}\frac{N_2}{K_1}\right)\\ \frac{dN_2}{dt} &= r_2 N_2\left(1-\frac{N_2}{K_2}+b_{21}\frac{N_1}{K_2}\right)\end{aligned}$$

Interacting Populations

To analyze these types of models

- Nondimensionalize the system
  - reduce the number of parameters
  - simplfy the system
- Solve for equilibria
- Analyze stability of equilibria
- Translate back to determine biological significance

Phase-Plane Techniques

Some defintions of stability

- Stable - if start small distance from equilibrium, remain small distance as $t \to \infty$
  - Lyapunov stable
  - locally stable
- Asymptotically stable - if start small distance from equilibrium, distance from equilibrium approaches zero as $t \to \infty$
  - locally asymptotically stable

Phase-Plane Techniques

- Linearization
- Bendixson-Dulac negative criterion
- Hopf bifurcation theorem
- Poincaré-Bendixson theorem
- Routh-Hurwitz Conditions

Linearization

Given:

$$\begin{aligned}\frac{dN}{dt} &= F(N,P)\\ \frac{dP}{dt} &= G(N,P)\end{aligned}$$

Linearization

Solve:

$$
\begin{aligned}
F(N^*, P^*) &= 0 \\
G(N^*, P^*) &= 0
\end{aligned}
$$

to find the equilibria, (N^*, P^*).

Let:

$$
\begin{aligned}
x(t) &= N(t) - N^* \\
y(t) &= P(t) - P^*
\end{aligned}
$$

Linearization

Then linearize about the equilibrium:

$$\frac{dx}{dt} = \left.\frac{\partial F}{\partial N}\right|_{(N^*,P^*)} x + \left.\frac{\partial F}{\partial P}\right|_{(N^*,P^*)} y$$

$$\frac{dy}{dt} = \left.\frac{\partial G}{\partial N}\right|_{(N^*,P^*)} x + \left.\frac{\partial F}{\partial P}\right|_{(N^*,P^*)} y$$

Or:

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

Linearization

Let:

$$J = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

Where J is known as the Jacobian matrix or the community matrix.
We now look for solutions of the form:

$$\begin{aligned} x(t) &= x_0 e^{\lambda t} \\ y(t) &= y_0 e^{\lambda t} \end{aligned}$$

Linearization

Substitute this back into the equations to obtain:

$$\begin{aligned} \lambda x_0 &= a_{11}x_0 + a_{12}y_0 \\ \lambda y_0 &= a_{21}x_0 + a_{22}y_0 \end{aligned}$$

or

$$\begin{pmatrix} a_{11}-\lambda & a_{12} \\ a_{21} & a_{22}-\lambda \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix} = 0$$

Linearization

From this, we obtain the characteristic equation

$$\lambda^2 - (a_1{}^1 + a_{22})\,\lambda + (a_{11}a_{22} - a_{12}a_{21}) \;=\; 0$$

Solving for the two roots of λ will determine the stability of the system.

Linearization

- If both roots of λ are real and negative, the equilibrium is a stable node.
- If both roots of λ are real and positive, the equilibrium is an unstable node.
- If the roots of λ are real and of opposite signs, the equilibrium is a saddle point.

