'SIMPLE' ECOSYSTEM MODELS (PART I)

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(HAND-OUT)

Reductionism

Reduce an infinitely complex "ecosystem" (i.e. a closed system which is part of nature, with its internal interactions and outside influences) to a set of equations describing it.
→ "modelling"

We assume that:

i) we know the variables that determine the state of the "system" i.e. state variables

ii) we know the interactions between the state variables, and can express them mathematically

iii) the system (or ecosystem) is either closed (i.e. no external influences) or open, but we know exactly what the external influences are, and can express them mathematically

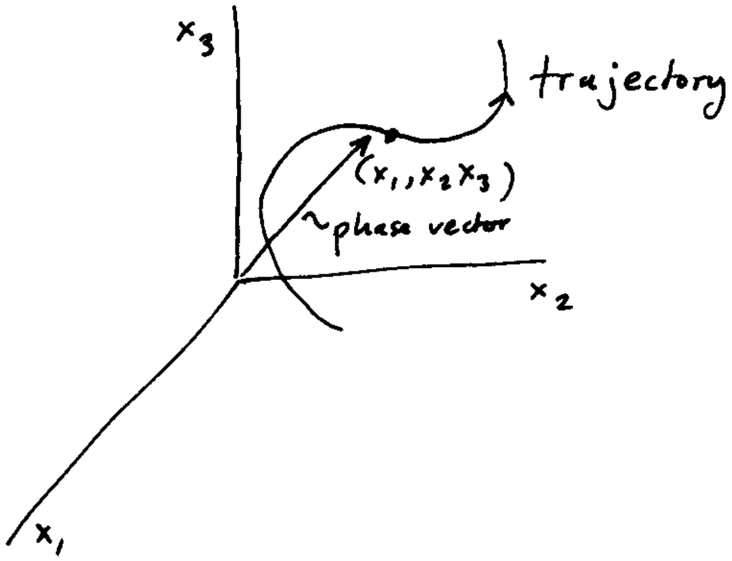
→ can lead to deterministic or stochastic models!

~ "dynamical systems"

Phase space (state space)

in general:
n state variables → n-dimensional state spa

$n = 3$



$x_1, x_2, x_3 =$ state variables

$x_1(t)$, $x_2(t)$, $x_3($

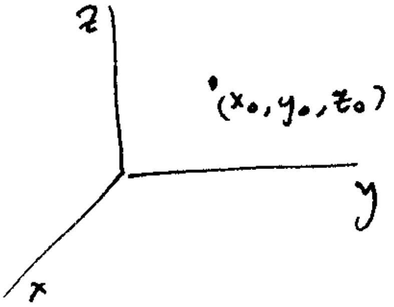
To describe a "system" we must know or choose a sufficient number of independent state variables to describe its behaviour, i.e. $\vec{x}(t)$ must be complete to dimension n. In addition we must know system properties

Example

Spring-mass system

The system properties are k and m.

In addition, we must know x and $v = \frac{dx}{dt}$ at a point in phase space in order to determine behaviour of the system. Knowing $x_0 = x(t_0)$ only is not enough, we mus also know $v_0 = v(t_0)$ to determine $(x(t), v(t)$ at all later time. x, v are state variables making up the phase space.



A stationary point or fixed poin or equilibrium point is where the system stays fixed

$$\vec{x}(t) = \vec{x}(t_0) = \vec{x}_0$$

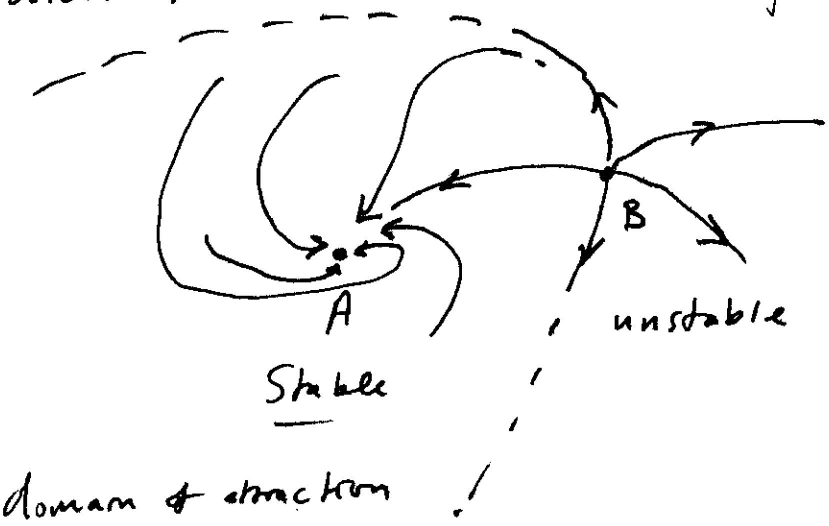
will remain there for all time

A stationary point can be stable (i.e. will return to it when slightly disturbed) or unstable (i.e. system moves away from it when slightly disturbed).

