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"Fifth Course on Mathematical Ecology
including and introduction to Ecological Economics"

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AN INTRODUCTION TO POPULATION DYNAMICS

Giulio De Leo

Universita' di Parma
Dipartimento di Scienze Ambientali
Parma, Italy

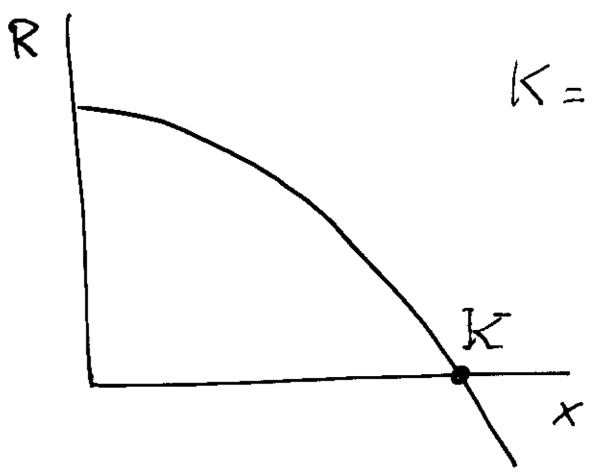
THE GROWTH OF BIOMASS

x = biomass of primary producers
(e.g., g dry weight m^{-2})

$$\dot{x} = R\,x$$

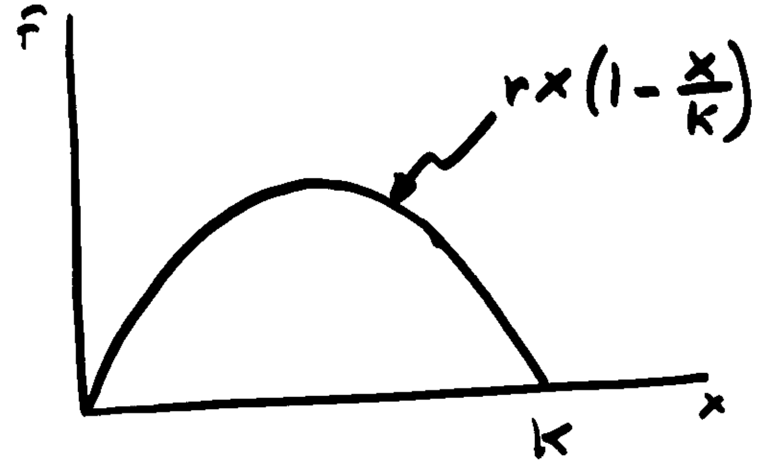
R = growth rate per unit biomass

In malthusian models R is constant. In reality, because of intraspecific competition or other interactions, R depends on x. In absence of facilitation or other positive feedbacks

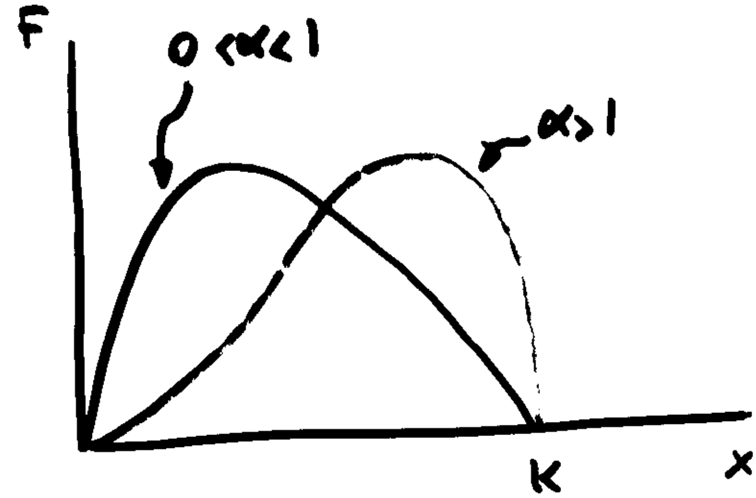


K = carrying capacity

Examples of growth rates

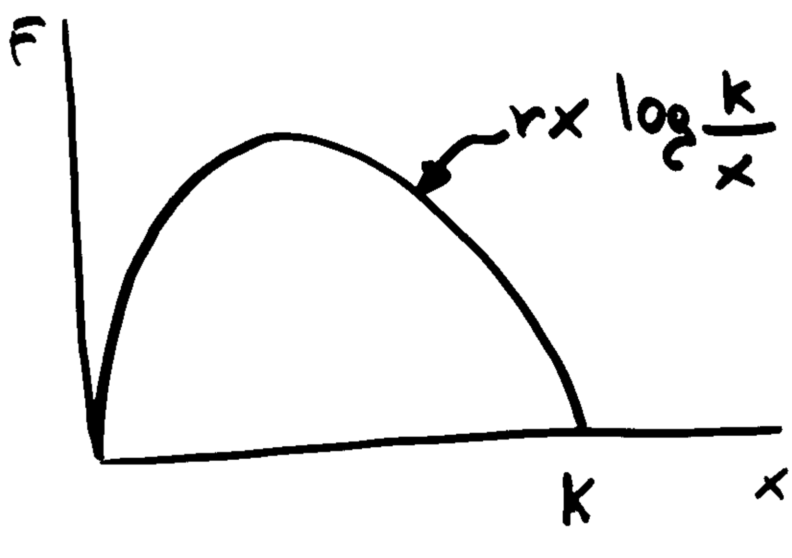


Logistic model



Modified logistic model

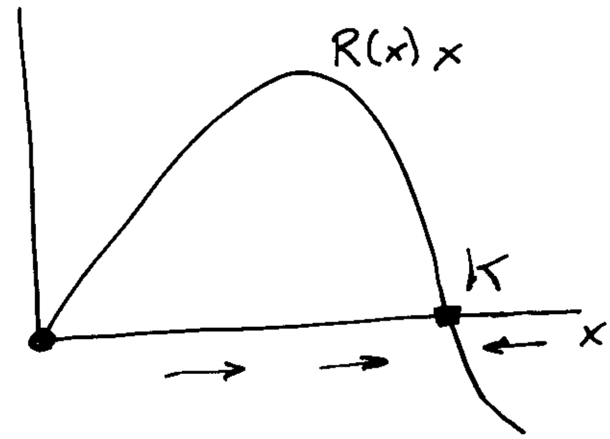
$$rx^{\alpha}\left(1-\frac{x}{K}\right)$$



Gompertz mode

EQUILIBRIA OF THE MODEL

$$\frac{dx}{dt} = R(x)\,x$$



$$\frac{dx}{dt} = 0 \quad \begin{array}{l} \nearrow \text{I. } x = 0 \\ \searrow \text{II. } R(x) = 0 \Rightarrow x = K \end{array}$$

