3. Continuous-time models for interacting species

(Ruth Baker notes Chapter 4).

We will consider two interacting species. This leads to a coupled system of 2 ordinary differential equations (ODEs).

Before going any further, let's do a quick revision of the relevant concepts which we will need from the Differential Equations I course.

3.1 Introduction

We will consider models of two species, u and v, whose dynamics can be described using the system of coupled ordinary differential equations

$$\frac{du}{dt} = f(u, v), \tag{3.1}$$

$$\frac{dv}{dt} = g(u, v), \tag{3.2}$$

where f and g are functions that model the interactions between the species.

Our "recipe" for analysing these models is to find their steady states, conduct a linear stability analysis and sketch the phase plane.

3.1.1 Steady states

The *steady states* (also called *stationary states* or *equilibrium points*), (u_s, v_s), satisfy

$f(u_s, v_s) = 0$ and $g(u_s, v_s) = 0$.

Note that these are the intersections of the *null clines*. Recall that the nullclines are the curves in phase space ((u, v) space) where either

$\frac{du}{dt} = 0$ or $\frac{dv}{dt} = 0$.

3.1.2 Linear stability analysis

Make a small perturbation from the steady state (u_s, v_s):

$$u(t) = u_s + \tilde{u} \qquad \text{and} \qquad \mathrm{v(t) = v_s + \tilde{v}.} \tag{3.3}$$

Substituting into equations (3.1-3.2) and retaining only first order terms in $\tilde{u}$, $\tilde{v}$ we have

$$\frac{d}{dt}\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} = \begin{pmatrix} f(u_s + \tilde{u}, v_s + \tilde{v}) \\ g(u_s + \tilde{u}, v_s + \tilde{v}) \end{pmatrix} \tag{3.4}$$

$$= \begin{pmatrix} f(u_s, v_s) \\ g(u_s, v_s) \end{pmatrix} + \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u_s, v_s)} \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} \tag{3.5}$$

$$= \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u_s, v_s)} \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix}. \tag{3.6}$$

As in the Differential Equations I course, we determine linear stability by consider the eigenvalues of the (constant) Jacobian matrix

$$\vec{J} = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u_s, v_s)} . \tag{3.7}$$

3.2 Interacting Populations

There are 3 basic types of interaction:

1. The growth of one population decreases, the growth of the other population increases – *predator-prey*.

2. The growth of both populations decreases – *competition*.

3. The growth of both populations increases – *mutualism (symbiosis)*.

3.2.1 Predator-Prey

Lotka-Volterra model. Let $N(t)$ be the density (biomass) of the prey and $P(t)$ the density (biomass) of the predators at time t.

Then:

$$\frac{dN}{dt} = aN - bNP, \tag{3.8}$$

$$\frac{dP}{dt} = cNP - dP, \tag{3.9}$$

with a, b, c, d positive parameters and $c < b$.

Here: a is linear birth rate, b is predation rate per predator, c is related to the conversion of predation to predator growth rate, and d is linear death rate.

We will also have some initial conditions: $N(0) = N_0$, $P(0) = P_0$, where N_0, P_0 are non-negative.

Non-dimensionalisation

Non-dimensionalising with $u = (\frac{c}{d})N$, $v = (\frac{b}{a})P$, $\tau = at$ and $\alpha = \frac{d}{a}$:

$$\frac{du}{d\tau} = u(1 - v) \quad := f(u, v), \tag{3.10}$$

$$\frac{dv}{d\tau} = \alpha v(u - 1) \quad := g(u, v), \tag{3.11}$$

with $u(0) = u_0, v(0) = v_0$.

Linear stability analysis

Steady states: $(u, v) = (0, 0)$ and $(u, v) = (1, 1)$.

The Jacobian, $\vec{J}$, is given by

$$\vec{J} = \begin{pmatrix} 1 - v_s & -u_s \\ \alpha v_s & \alpha(u_s - 1) \end{pmatrix}. \tag{3.12}$$

At $(0, 0)$ we have

$$\vec{J} = \begin{pmatrix} 1 & 0 \\ 0 & -\alpha \end{pmatrix}, \tag{3.13}$$

with eigenvalues 1, $-\alpha$. Therefore the steady state $(0, 0)$ is an unstable saddle.

At $(1, 1)$ we have

$$\vec{J} = \begin{pmatrix} 0 & -1 \\ \alpha & 0 \end{pmatrix}, \tag{3.14}$$

with eigenvalues $\pm i\sqrt{\alpha}$. Therefore the steady state $(1, 1)$ is a centre (not linearly stable).