Global stability: if the system returns to a fixed point no matter where it is started from

Neighbourhood stability: if stability is true for displacements in the neighborhood of the fixed point

Region of attraction: the region in phase space which is attracted to a fixed point



domain of attraction
for A

Types of stability

e.g. $X_{n+1} = X_e + k(X_n - X_e)$ discrete system recurrence

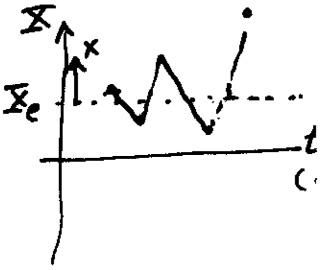
k, X constants

n - n^{th} year

equilibrium if $X_{n+1} = X_n \rightarrow X_n = X_e$

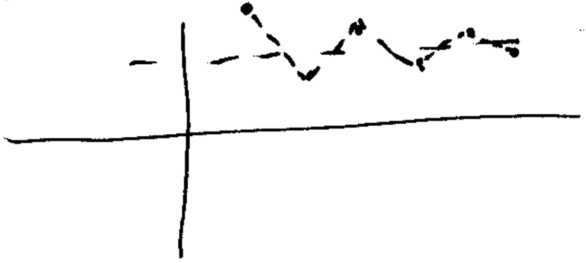
let $X_n = X_e + x_n$

then $x_{n+1} = k\,x_n$

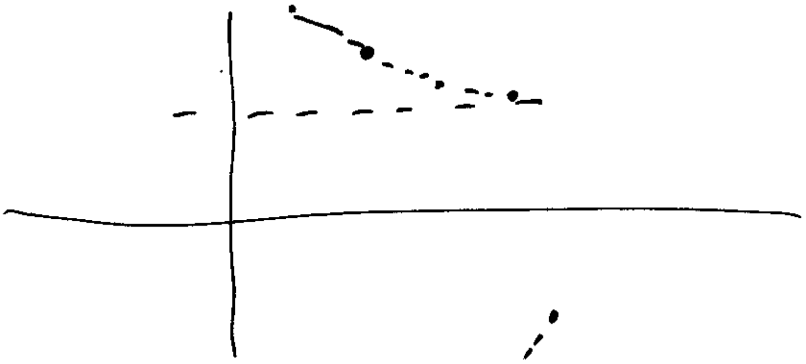


if $k < -1 \Rightarrow$ divergent oscillation

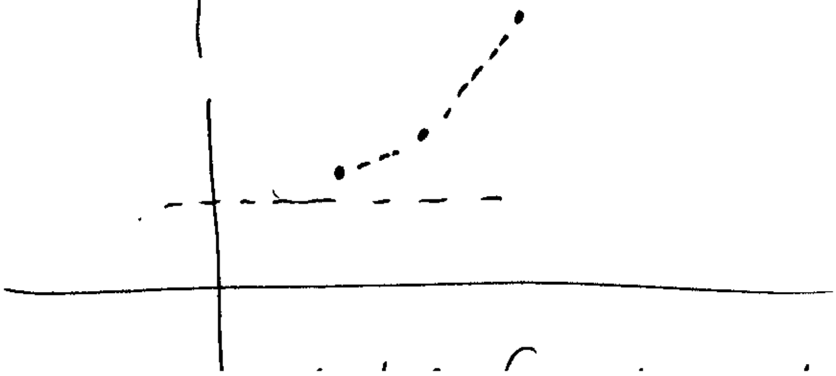
$-1 < k < 0 \Rightarrow$ convergent oscillation