2 EQUILIBRIA

Stability can be assessed via linearization

I. For x small $(x \sim 0)$

$$\frac{dx}{dt} \simeq R(0)\cdot 0 + \left.\frac{d\,[R(x)\,x]}{dx}\right|_{x=0} x + \cancel{\dots} =$$

$$= R(0)\,x$$

As $R(0) > 0$ $\quad x$ increases $\Rightarrow$ Eq. is unstable

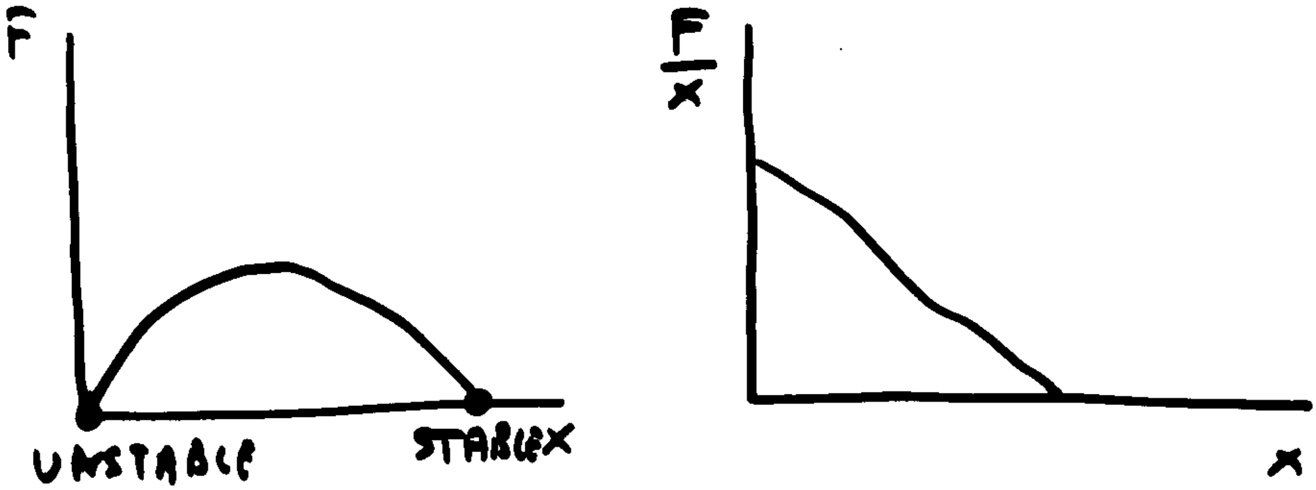
II. For x close to K

$$\frac{dx}{dt} \simeq R(K)K + \left.\frac{d\,[R(x)\,x]}{dx}\right|_{x=K} (x-K) + \cancel{\dots}$$

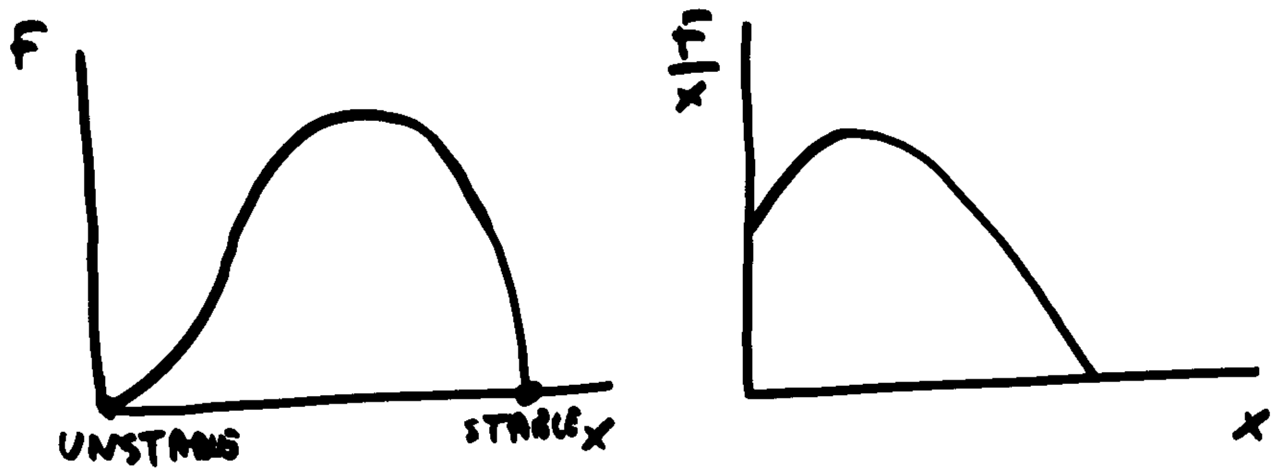
$$\frac{d\,(x-K)}{dt} \simeq R'(K)\,K\,(x-K)$$