Linearization

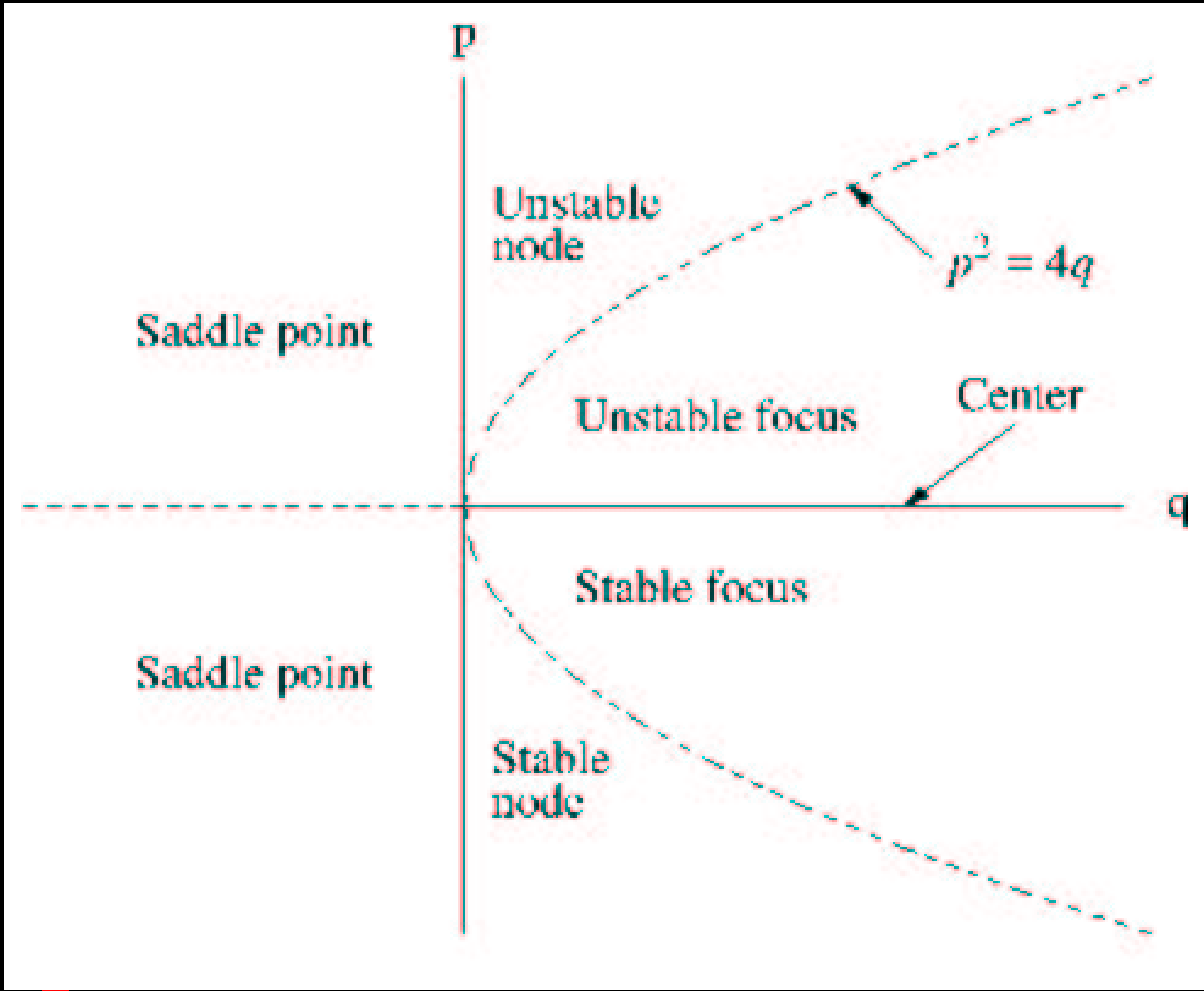
- If the roots of λ are complex with negative real parts, the equilibrium is a stable focus.
- If the roots of λ are complex with positive real parts, the equilibrium is an unstable focus.
- If the roots of λ are purely complex, the equilibrium of the linearized system is a center, but the original nonlinear system will have a center or a stable or unstable focus depending upon the exact nature of the nonlinear terms.

Routh-Hurwitz conditions

Routh-Hurwitz conditions give the necessary and sufficient conditions for all roots of the characteristic polynomial to have negative real roots thus implying asymptotic stability.

$$
\begin{aligned}
p = TrJ = a_11 + a_22 &< 0 \\
q = detJ = a_11a_22 - a_12a_21 &> 0
\end{aligned}
$$

Stability



p
q
Unstable
node
$p^2 = 4q$
Saddle point
Unstable focus
Center
Stable focus
Saddle point
Stable
node

Bendixson negative criterion

Bendixson's negative criterion

Consider the dynamical system, $\frac{dx}{dt} = F(x,y), \frac{dy}{dt} = G(x,y)$, where F and G are continuously differentiable functions on some simply connected domain $D \subset \Re^2$. If $\nabla \cdot (F,G) = \frac{\partial F}{\partial x} + \frac{\partial G}{\partial y}$ is of one sign in D, there cannot be a closed orbit contained within D.

Bendixson-Dulac negative criterion

Additionally, we have the Bendixson's-Dulac's negative criterion.

Let B be a smooth function on $D \subset \Re^2$ (with above assumptions). If $\nabla \cdot (BF, BG) = \frac{\partial BF}{\partial x} + \frac{\partial BG}{\partial y}$ is of one sign in D, there cannot be a closed orbit contained within D.