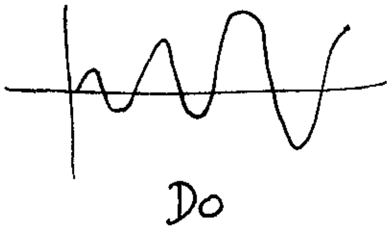
$0 < k < +1$

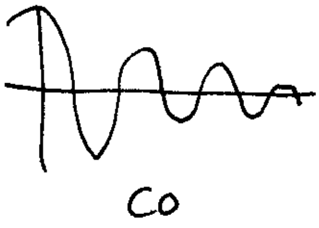


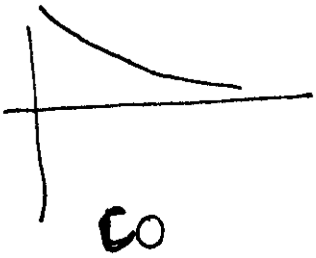
- $k > +1$

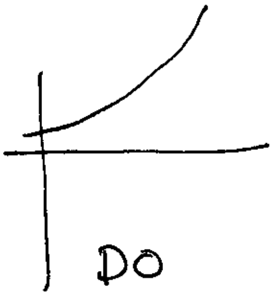


Continuous systems

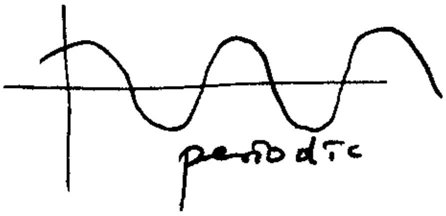




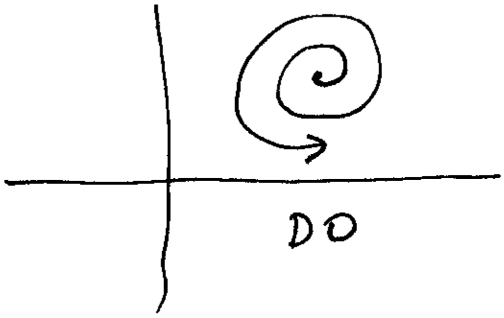


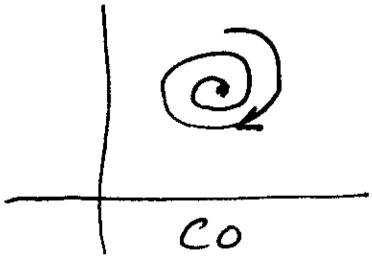


+

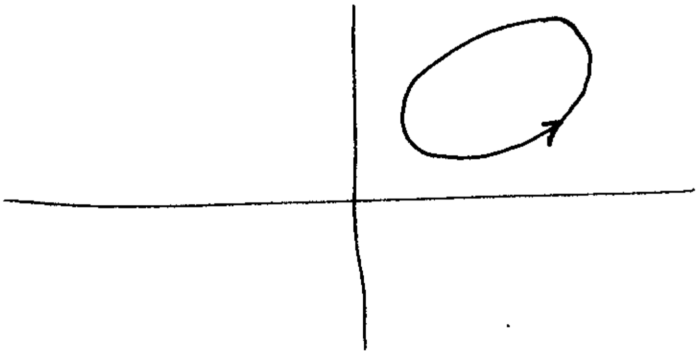


in phase space:

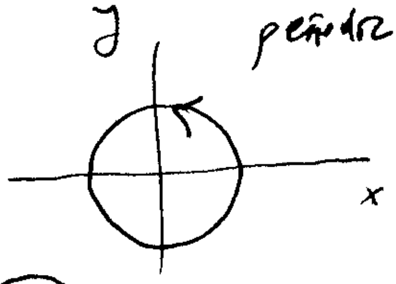




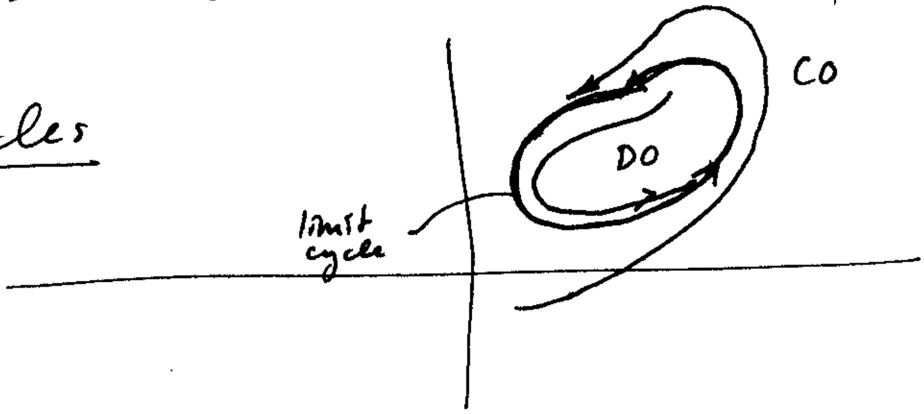
periodic



e.g. $\frac{dx}{dt} = ay$, $\frac{dy}{dt} = -ax$ $\Big\}$ $\frac{dx^2}{dt^2} + a^2 x = 0$

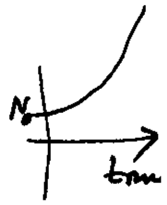


Limit cycles



Single species:

Growth :
$$\frac{dN}{dt} = aN \quad \Rightarrow \underline{N = N_0 e^{at}}$$



population grows indefinitely with growth rate a.