As $R'(K)\,K < 0$ $\quad \|x-K\|$ decreases $\Rightarrow$ Eq. is stable

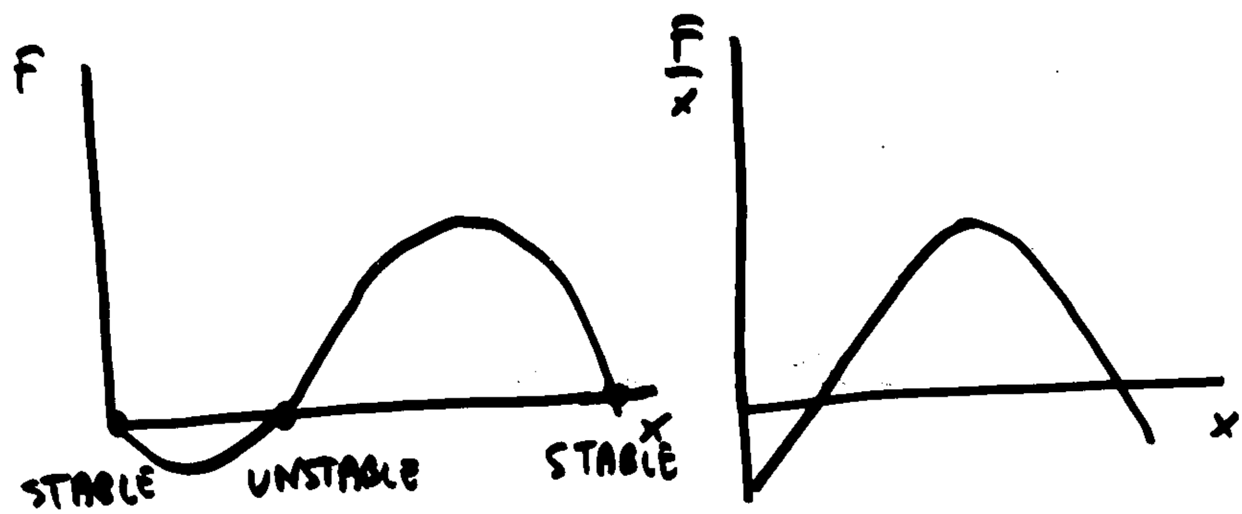
CLASSIFICATION OF GROWTH CURVES



PURE COMPENSATION



DEPENSATION



CRITICAL DEPENSATION

EQUILIBRIA OF THE MODEL

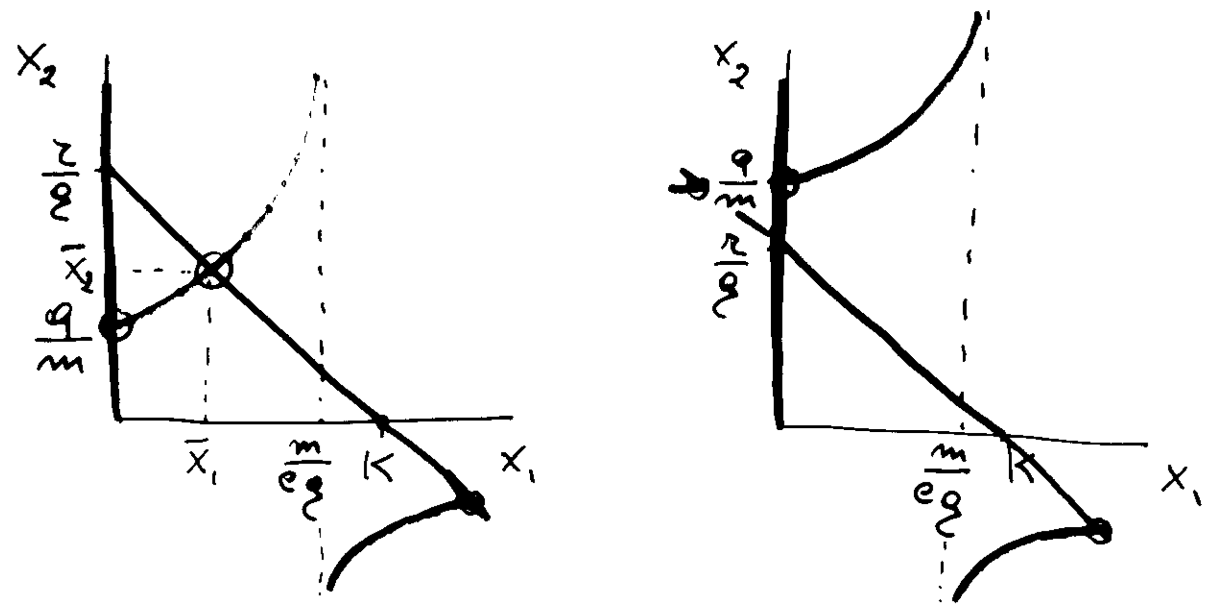
$$\frac{dx_1}{dt} = x_1\left[r\left(1-\frac{x_1}{K}\right) - g\,x_2\right] = 0$$

$$\frac{dx_2}{dt} = (-m + e g x_1)\,x_2 + q = 0$$

- $\dot{x}_1 = 0 \;\begin{cases} x_1 = 0 \\ x_2 = \dfrac{r}{g}\left(1-\dfrac{x_1}{K}\right) \end{cases}$

- $\dot{x}_2 = 0 \longrightarrow x_2 = \dfrac{q}{-egx_1 + m}$

Geometrically, equilibria are found as intersections between curves defined by $\dot{x}_1 = 0$ and $\dot{x}_2 = 0$



There are two cases

1)- <u>Low migration</u> $\left(q < \frac{mr}{g}\right)$

Two equilibria (meaningful!)

I. $x_1 = 0$

$x_2 = \frac{q}{m}$

GRASSLAND IS DESTROYED

II. $x_1 = \bar{x}_1$

$x_2 = \bar{x}_2 = \frac{q}{m - eg\bar{x}_1}$

$\bar{x}_1$ is solution of

$$\frac{r}{g}\left(1 - \frac{x_1}{K}\right)(m - egx_1) - q = 0$$

2)- <u>High migration</u> $\left(q > \frac{mr}{g}\right)$

One meaningful equilibrium

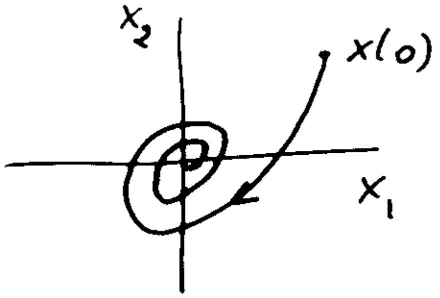
$x_1 = 0 \qquad x_2 = \frac{q}{m}$

How to study the stability?

STABILITY

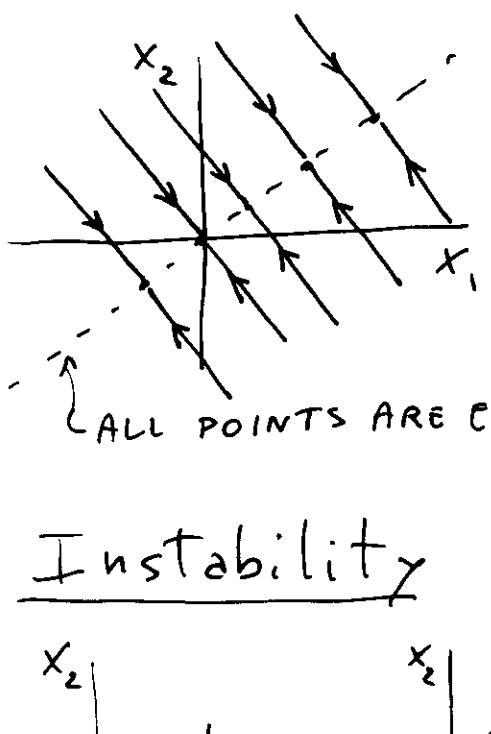
Remark: $x=0$ is always an equilibrium in linear autonomous systems

Asymptotic stability (strong, exponential)



$$\|x(t)\| = \|\phi(t)\, x(0)\| \to 0 \quad \forall x(0)$$

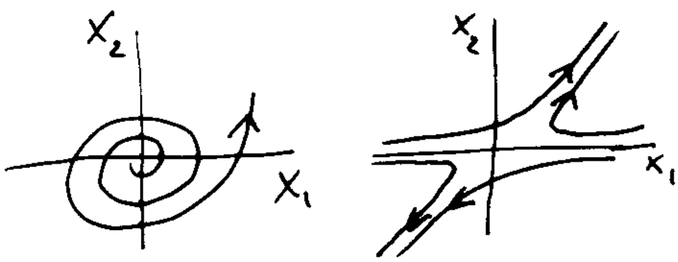
Simple stability (neutral, critical, weak)



$$\exists\, x(0): \quad \|\phi(t)\, x(0)\| \not\to 0$$

$$\nexists\, x(0): \quad \|\phi(t)\, x(0)\| \to \infty$$

Instability



$$\exists\, x(0): \|\phi(t)\, x(0)\| \to \infty$$

THE LINEARIZATION METHOD

Given the dynamical system

$$\begin{cases} \dot{x}_1 = f_1(x_1, x_2 \dots x_n) \\ \dot{x}_2 = f_2(x_1, x_2 \dots x_n) \\ \vdots \\ \dot{x}_n = f_n(x_1, x_2 \dots x_n) \end{cases}$$

and an equilibrium $\bar{x} = (\bar{x}_1, \bar{x}_2 \dots \bar{x}_n)$, build the corresponding Jacobian (linearization matrix)

$$J_{\bar{x}} = \begin{bmatrix} \frac{\partial f_1(\bar{x})}{\partial x_1} & \frac{\partial f_1(\bar{x})}{\partial x_2} & \dots & \frac{\partial f_1(\bar{x})}{\partial x_n} \\ \vdots & & & \\ \frac{\partial f_n(\bar{x})}{\partial x_1} & \frac{\partial f_n(\bar{x})}{\partial x_2} & \dots & \frac{\partial f_n(\bar{x})}{\partial x_n} \end{bmatrix}$$