Other theorems

- The Hopf bifurcation theorem gives conditions necessary for the existence of real periodic solutions of a real system of ordinary differential equations.
- Poincaré-Bendixson theorem can also be used to prove the existence of periodic orbits.

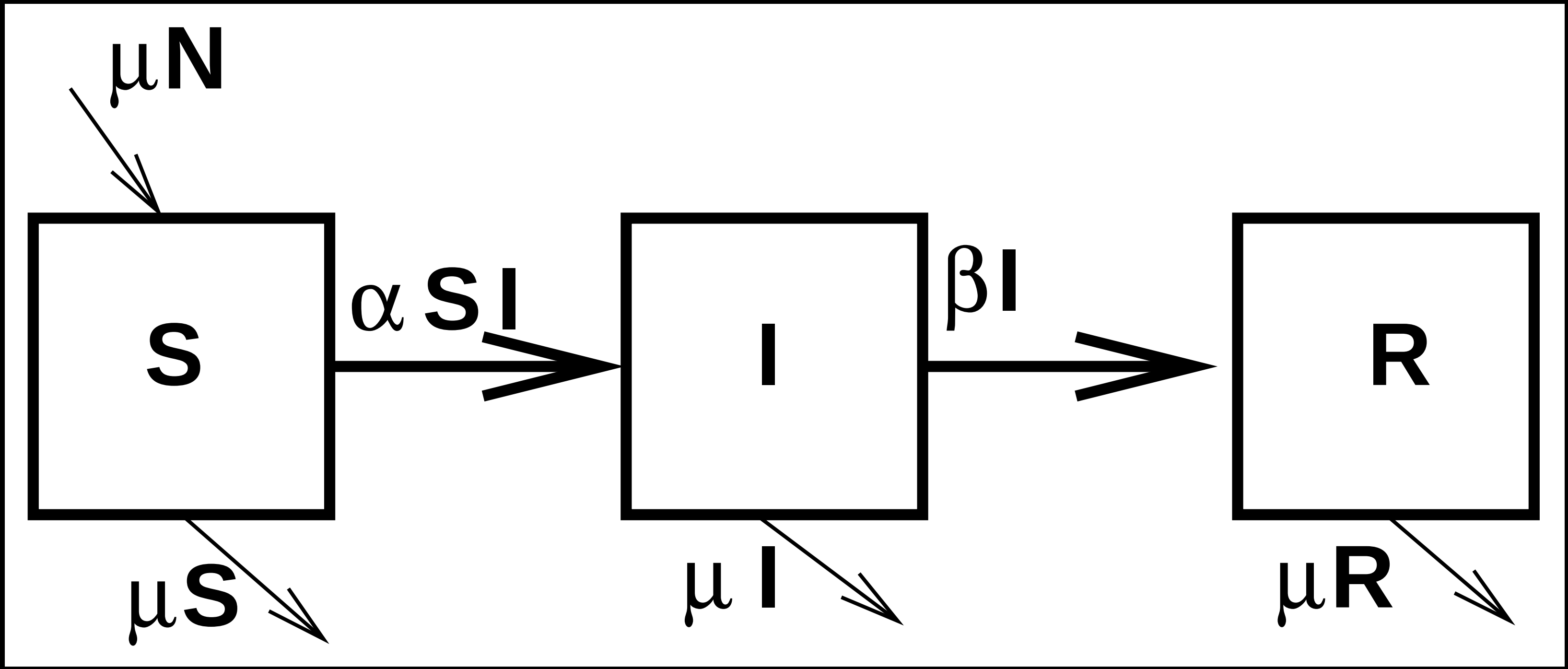
Examples from Epidemiology

Divide population up into distinct classes

- $S =$ Susceptibles
- $I =$ Infectives
- $R =$ Recovered

Classes used depend on disease dynamics

SIR Model



SIR Model - constant population

$$
\begin{aligned}
\frac{dS}{dt} &= \mu(S+I+R) - \alpha SI - \mu S \\
\frac{dI}{dt} &= \alpha SI - \beta I - \mu I \\
\frac{dR}{dt} &= \beta I - \mu R \\
N &= S+I+R
\end{aligned}
$$

$S(0) = S_0, I(0) = I_0, R(0) = 0$. All parameters are assumed to be positive.

Questions for Epidemic Models

Given all parameters and initial conditions

- Does the infection spread or die out?
- If it does spread, how does it develop with time?
- When will it start to decline?