Ultimately a growing population has to limit itself, either by depleting resources, or by disease, death etc. If we put linear limitation (e.g. mortality)

$$\frac{dN}{dt} = \underset{\text{growth}}{\underline{\underline{aN}}} - \underset{\text{mortality}}{\underline{\underline{bN}}}$$

then the behaviour will depend on(a − b, and will become unbounded for a > b.

Most populations can be idealized with some nonlinear form of self limitation, e.g.

$$\frac{dN}{dt} = aN - bN^2$$

which is called the logistics eq^n.

For large time, it is hoped that an equilibrium will be reached. In fact the equilibrium value is

$$N = \left(\frac{a}{b}\right) \qquad \text{for } \frac{dN}{dt} = 0$$

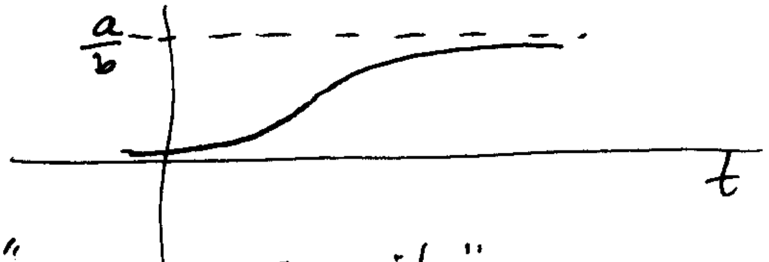
A solution can be seeked in the form $N = e^{at}.x(t)$, then

$$\frac{dN}{dt} = \cancel{a e^{at} x(t)} + e^{at}\frac{dx}{dt} = \cancel{a e^{at} x(t)} - b e^{2at} x^2(t)$$

or $$\frac{dx}{dt} = -b e^{at} x^2 \Rightarrow \underline{-\frac{1}{x^2}\frac{dx}{dt} = b e^{at}}$$

integrates to $$\frac{1}{x} = \frac{b}{a} e^{at} + c \Rightarrow x = \frac{1}{\frac{b}{a} e^{at} + c}$$

$$\therefore N = \frac{a}{b}\left(\frac{e^{at}}{e^{at} + c_0}\right)$$



$\frac{a}{b}$ is called the "carrying capacity".

Stability Analysis:

For single species described by the (generally non-linear) equation

$$\frac{dN}{dt} = \underset{\sim}{F(N(t))}$$

Growth rate $F(N)$. An equilibrium pt will be

$$F(N^*) = 0$$

where N^* is a solution of the above eqn. Let us perturb the equilibrium so that

$$N(t) = N^* + x(t)$$

then Taylor expansion around $F(N^*) = 0$ gives

$$\frac{dN}{dt} = \underbrace{F(N^*)}_{=0} + \left(\frac{\partial F}{\partial N}\right)_{N_*}(N-N_*) + \cdots$$

Neglecting higher order terms

$$\frac{d\,x(t)}{dt} = A\;x(t)$$

where $$A = \left(\frac{dF}{dN}\right)_{N_*}$$

Sol^n $$x = x_0\, e^{At} \Rightarrow N = (N_0 - N_*)\,e^{At}$$

$\underline{\text{unstable for } A >}$

e.g for the logistic growth $$\frac{dN}{dt} = \underbrace{aN - bN^2}_{F(N)}$$

$$\frac{\partial F}{\partial N} = a - 2bN$$

Near the equilibrium pt $N_* = \frac{a}{b}$

$$\left(\frac{\partial F}{\partial N}\right)_{N_*} = a - 2\cancel{b}\,\frac{a}{\cancel{b}} = \underline{\underline{-a < 0}}$$

for $a > 0$

stable for $a > 0$

In general, a multi-species population $(i=1, \dots m)$ has

$$\frac{dN_i(t)}{dt} = F_i\left(N_1(t), N_2(t), N_3(t), \dots N_m(t), t\right)$$

where the growth rate of the i'th species at time t is given by a function F_i of the other species, and time t.

Systems where there is no explicit dependence of F_i on t are called <u>autonomous systems</u>.

$$\frac{dN_i}{dt} = F_i\left(N_1, N_2, \dots N_m\right).$$

The equilibrium populations N_i^* are given by

$$0 = F_i\left(N_1^*, N_2^*, \dots N_m^*\right).$$

Again perturbing about the equilibrium pts,

$$N_i(t) = N_i^* + x_i(t)$$

and Taylor expanding F_i, and keeping first order terms yields

$$\frac{dx_i}{dt} = \sum_{j=1}^{m} a_{ij}\, x_j(t)$$

where

$$a_{ij} = \left(\frac{\partial F_i}{\partial N_j}\right)_*$$

in matrix notation

$$\frac{d\vec{x}(t)}{dt} = A \cdot \vec{x}(t)$$

where $\vec{x}$ is a $m \times 1$ state vector, and A is the $m \times m$ community matrix.