Let $\Delta = x - \bar{x}$. Approximately

$$\frac{d\Delta}{dt} = J_{\bar{x}} \Delta$$ Linearized system

The linearized system

the equilibrium point

$$\frac{d\Delta}{dt} = J_{\bar{x}}\,\Delta \qquad \text{where } \Delta = x - \bar{x}$$

Solution

$$x(t) = \phi(t)\,x(0) \qquad \phi(t) = \text{transition matrix}$$

$$\phi(t) = e^{J_{\bar{x}} t}$$

Relationship with eigenvalues + eigenvectors

$\det(\lambda I - J_{\bar{x}})$ ⇒ characteristic polynomial

$\det(\lambda I - J_{\bar{x}}) = 0$ ⇒ characteristic equation

⇓

$\lambda_1, \lambda_2, \ldots \lambda_n$ ⇒ eigenvalues

$J_{\bar{x}}\, w_i = \lambda_i\, w_i \qquad w_i$ = eigenvector.

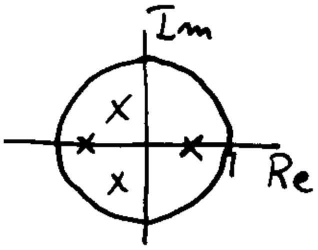
$$\Rightarrow \quad x(t) = \sum_i c_i\, e^{\lambda_i t}\, w_i$$

(N.B.: λ_i supposed distinct)

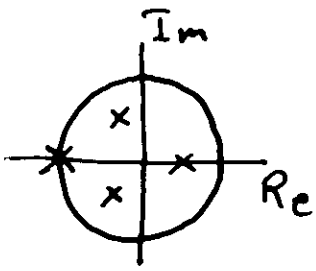
STABILITY AND EIGENVALUES

Remark: distinct eigenvalues

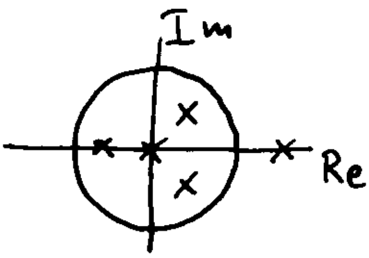
Discrete time : $x(t) = \sum_i c_i w_i \lambda_i^{\,t}$



$\|\lambda_i\| < 1 \quad \forall i$ ASYMPT. STABILITY



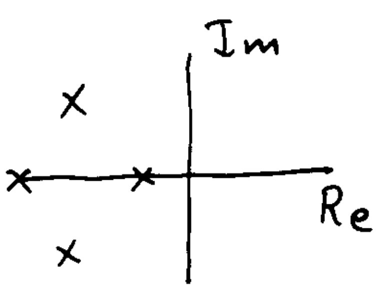
$\|\lambda_i\| \leq 1 \quad \forall i$
$\exists j : \|\lambda_j\| = 1$ SIMPLE STABILITY

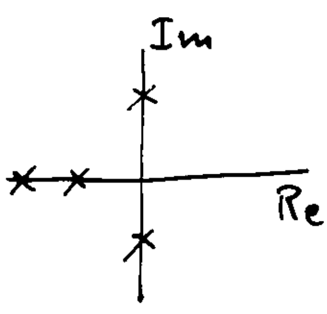


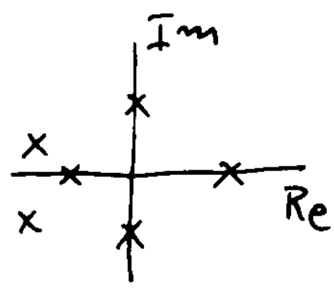
$\exists j : \|\lambda_j\| > 1$ INSTABILITY

Continuous Time : $x(t) = \sum_i c_i w_i e^{\lambda_i t}$

Replace $\|\lambda_i\| < 1$ with $Re(\lambda_i) < 0$







ASYMPT. STAB. SIMPLE STAB. INSTABILITY

DOMINANT EIGENVALUE AND EIGENVECTOR

Discrete time

$$x(t) = \sum_i c_i w_i \lambda_i^t \qquad \|\lambda_1\| > \|\lambda_2\| \ldots \|\lambda_n\|$$

$$\lim_{t \to \infty} \frac{x(t)}{\lambda_1^t} = c_1 w_1$$

$\lambda_1 =$ eigenvalue with largest modulus =

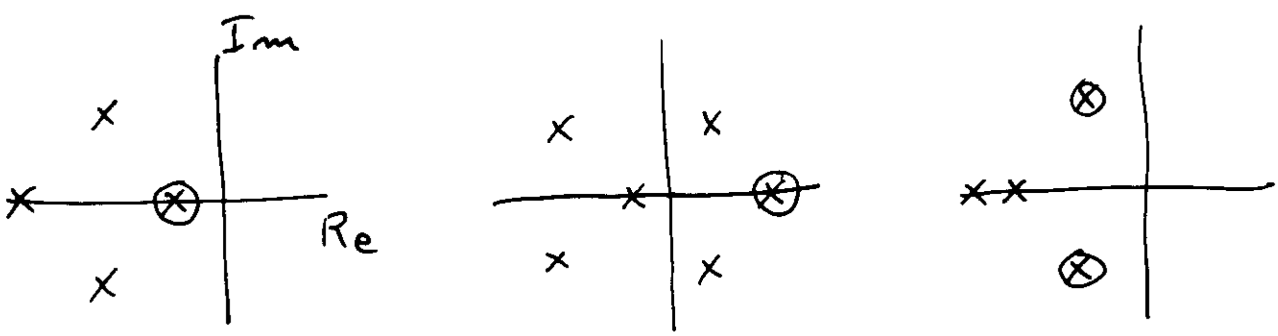
= dominant eigenvalue

$w_1 =$ dominant eigenvector

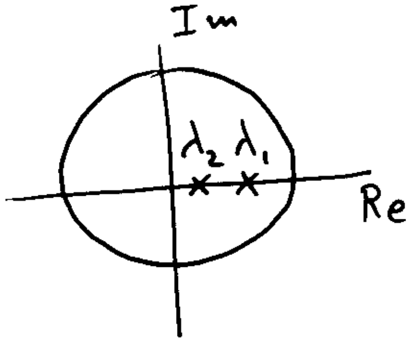
Continuous time

$$x(t) = \sum_i c_i w_i e^{\lambda_i t}$$

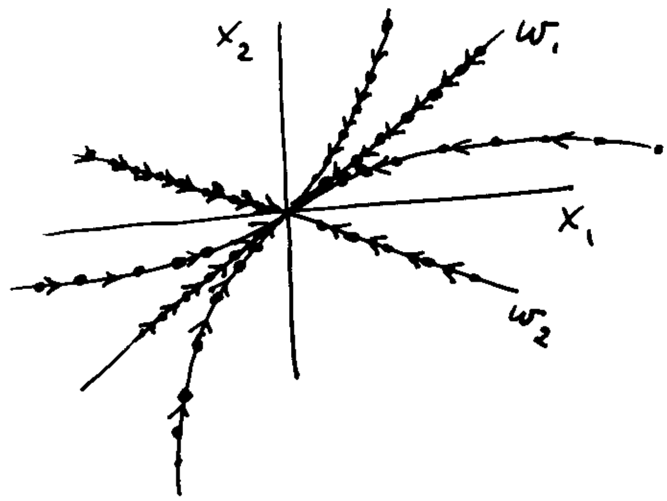
$\lambda_{dom} =$ eigenvalue with max real part