Equilibria

Note: Since N is a constant, we can solve for only S and I, then if we need R, we can calculate it easily.

$$\begin{aligned} \frac{dS}{dt} &= \mu N - \alpha S I - \mu S = 0 \\ \frac{dI}{dt} &= \alpha S I - \beta I - \mu I = 0 \end{aligned}$$

Equilibria

Gives two equilibria:

$$S^* = N \quad , \quad I^* = 0$$

$$S^* = \frac{\beta + \mu}{\alpha} \quad , \quad I^* = \frac{\mu \left(\alpha N - \beta - \mu\right)}{\alpha \left(\beta + \mu\right)}$$

Let

$$\begin{aligned} F(S, I) &= \mu N - \alpha S I - \mu S \\ G(S, I) &= \alpha S I - \beta I - \mu I \end{aligned}$$

Stability

Then

$$
\begin{aligned}
\frac{\partial F}{\partial S} &= -\alpha I - \mu \\
\frac{\partial F}{\partial I} &= -\alpha S \\
\frac{\partial G}{\partial S} &= \alpha I \\
\frac{\partial G}{\partial I} &= \alpha S - \beta - \mu
\end{aligned}
$$

Stability

First, let's evaluate the stability of $S^* = N, I^* = 0$
The elements of the Jacobian evaluated at this equilibrium are:

$$
\begin{aligned}
a_{1}1 &= -\mu \\
a_{12} &= -\alpha N \\
a_{21} &= 0 \\
a_{22} &= \alpha N - \beta - \mu
\end{aligned}
$$

Stability

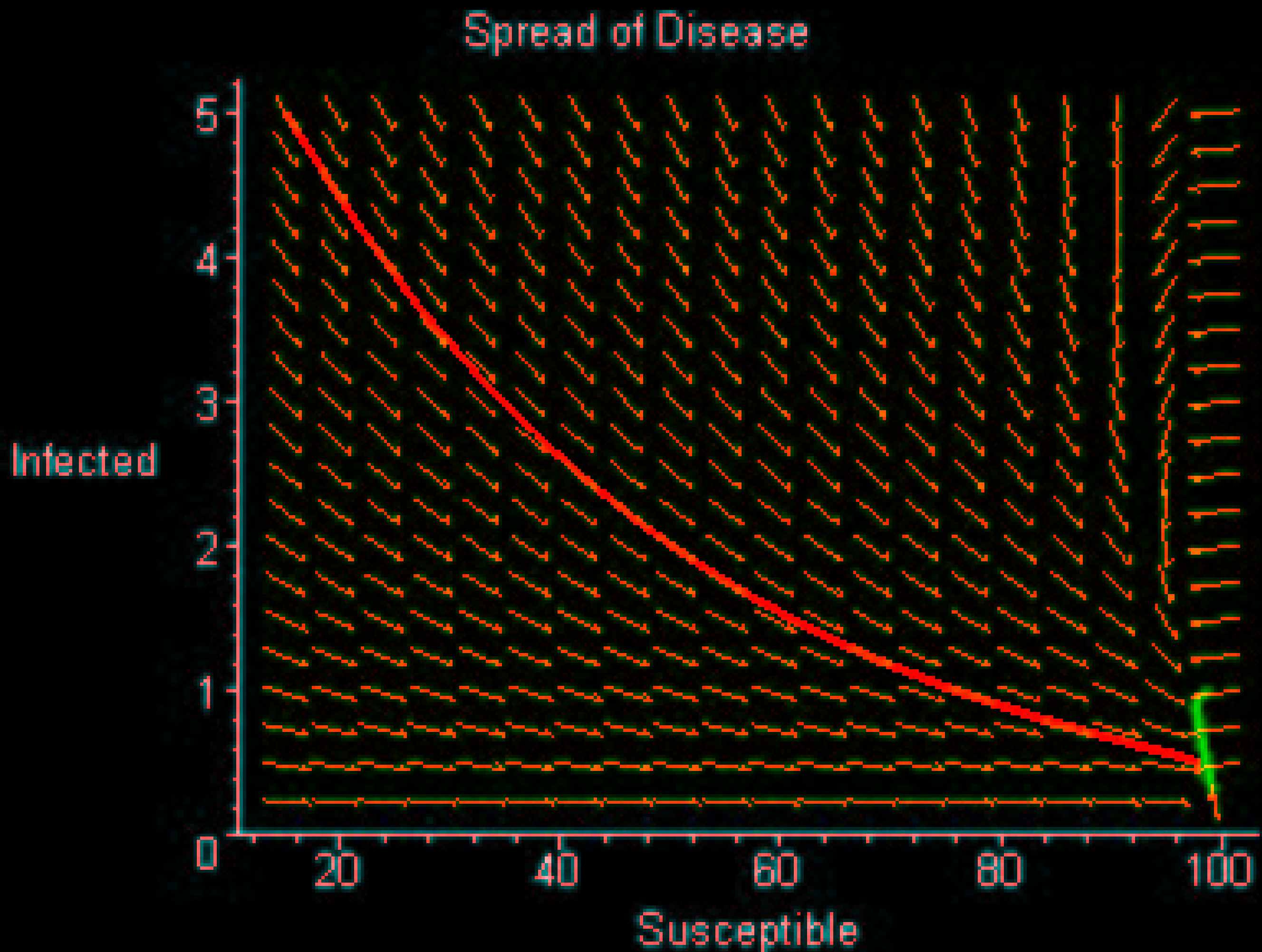
Applying the Routh-Hurwitz conditions:

$$\begin{aligned} a_11 + a_22 &= -\beta - 2\mu \\ a_{11}a_22 - a_{12}a_21 &= \mu\left(\beta + \mu - \alpha N\right) \end{aligned}$$

Clearly, $-\beta - 2\mu < 0$
However, $\mu\left(\beta + \mu - \alpha N\right) > 0$ only if $\alpha N < \beta + \mu$

Therefore, $S^* = N, I^* = 0$ is asymptotically stable if $\alpha N < \beta + \mu$

Disease dies out



Stability

Now, let's evaluate the stability of $S^* = \frac{\beta+\mu}{\alpha}$, $I^* = \frac{\mu(\alpha N-\beta-\mu)}{\alpha(\beta+\mu)}$

The elements of the Jacobian evaluated at this equilibrium are:

$$
\begin{aligned}
a_{11} &= -\mu - \frac{\mu\left(\alpha N - \beta - \mu\right)}{\beta + \mu} \\
a_{12} &= -\beta - \mu \\
a_{21} &= \frac{\mu\left(\alpha N - \beta - \mu\right)}{\beta + \mu} \\
a_{22} &= 0
\end{aligned}
$$

Stability

Applying the Routh-Hurwitz conditions:

$$
\begin{aligned}
a_{11} + a_{22} &= -\mu - \frac{\mu\left(\alpha N - \beta - \mu\right)}{\beta + \mu} \\
a_{11}a_{22} - a_{12}a_{21} &= \left(\beta + \mu\right)\left(\frac{\mu\left(\alpha N - \beta - \mu\right)}{\beta + \mu}\right)
\end{aligned}
$$

Stability

Both

$$
\begin{aligned}
-\mu - \frac{\mu\left(\alpha N - \beta - \mu\right)}{\beta + \mu} &< 0 \\
(\beta + \mu)\left(\frac{\mu\left(\alpha N - \beta - \mu\right)}{\beta + \mu}\right) &< 0
\end{aligned}
$$