3.2.2 Analytic solution

Note that:

$$\frac{du}{dv} = \frac{u(1-v)}{\alpha(u-1)v} \quad \Rightarrow \quad \int \frac{u-1}{u} du = \int \frac{1-v}{\alpha v} dv. \tag{3.15}$$

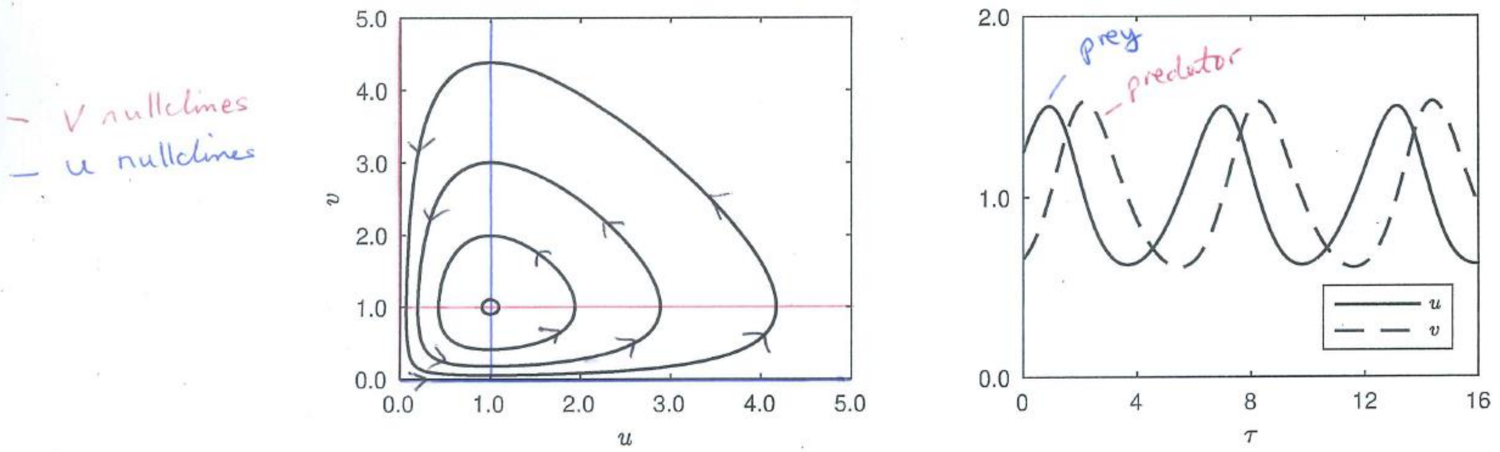
Hence

$$H = \text{constant} = \alpha u + v - \alpha \ln u - \ln v. \tag{3.16}$$

This can be rewritten as

$$\left(\frac{e^v}{v}\right)\left(\frac{e^u}{u}\right)^\alpha = e^H, \tag{3.17}$$

from which we can deduce that the trajectories in the (u, v) plane take the form shown in the figure below.



Thus u and v exhibit temporal oscillations, which are out of phase.

Eg. Hare-lynx 1845-1935 (Hudson Bay).

End of Lecture 3-1

Summary of previous lecture

- Brief revision of key material from Differential Equations 1 that is needed for this course (phase planes – linear stability analysis, null clines)
- Lotka-Volterra predator-prey model

$$\frac{dN}{dt} = aN - bNP,$$
$$\frac{dP}{dt} = cNP - dP,$$

3.3 A more realistic predator-prey model

The Lotka-Volterra model assumes that growth of prey goes to infinity as the prey population goes to infinity, and also that predation goes to infinity as the prey population goes to infinity.

A more realistic model (proposed for aphids-ladybirds) takes the form:

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) - \frac{kNP}{N+D}, \quad (3.18)$$
$$\frac{dP}{dt} = SP(1 - \frac{\alpha P}{N}), \quad (3.19)$$

where $N(t)$ is the aphid density (prey), $P(t)$ is the ladybird density (predator), t is time, and r, K, k, D, S, α are positive parameters.

After non-dimensionalisation (**Exercise**):

$$\frac{du}{d\tau} = u(1-u) - \frac{auv}{d+u}, \tag{3.20}$$

$$\frac{dv}{d\tau} = bv(1-\frac{v}{u}), \tag{3.21}$$

where a, b, d are positive constants.

3.3.1 Steady States and Linear Stability Analysis

Steady states: $(u_s, v_s) = (0, 0)$.

Non-trivial steady states: (u_s, v_s) satisfy

$$v_s = u_s \quad \text{where} \quad (1-u_s) = \frac{au_s}{d+u_s}, \tag{3.22}$$

and hence

$$u_s = \frac{1}{2}\left[-(a+d-1) + \sqrt{(a+d-1)^2 + 4d}\right], \tag{3.23}$$

is the only positive steady state.