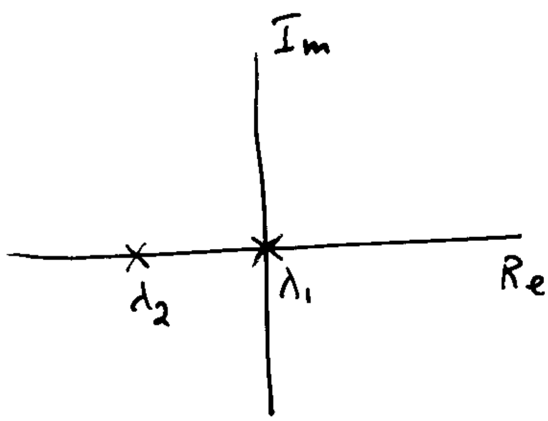


APPROACH TO DOMINANT EIGENVECTOR

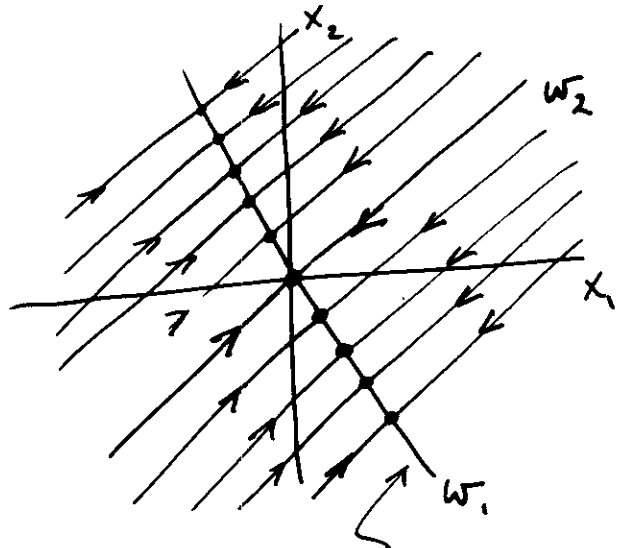


DISCRETE

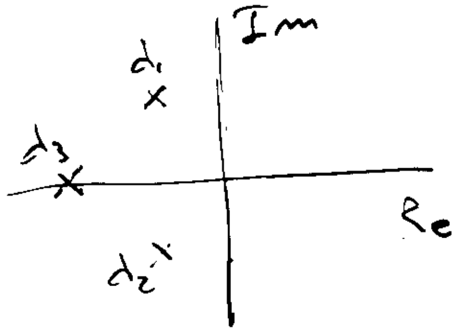




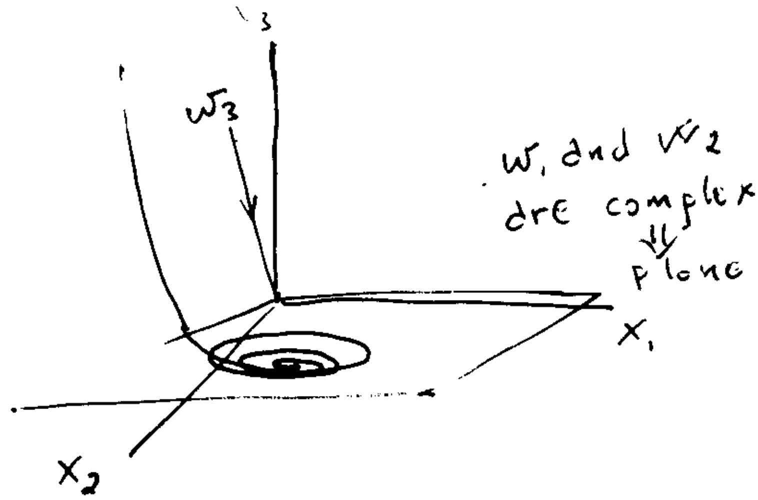
CONTINUOUS

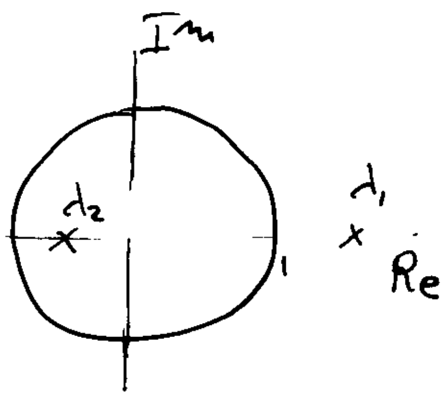


EVERY POINT IS AN EQUILIBRIUM

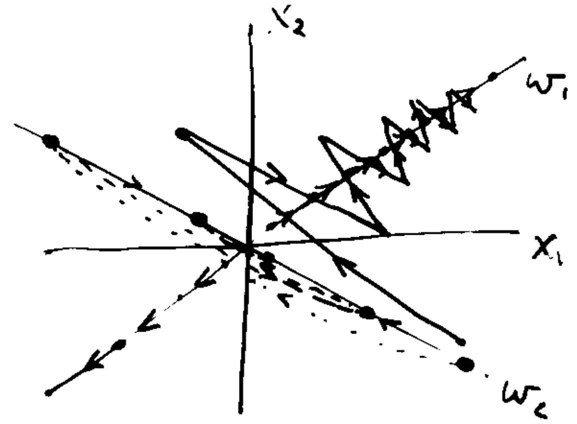


CONTINUOUS

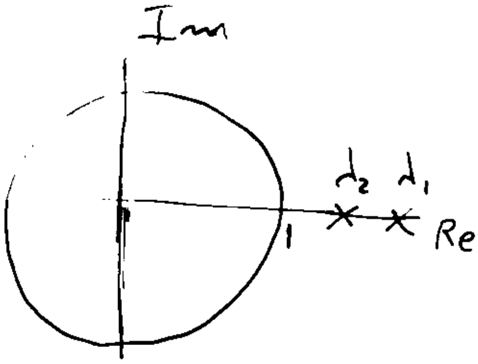




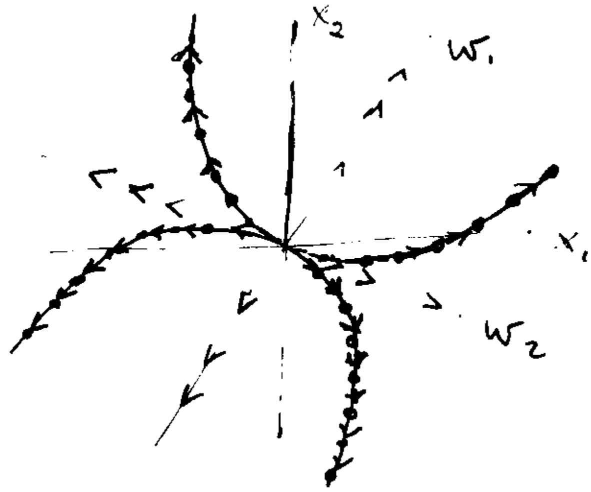
DISCRETE



Negative eigenvalues correspond to oscillations



DISCRETE



Sometimes the dominant eigenvector is not actually approached. It gives the "main" direction of divergence

Studying the stability of the linearized system (eigenvalues $\lambda_1, \dots \lambda_m$ of $J_{\bar{x}}$) can help one assess the stability of the equilibrium $\bar{x}$ in the nonlinear system.