The analogue multispecies solution is

$$x_i(t) = \sum_{j=1}^{M} C_{ij} \, e^{\lambda_j t}$$

where C_{ij} are constants depending on the initial values $N_i(0) = N_1^* + x_1(0)$ perturbed from the equilibrium points. The λ_j are constants which characterize the dynamical behaviour of the system in time

$$\lambda \, x_i(t) = \sum_{j=1}^{m} a_{ij} \, x_j(t)$$

obtained by substituting each solution $e^{\lambda t}$ in to the equations. The above equation is identical to

$$(A - \lambda I)\,\vec{x}(t) = 0$$

which has a solution if

$$\det|A - \lambda I| = 0$$

i.e the λ_j $(j=1,..m)$ are the eigenvalues of the community matrix A.

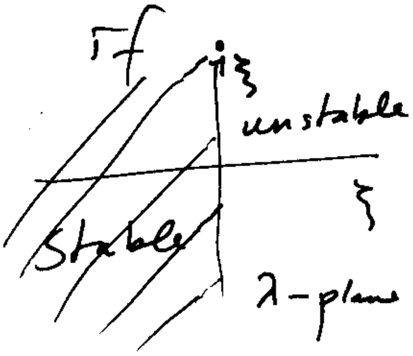
$$\det|A - \lambda I| = 0$$

is an mth order polynomial equation, known as the characteristic eqⁿ. The roots are in general some complex numbers $\lambda = \xi + i\xi$, so that

$$e^{\lambda t} = \underbrace{e^{\xi t}}_{\text{growth/decay}} (\underbrace{\cos \xi t + i\sin \xi t}_{\text{oscillatory part}})$$

Solutions are only stable if

$$\xi = Re(\lambda) < 0$$



Discrete systems:

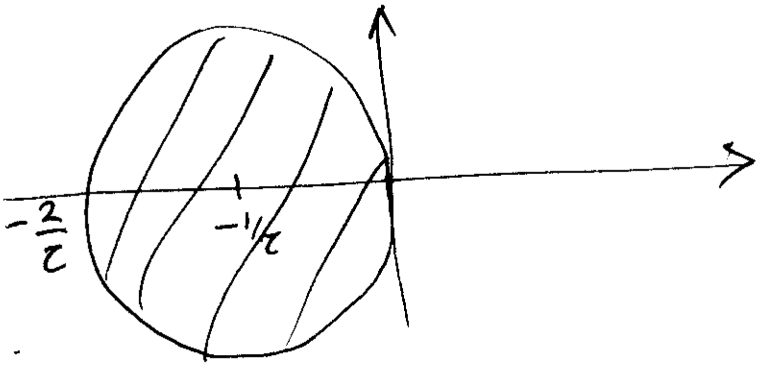
$$\frac{dN_i}{dt} = \frac{N_i(t+\tau) - N_i(t)}{\tau} = F_i(N_1, \ldots N_m)$$

$$\left(\frac{d\vec{x}}{dt} = A\vec{x}\right)$$

let $\cancel{N}_i(t+\tau) = e^{\lambda\tau} \cancel{N}_i(t)$

$$\frac{d\cancel{N}_i}{dt} = \frac{e^{\lambda\tau}\cancel{N}_i(t) - \cancel{N}_i(t)}{\tau} = \frac{e^{\lambda\tau} - 1}{\tau}$$

stability $\left|\frac{e^{\lambda\tau}-1}{\tau}\right| < 0$



discrete systems less stable

additional instability due to discretization.

2-species interaction:

Lotka-Volterra equations

H = prey
P = predator

$$\frac{dH(t)}{dt} = H(t)\left[a - \alpha P(t)\right] = \underbrace{aH}_{\text{growth}} - \alpha \underbrace{PH}_{\text{predation}} \equiv F_1$$

$$\frac{dP}{dt} = P(t)(-b + \beta H(t) = \underbrace{-bP}_{\text{mortality}} + \underbrace{\beta PH}_{\text{predation}} \equiv F_2$$

Equilibrium : $\frac{dH}{dt} = \frac{dP}{dt} = 0 \qquad P_* = \frac{a}{\alpha} \;, \quad H_* = \frac{b}{\beta}$

Stability analysis near (P_*, H_*) :