The Jacobian at (u_s, v_s) is

$$\boldsymbol{J} = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u_s,v_s)} \tag{3.24}$$

The eigenvalues, λ, satisfy

$$\left(\lambda - \frac{\partial f}{\partial u}\right)\left(\lambda - \frac{\partial g}{\partial v}\right) - \frac{\partial f}{\partial v}\frac{\partial g}{\partial u} = 0 \quad \Longrightarrow \quad \lambda^2 - \left(\frac{\partial f}{\partial u} + \frac{\partial g}{\partial v}\right)\lambda + \left(\frac{\partial f}{\partial u}\frac{\partial g}{\partial v} - \frac{\partial f}{\partial v}\frac{\partial g}{\partial u}\right) = 0. \tag{3.25}$$

Hence

$$\lambda^2 - \alpha\lambda + \beta = 0 \quad \Longrightarrow \quad \lambda = \frac{\alpha \pm \sqrt{\alpha^2 - 4\beta}}{2}, \tag{3.26}$$

where

$$\alpha = -u_s + \frac{au_s^2}{(u_s+d)^2} - b, \quad \beta = b\left(u_s - \frac{au_s^2}{(u_s+d)^2} - (u_s - 1)\right). \tag{3.27}$$

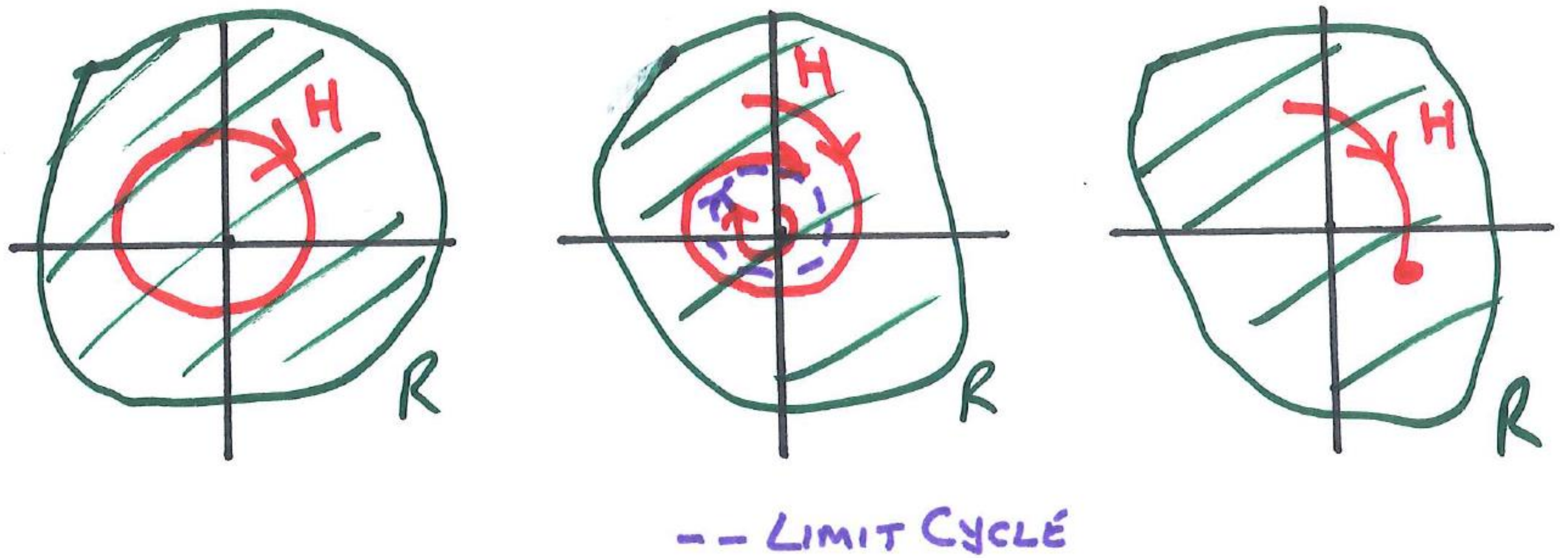
Note that

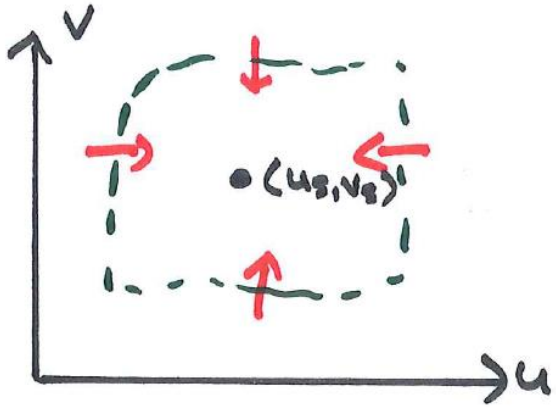
$$\beta = 1 - \frac{au_s^2}{(u_s+d)^2} = 1 - \frac{u_s(1-u_s)}{(u_s+d)} = \frac{(u_s+d) - u_s + u_s^2}{u_s+d} = \frac{d + (u_s)^2}{d + u_s} > 0. \tag{3.28}$$