are true if $\alpha N > \beta + \mu$

Stability

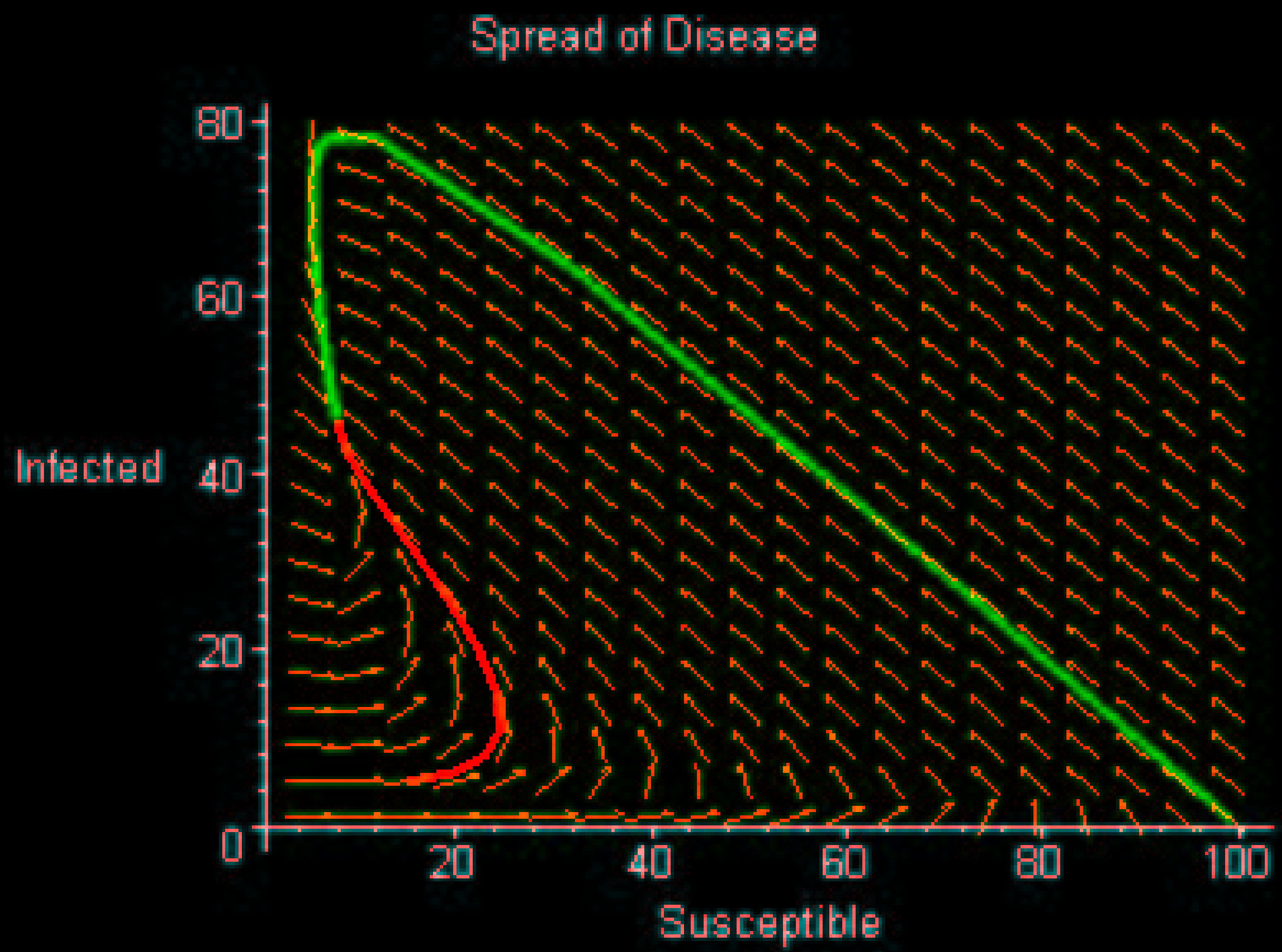
Therefore,

$$S^* = \frac{\beta + \mu}{\alpha} \quad , \quad I^* = \frac{\mu\left(\alpha N - \beta - \mu\right)}{\alpha\left(\beta + \mu\right)}$$

is asymptotically stable if $\alpha N < \beta + \mu$

But what about limit cycles?

Epidemic


Spread of Disease
Infected
80
60
40
20
0
20
40
60
80
100
Susceptible

Bendixson's Negative Criteria

Recall, we need

$$\nabla \cdot (F, G) = \frac{\partial F}{\partial S} + \frac{\partial G}{\partial I}$$

to be of one sign in our region of interest, D.

Define D to be all positive values in $\Re^2$.

Bendixson's Negative Criteria

$$\frac{\partial F}{\partial S} + \frac{\partial G}{\partial I} \;=\; -\alpha I - \mu + \alpha S - \beta - \mu$$

So this will be of one sign, negative, if $\alpha N < \beta + \mu$ since $S \leq N$.

Therefore there are no limit cycles in D.

R_0 *Basic reproduction rate*

- R_0 is defined to be the number of secondary infections produced by one primary infection in a wholly susceptible population.
- So if $R_0 > 1$, then the disease will spread.
- For SIR model, R_0 is calculated by linearizing the equation for $\frac{dI}{dt}$ about $I = 0$, which we have already done.
- So the criteria for determining if the epidemic will spread is, $R_0 \equiv \frac{\alpha N}{\beta + \mu}$.

Conclusions

There are many other applications of differential equation models in biology. Once a basic set of equations has been developed, there are a number of standard techinques used to analyze the stability of the equations.

We will take time in the lab to explore these and other equations.

Acknowledgements

- Murray, J. D., Mathematical Biology, Springer-Verlag, 1989.
- Kot, Mark, Elements of Mathematical Ecology, Cambridge University Press, 2001.
- Arrowsmith, D.K. and C.M. Place, Ordinary Differential Equations, Chapman and Hall, 1982.

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