Community matrix

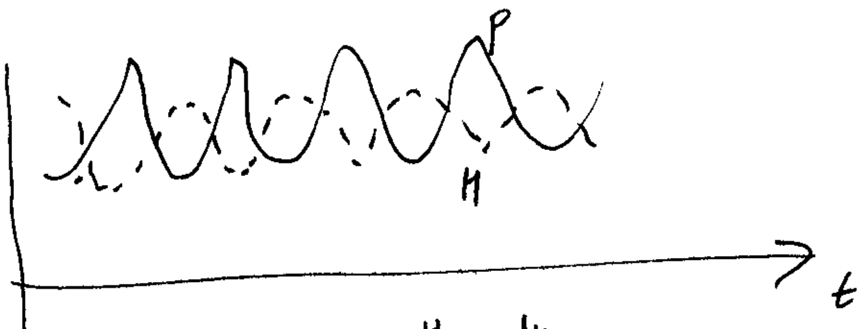
$$A = \begin{pmatrix} \left.\frac{\partial F_1}{\partial H}\right|_* & \left.\frac{\partial F_1}{\partial P}\right|_* \\ \left.\frac{\partial F_2}{\partial H}\right|_* & \left.\frac{\partial F_2}{\partial P}\right|_* \end{pmatrix} = \begin{pmatrix} a - \alpha P_* & -\alpha H_* \\ +\beta P_* & -b + \beta H_* \end{pmatrix}$$

$$= \begin{pmatrix} 0 & -\alpha \frac{b}{\beta} \\ +\beta \frac{a}{\alpha} & 0 \end{pmatrix}$$

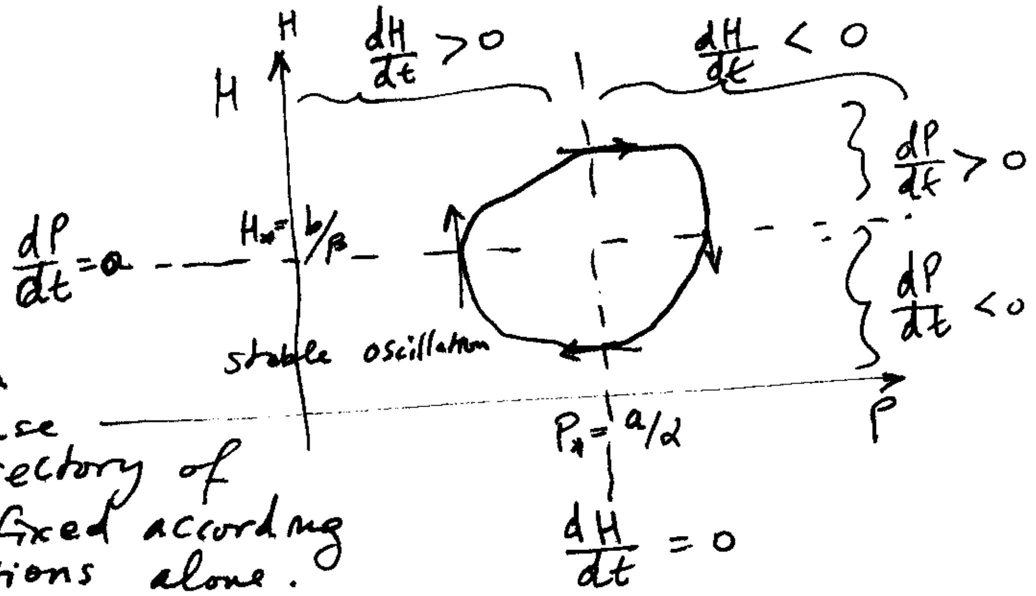
eigenvalues

$$\det \begin{vmatrix} -\lambda & -\alpha b/\beta \\ \beta a/\alpha & -\lambda \end{vmatrix} = 0$$

$$\lambda^2 + ab = 0 \qquad \lambda_{1,2} = \pm i \sqrt{ab}$$



phase space



This is however, a pathological case because the trajectory of the system is fixed according to initial conditions alone.

Volterra equations with logistics

$$\frac{dH}{dt} = aH - \underbrace{AH^2}_{\text{logistic control}} - \alpha HP$$

$$\frac{dP}{dt} = -bP + \beta PH$$

Limits (i) when there is no predator → logistic eqn

(ii) no logistic $A = 0$ prey-predator, conservative

Equilibrium?