<u>Criterion 1</u> (Stability)

If $Re(\lambda_i) < 0 \quad \forall i$, $\bar{x}$ is asymptotic. stable

<u>Criterion 2</u> (Instability)

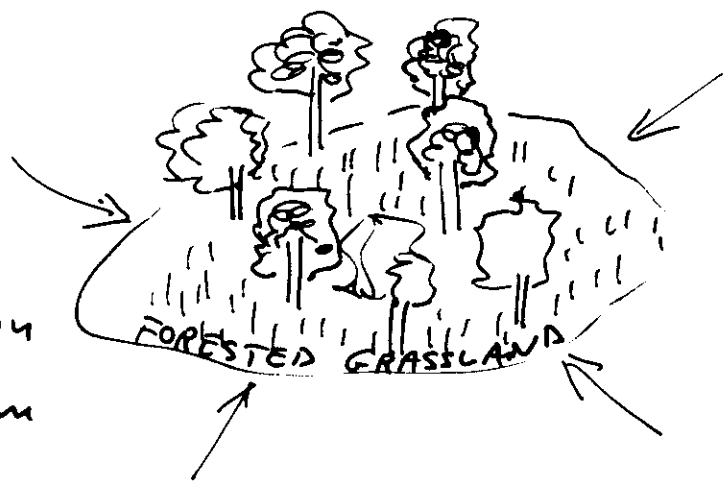
If $Re(\lambda_j) > 0$ for at least one j, $\bar{x}$ is unstable

<u>Remark</u>

If $Re(\lambda_i) \leq 0$ with $Re(\lambda_j) = 0$ for one or more j, $\bar{x}$ may be stable or unstable (Linearization fails! Quadratic terms are important!)

OVERGRAZING DUE TO MIGRATION

In tropical countries there has been a deterioration of forested grassland due to immigration of herbivores from surrounding dry flatlands



$x_1 =$ grass biomass

$x_2 =$ herbivore biomass

$$\dot{x}_1 = r\, x_1 \left(1 - \frac{x_1}{K}\right) - g\, x_1 x_2$$

$$\dot{x}_2 = -m\, x_2 + e\, g\, x_1 x_2 + q$$

$R(x_1) =$ logistic growth rate $= r\left(1 - \frac{x_1}{K}\right)$

$g =$ grazing parameter

$m =$ herbivore natural mortality

$e =$ conversion efficiency

$q =$ immigration rate

STABILITY IN THE OVERGRAZING MODEL

The "generic" Jacobian is

$$J = \begin{bmatrix} r\left(1-\frac{x_1}{K}\right) - r\frac{x_1}{K} - g x_2 & -g x_1 \\ \\ e g x_2 & -m + e g x_1 \end{bmatrix}$$

I. Equilibrium corresponding to overgrazed grassland

$x_1 = 0 \qquad x_2 = \frac{q}{m}$

$$J = \begin{bmatrix} r - g\frac{q}{m} & 0 \\ \\ e g \frac{q}{m} & -m \end{bmatrix}$$

$\lambda_1 = r - g\frac{q}{m} \qquad \lambda_2 = -m$

Low migration $\lambda_1 > 0, \lambda_2 < 0$ <u>SADDLE</u>

High migration $\lambda_1 < 0, \lambda_2 < 0$ <u>STABLE NODE</u>

II. Equilibrium corresponding to non overgrazed grassland (low migration)

$x_1 = \bar{x}_1 > 0 \qquad \bar{x}_2 = \dfrac{q}{m - eg\bar{x}_1}$

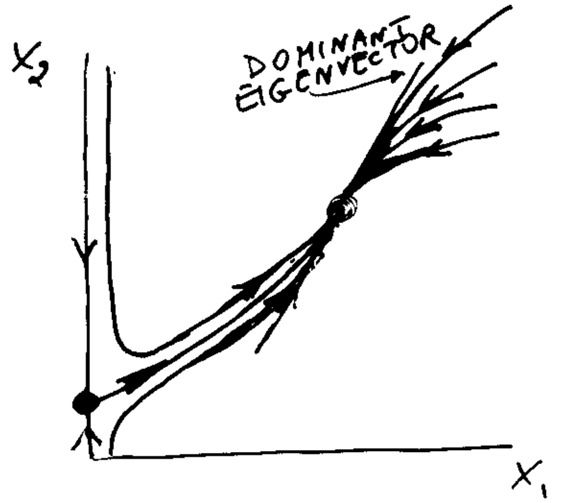
$\bar{x}_1$ solution of $\dfrac{r}{g}\left(1 - \dfrac{x_1}{k}\right)(m - egx_1) - q = 0$

$$J = \begin{bmatrix} r\left(1 - \dfrac{2\bar{x}_1}{k}\right) - g\bar{x}_2 & -g\bar{x}_1 \\ & \\ eg\bar{x}_2 & -m + eg\bar{x}_1 \end{bmatrix}$$

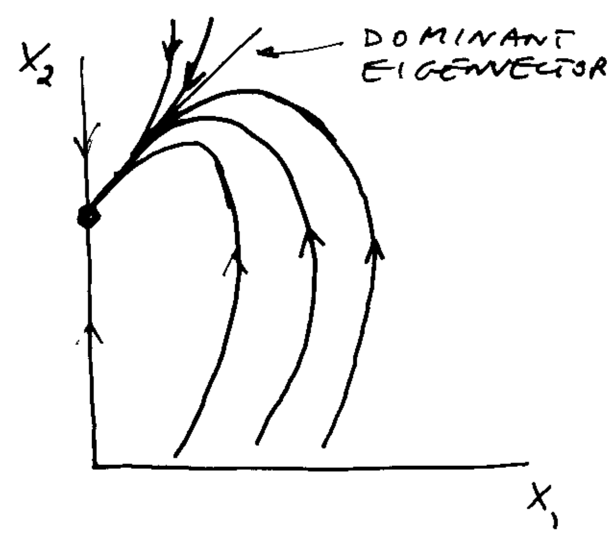
One can show that $Re(\lambda_1, \lambda_2) < 0$.