Thus, if $\alpha < 0$ we have either a stable node ($\alpha^2 - 4\beta > 0$) or stable focus ($\alpha^2 - 4\beta < 0$) at the steady state (u_s, v_s). If $\alpha > 0$ we have an unstable steady state at (u_s, v_s) (either node or spiral).

3.3.2 Limit cycle dynamics

Poincaré-Benedixon Theorem: Let R be a closed bounded region consisting of non-singular points of a 2x2 system: $\frac{d\mathbf{x}}{dt} = \mathbf{X}(\mathbf{x})$ such that some positive half-path H of the system lies entirely in R. Then, either H is itself a closed path, or it approaches a closed path, or it terminates at an equilibrium point.

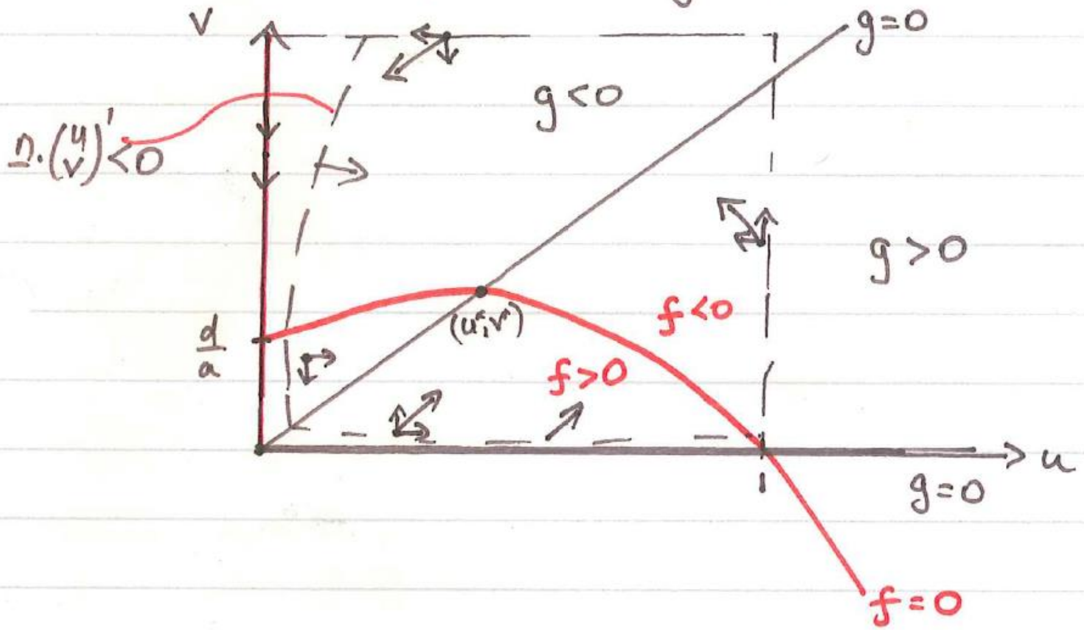



v
(u_s, v_s)
u

$$\frac{du}{d\tau} = u(1-u) - \frac{auv}{d+u},$$
$$\frac{dv}{d\tau} = bv(1-\frac{v}{u}),$$

$u' = f(u,v)$
$v' = g(u,v)$

Nullclines are $f(u,v)=0$, $g(u,v)=0$.