$$a - AH_* - \alpha P_* = 0$$

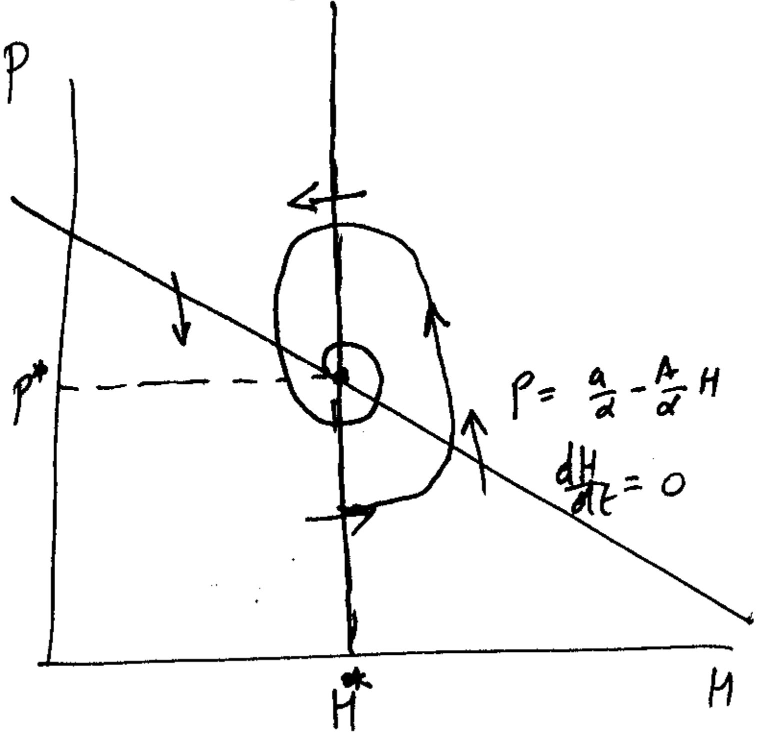
$$-b + \beta H_* = 0$$

$$H_* = \frac{b}{\beta} \qquad P_* = \frac{a}{\alpha} - \frac{A}{\alpha}\frac{b}{\beta}$$

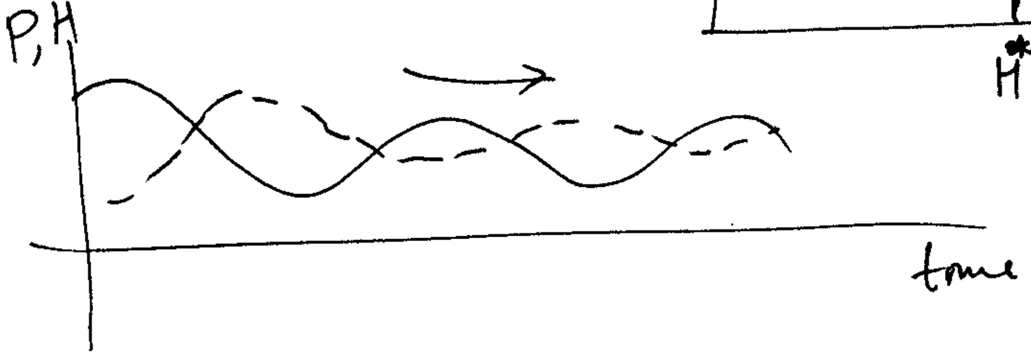
Phase plane:

$$\frac{dH}{dt} = 0 \Rightarrow a - AH - \alpha P = 0$$

$$\frac{dP}{dt} = 0 \Rightarrow -b + \beta H = 0$$



dissipative system.



Other forms of predator – prey systems:

There are a large number of ways in which the various terms in the ecosystem equations are formulated, e.g. the growth, predation and mortality terms are represented, based on biological 'common-sense'.

A simple extension of the predation term is

$$\frac{\alpha HP}{H + D}$$

instead of the αHP term previously used. This simply states that there will be a saturation

Similarly the predator equation has alternatively been given as

$$\frac{dP(t)}{dt} = s\,P(t)\left[1 - \frac{P(t)}{\gamma H(t)}\right]$$

$$= sP - (s/\gamma)\,P^2/H$$

the growth of the Predator occurs linearly and its mortality is proportional to P^2/H i.e. the self-control is of logistic form, but the loss or death increases if less and less amount of prey is available.

A composite model is then

$$\frac{dH}{dt} = rH\left[1 - \frac{H}{K}\right] - \frac{kPH}{H+D}$$

$$\frac{dP}{dt} = sP\left[1 - \frac{P}{\gamma H}\right]$$

An analysis of this system shows equilibrium values

$$P_* = \gamma H_*\ , \qquad 1 - \frac{H^*}{K} - \frac{(k\gamma/r)\,H^*}{H+D} = 0$$