This equilibrium, when it exists, is a stable node or focus

LOW MIGRATION

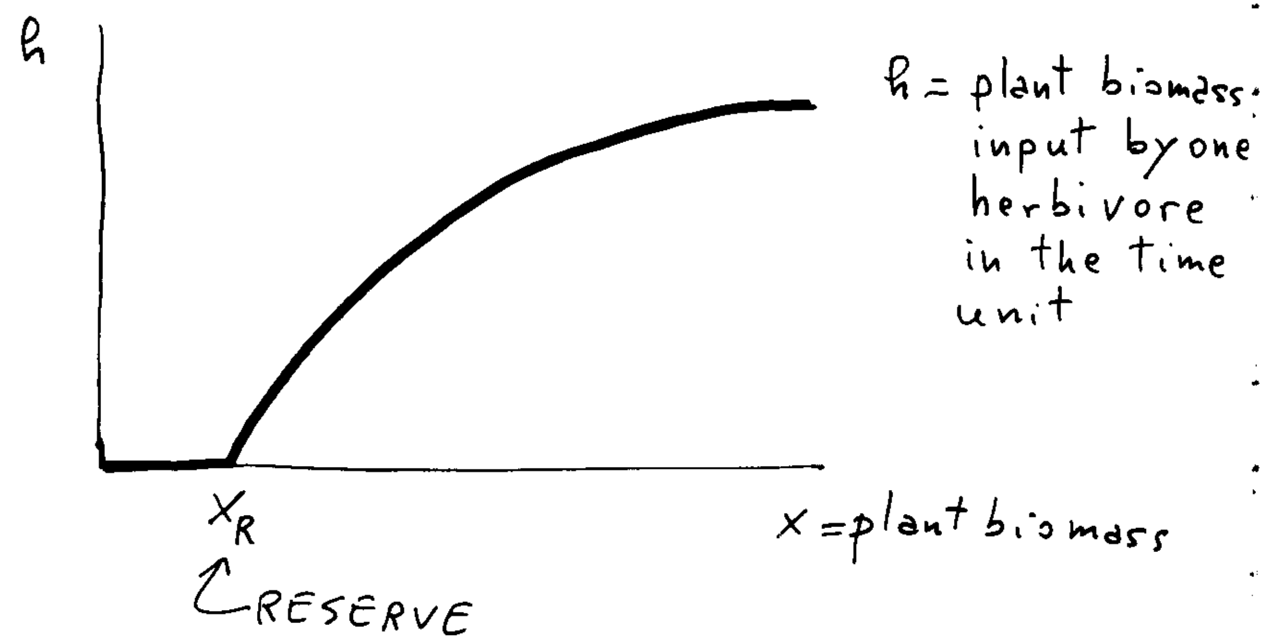


HIGH MIGRATION



MORE REALISM IN DESCRIBING THE GRAZING PROCESS

- Part of the plant biomass is not accessible to herbivores (underground organs, nonpalatable tissues, etc.)
- Each herbivore cannot ingest more than a certain amount of biomass per unit time



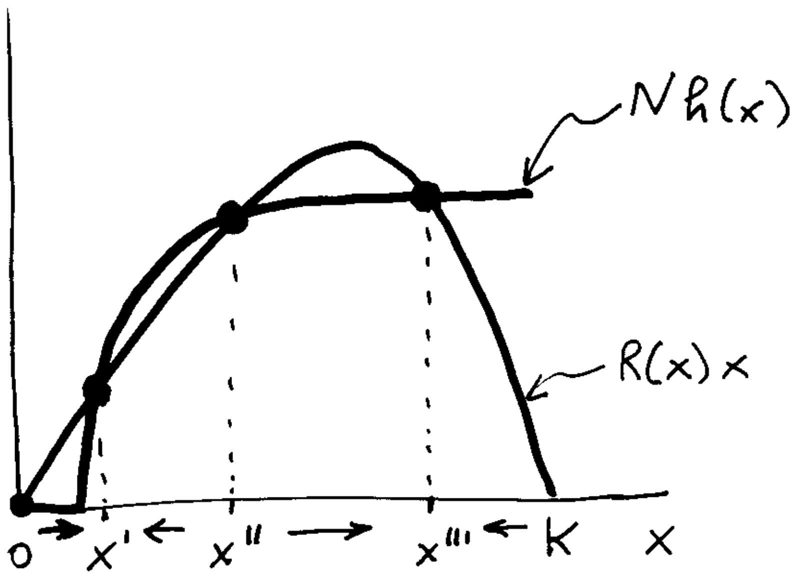
THE NOY-MEIR (1975) MODEL

$$\frac{dx}{dt} = R(x)x - Nh(x)$$

$N =$ No. of herbivores

N is treated as an exogenous parameter

Equilibria and their stability



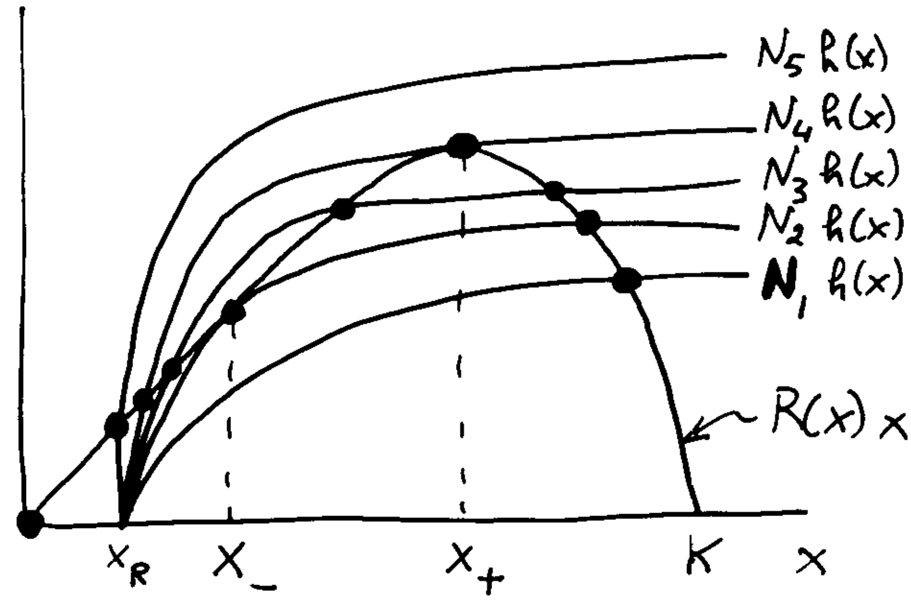
$\dot{x} > 0$ if $0 < x < x'$ or $x'' < x < x'''$