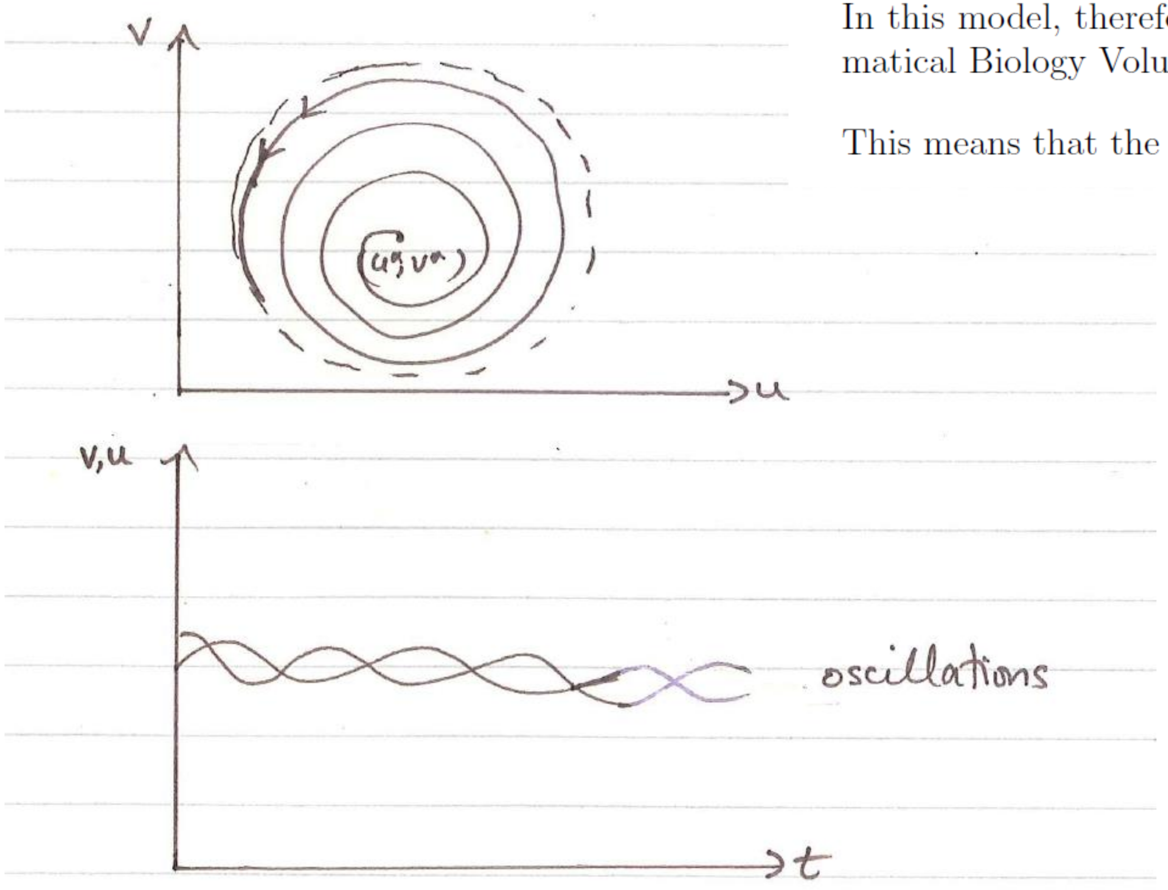


$f(u,v) = u(1-u) - \frac{auv}{u+d} = 0$

$\Rightarrow v = \frac{u(1-u)(u+d)}{au}$

$g(u,v) = bv(1-\frac{v}{u}) = 0$

$\Rightarrow v=0,\ v=u$



In this model, therefore, for $\alpha > 0$, we have limit cycle dynamics (See J. D. Murray, Mathematical Biology Volume I (Chapter 3.4) for more details).

This means that the predator and prey population densities oscillate out-of-phase.

Summary

- We considered a more realistic model for predator-prey dynamics
- Limit cycles

End of Lecture 3-2

Summary of Previous Lecture

- We considered a more realistic model for predator-prey dynamics
- Limit cycles

In this lecture we will consider

- Competition
- Mutualism (Symbiosis)

3.4 Competition

Lotka-Volterra competition model:

$$\frac{\mathrm{dN_1}}{\mathrm{dt}} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right), \tag{3.29}$$

$$\frac{\mathrm{dN_2}}{\mathrm{dt}} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_2}\right), \tag{3.30}$$

where K_1, K_2, r_1, r_2, b_{12}, b_{21} are positive constants.

We will have initial conditions $N_1(0) = N_1^0, N_2(0) = N_2^0$.

Non-dimensionalise: $u_1 = \frac{N_1}{K_1}, u_2 = \frac{N_2}{K_2}, \tau = r_1 t, \rho = \frac{r_2}{r_1}, \alpha_{12} = b_{12}\frac{K_2}{K_1}, \alpha_{21} = b_{21}\frac{K_1}{K_2}$:

$$\frac{\mathrm{d}u_1}{\mathrm{d}\tau} = u_1(1 - u_1 - \alpha_{12}u_2) := f_1(u_1, u_2), \tag{3.31}$$

$$\frac{\mathrm{d}u_2}{\mathrm{d}\tau} = \rho u_2(1 - u_2 - \alpha_{21}u_1) := f_2(u_1, u_2). \tag{3.32}$$

3.4.1 Steady States and Linear Stability Analysis

The steady states are

$$(u_{1,s}, u_{2,s}) = (0, 0), \quad (u_{1,s}, u_{2,s}) = (1, 0), \quad (u_{1,s}, u_{2,s}) = (0, 1), \tag{3.33}$$

and

$$(u_{1,s}, u_{2,s}) = \frac{1}{1 - \alpha_{12}\alpha_{21}}(1 - \alpha_{12}, 1 - \alpha_{21}), \tag{3.34}$$

if $\alpha_{12} < 1$ and $\alpha_{21} < 1$ *or* $\alpha_{12} > 1$ and $\alpha_{21} > 1$.