$\dot{x} < 0$ if $x' < x < x''$ or $x > x'''$

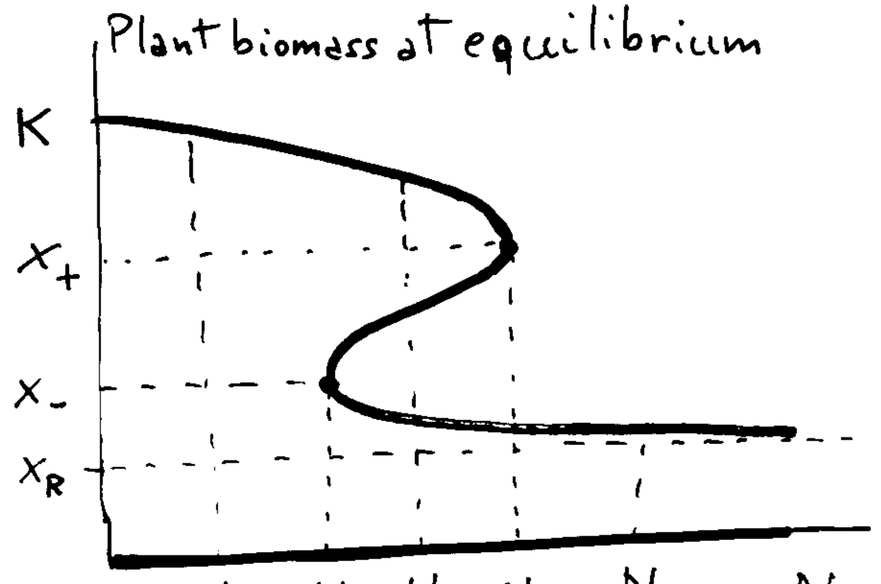
0 and x'' are unstable

x' and x''' are stable

LETTING THE NUMBER N OF HERBIVORES VARY



$N_1 < N_2 < N_3 < N_4 < N_5$



WE CAN HAVE MULTIPLE STABLE EQUILIBRIA

COMPETITION FOR ONE RESOURCE

R = resource $= R_0 - h_1 x_1 - h_2 x_2$

D = resource deficit $= R_0 - R = h_1 x_1 + h_2 x_2$

$$\dot{x}_1 = [r_1 - \gamma_1 (h_1 x_1 + h_2 x_2)]\, x_1$$

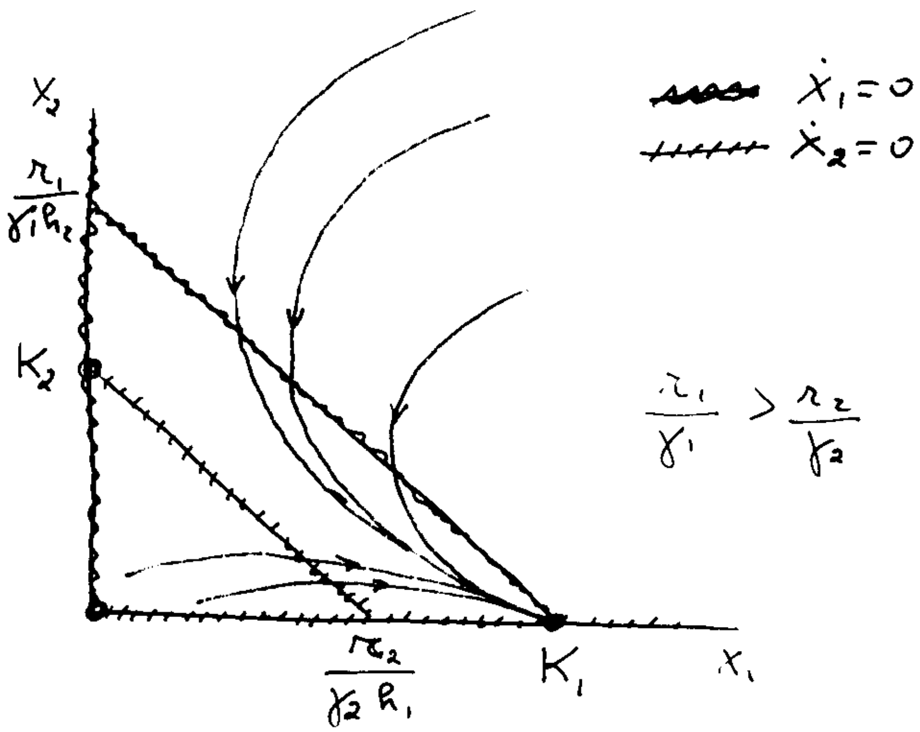
$$\dot{x}_2 = [r_2 - \gamma_2 (h_1 x_1 + h_2 x_2)]\, x_2$$

SENSITIVITY TO RESOURCE DEFICIT

It is a particular kind of Volterra competition model

Exclusion principle

The species with smaller $\frac{r}{\gamma}$ is doomed to extinction



A MODEL OF INTERSPECIFIC COMPETITION

x_1, x_2 = population sizes of competing populations

$$\dot{x}_1 = (r_1 - \beta_1 x_1)x_1 - \beta_{12} x_1 x_2 = \frac{r_1}{K_1}\left(K_1 - x_1 - \alpha_{12} x_2\right)x_1$$

$$\dot{x}_2 = (r_2 - \beta_2 x_2)x_2 - \beta_{21} x_1 x_2 = \frac{r_2}{K_2}\left(K_2 - x_2 - \alpha_{21} x_1\right)x_2$$

VOLTERRA COMPETITION MODEL

r_1, r_2 = intrinsic rates of increase

β_1, β_2 = <u>intra</u>specific competition coefficients

β_{12}, β_{21} = <u>inter</u>specific competition coefficients

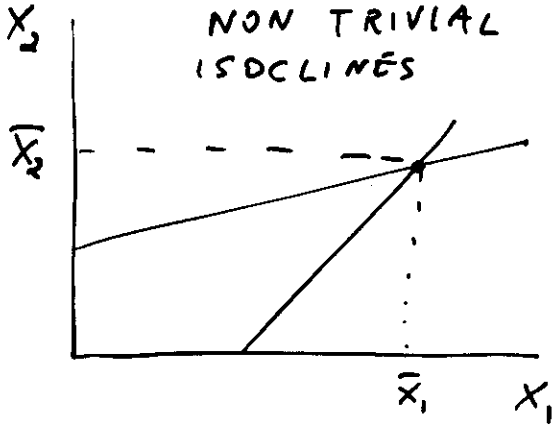
K_1, K_2 = carrying capacities of each population when other population is not present

α_{12}, α_{21} = rescaled <u>inter</u>specific competition coefficients $= \dfrac{\beta_{12}}{\beta_1}, \dfrac{\beta_{21}}{\beta_2}$

A MODEL OF SYMBIOSIS

$$\dot{X}_1 = (r_1 - \beta_1 x_1 + s_1 x_2)\, x_1$$
$$\dot{X}_2 = (r_2 - \beta_2 x_2 + s_2 x_1)\, x_2$$

SYMBIOSIS COEFFICIENTS



EQUILIBRIUM $\bar{x}$ EXISTS ONLY IF $\beta_1 \beta_2 > s_1 s_2$

$$V(x_1, x_2) = \frac{1}{s_1}\left(x_1 - \bar{x}_1 - \bar{x}_1 \ln \frac{x_1}{\bar{x}_1}\right) + \frac{1}{s_2}\left(x_2 - \bar{x}_2 - \bar{x}_2 \ln \frac{x_2}{\bar{x}_2}\right)$$

$$\dot{V}(x_1, x_2) = -\frac{\beta_1}{s_1}(x_1 - \bar{x}_1)^2 + 2(x_1 - \bar{x}_1) - \frac{\beta_2}{s_2}(x_2 - \bar{x}_2)^2$$

It is easy to verify that, with the condition $\beta_1 \beta_2 > s_1 s_2$, this quadratic function is negative definite

$\Downarrow$

STABILITY OF $\bar{x}$, ALL POINTS IN THE POSITIVE QUADRANT ARE ATTRACTED TO $\bar{x}$