The Jacobian (community matrix) is

$$\mathbf{J} = \begin{pmatrix} 1 - 2u_1 - \alpha_{12}u_2 & -\alpha_{12}u_1 \\ -\rho\alpha_{21}u_2 & \rho(1 - 2u_2 - \alpha_{21}u_1) \end{pmatrix}. \tag{3.35}$$

Steady state $(u_{1,s}, u_{2,s}) = (0, 0)$.

$$\mathbf{J} - \lambda\mathbf{I} = \begin{pmatrix} 1-\lambda & 0 \\ 0 & \rho - \lambda \end{pmatrix} \tag{3.36}$$

So, we see that $\lambda = 1, \rho$.

Therefore $(0, 0)$ is an unstable node.

Steady state $(u_{1,s}, u_{2,s}) = (1, 0)$**.**

$$\mathbf{J} - \lambda \mathbf{I} = \begin{pmatrix} -1-\lambda & -\alpha_{12} \\ 0 & \rho(1-\alpha_{21}) - \lambda \end{pmatrix} \tag{3.37}$$

So, we see that $\lambda = -1, \rho(1-\alpha_{21})$.

Therefore $(1, 0)$ is a stable node if $\alpha_{21} > 1$ and a saddle point if $\alpha_{21} < 1$.

Steady state $(u_{1,s}, u_{2,s}) = (0, 1)$**.**

$$\mathbf{J} - \lambda \mathbf{I} = \begin{pmatrix} 1-\alpha_{12}-\lambda & 0 \\ -\rho\alpha_{21} & -\rho - \lambda \end{pmatrix} \tag{3.38}$$

So, we see that $\lambda = -\rho, 1-\alpha_{12}$.

Therefore $(0, 1)$ is a stable node if $\alpha_{12} > 1$ and a saddle point if $\alpha_{12} < 1$.

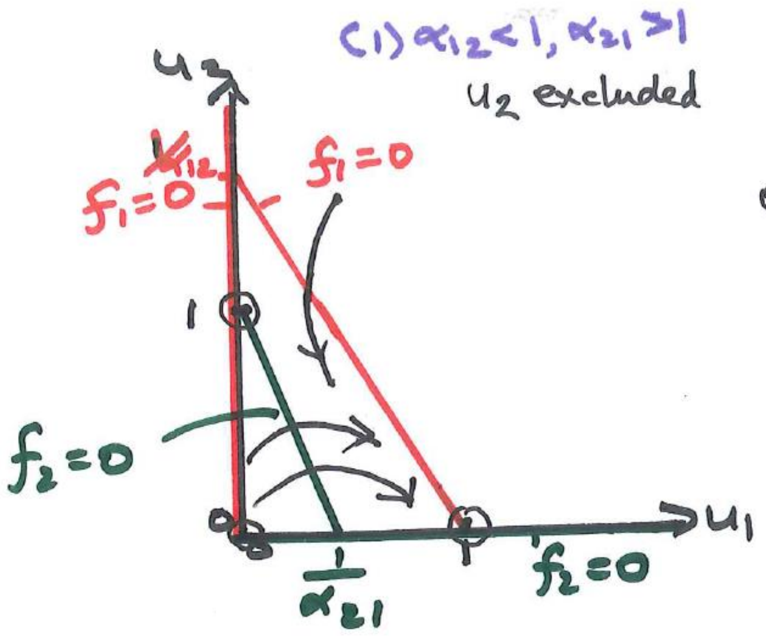
Steady state $(u_{1,s}, u_{2,s}) = \frac{1}{1-\alpha_{12}\alpha_{21}}(1-\alpha_{12}, 1-\alpha_{21})$.

$$\mathbf{J} - \lambda\mathbf{I} = \frac{\mathbf{1}}{\mathbf{1} - \alpha_{\mathbf{12}}\alpha_{\mathbf{21}}} \begin{pmatrix} \alpha_{21} - 1 - \lambda & \alpha_{12}(\alpha_{12} - 1) \\ \rho\alpha_{21}(\alpha_{21} - 1) & \rho(\alpha_{21} - 1) - \lambda \end{pmatrix}. \tag{3.39}$$

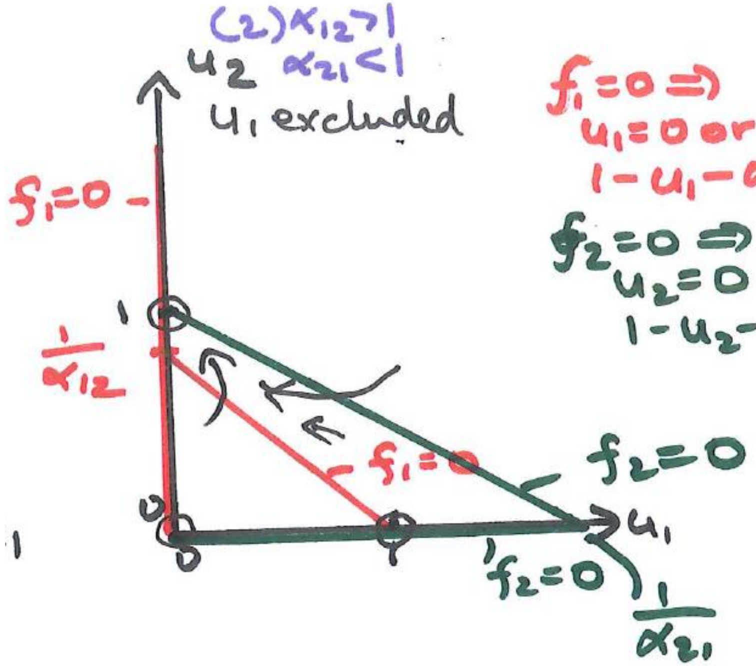
Existence and stability depends on α_{12} and α_{21}.

$f_1 = 0 \Rightarrow$
$u_1 = 0$ or
$1 - u_1 - \alpha_{12} u_2 = 0$

$f_2 = 0 \Rightarrow$
$u_2 = 0$ or
$1 - u_2 - \alpha_{21} u_1 = 0$

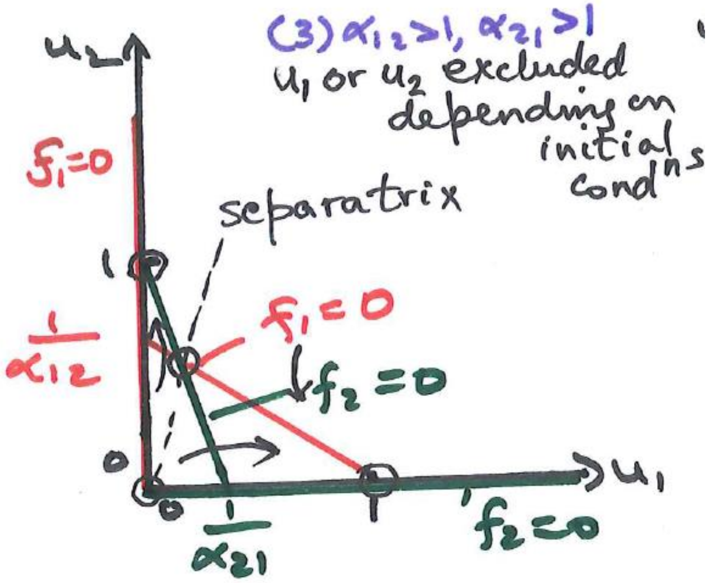


o - steady states

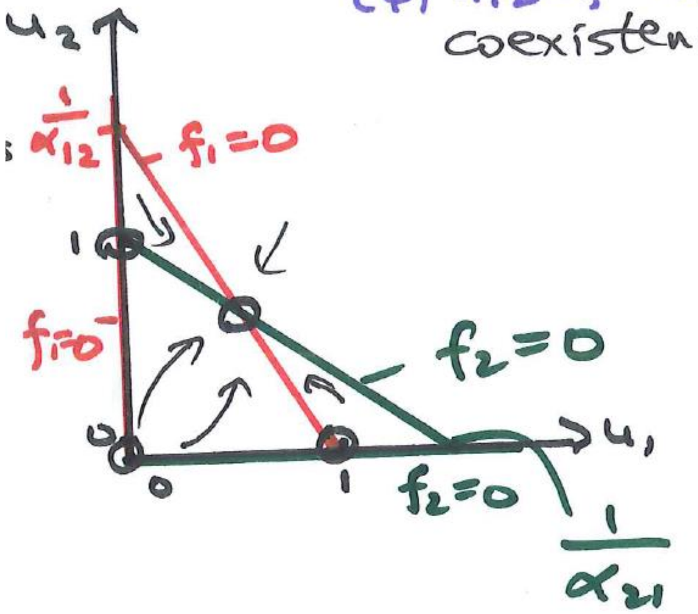


$f_1 = 0 \Rightarrow$
$u_1 = 0$ or
$1 - u_1 - \alpha_{12} u_2 = 0$

$f_2 = 0 \Rightarrow$
$u_2 = 0$ or
$1 - u_2 - \alpha_{21} u_1 = 0$



(4) $\alpha_{12}<1$, $\alpha_{21}<1$
coexistence



Ecological implications:

1. In case (1) $\alpha_{12} < 1 ==> b_{12}\frac{K_2}{K_1} < 1$ while $\alpha_{21} > 1 ==> b_{21}\frac{K_1}{K_2} > 1$, so u_1 (that is, N_1) is the better competitor (*competitive exclusion*).

2. In case (1) we cannot eliminate N_1 by culling alone. We must also increase α_{12}, that is, increase $b_{12}\frac{K_2}{K_1}$.

Acid-Mediated Invasion Hypothesis

- A bi-product of the glycolytic pathway is lactic acid – this lowers the extracellular pH so that it favours tumour cell proliferation AND it is toxic to normal cells.

Robert A Gatenby

- **R.A. Gatenby and E.T. Gawslinski, A reaction-diffusion model of cancer invasion, Cancer Research, 56, 5745-5753 (1996)**

3.5 Mutualism (Symbiosis)

We consider a very similar ordinary differential equation model for two species, but this time with positive interactions,

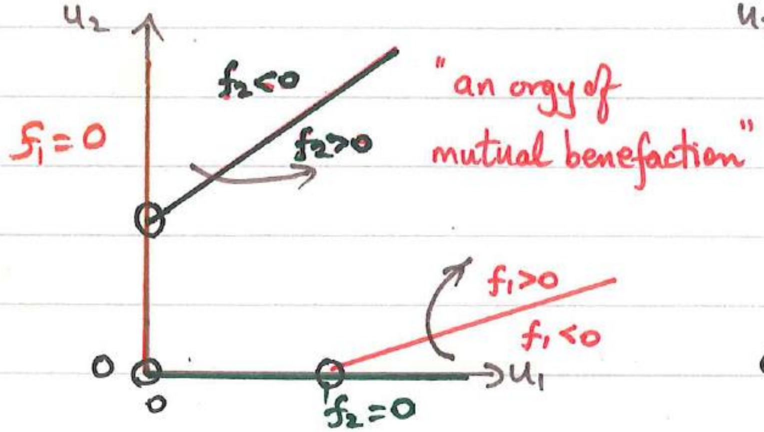
$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left(1 - \frac{N_1}{K_1} + b_{12}\frac{N_2}{K_1}\right), \tag{3.40}$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2 \left(1 - \frac{N_2}{K_2} + b_{21}\frac{N_1}{K_2}\right), \tag{3.41}$$

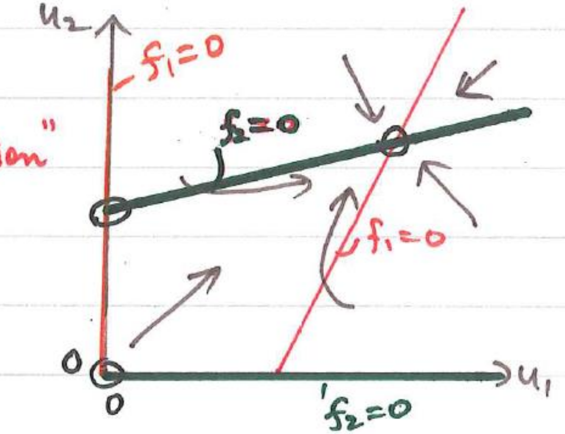
where K_1, K_2, r_1, r_2, b_{12}, b_{21} are positive constants. The model can be non-dimensionalised to give

$$\frac{\mathrm{d}u_1}{\mathrm{d}\tau} = u_1(1 - u_1 + \alpha_{12}u_2) := f_1(u_1, u_2), \tag{3.42}$$

$$\frac{\mathrm{d}u_2}{\mathrm{d}\tau} = \rho u_2(1 - u_2 + \alpha_{21}u_1) := f_2(u_1, u_2). \tag{3.43}$$



u_2
$f_1=0$
$f_2<0$
$f_2>0$
$f_1>0$
$f_1<0$
0
0
$f_2=0$
u_1
"an orgy of mutual benefaction"



u_2
$f_1=0$
$f_2=0$
$f_1=0$
0
0
$f_2=0$
u_1
o steady states

Summary

- Considered a model for competition
- Considered a model for mutualism (symbiosis)

End of Lecture 3-3