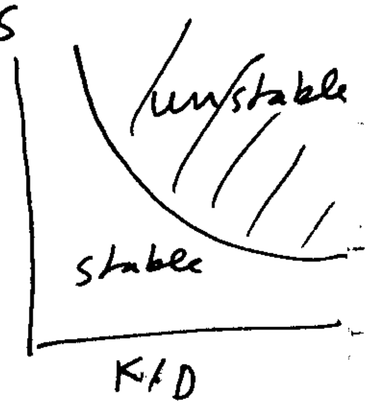
Letting $\alpha = k\gamma/r$, $\beta = D/K$, then

$$H^* = D(1-\alpha-\beta+R)/2\beta$$

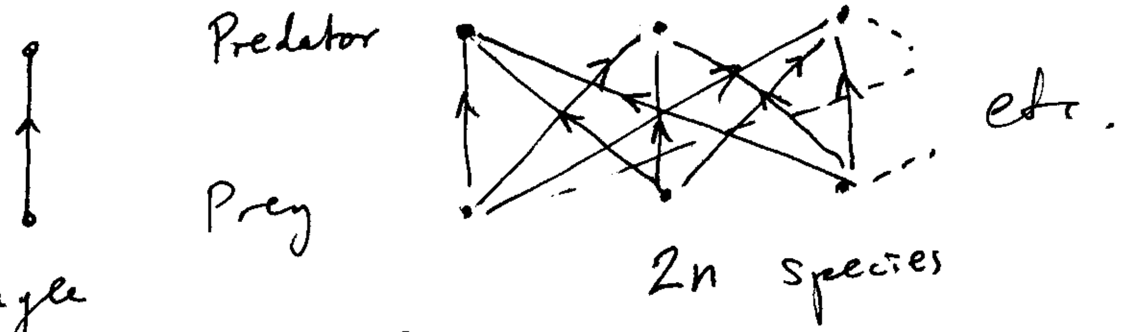
where $R = ((1-\alpha-\beta)^2 + 4\beta)^{1/2}$

Stability: $\lambda^2 + A\lambda + B = 0$

yields $\frac{s}{r} > \frac{2(\alpha-R)}{1-\alpha+\beta+R}$



Multiple prey - multiple predator models



Lotka-Volterra analogue:

$$\frac{dH_i(t)}{dt} = H_i(t)\left[a_i - \sum_{j=1}^{n} \alpha_{ij} P_j(t)\right]$$

$$\frac{dP_i(t)}{dt} = P_i(t)\left[-b_i + \sum_{j=1}^{n} \beta_{ij} H_j(t)\right]$$

$i = 1, 2, \ldots n.$ $a_i, b_i, \alpha_{ij}, \beta_{ij} > 0$

equilibrium points:

$$a_i - \sum \alpha_{ij} P_j = 0 \quad \Rightarrow \quad \underline{\alpha}\, P^* = \underline{a}$$

$$-b_i + \sum \beta_{ij} H_j = 0 \quad \Rightarrow \quad \underline{\beta}\, H^* = \underline{b}$$

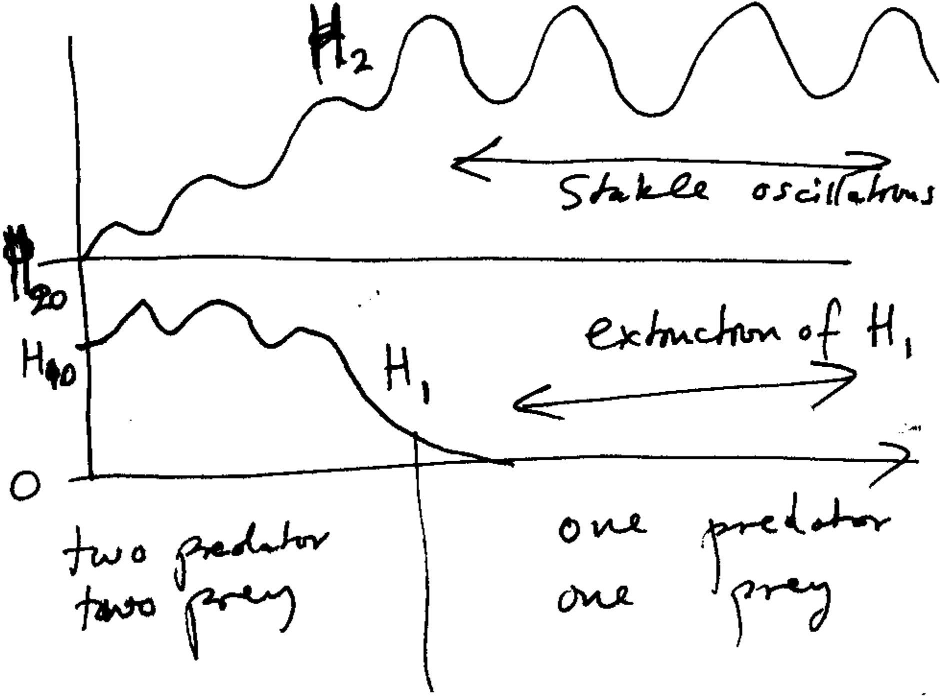
Community matrix $A = \left(\begin{array}{c|c} 0 & -\underline{\alpha}^* \\ \hline \beta^* & 0 \end{array}\right)$

Where $\alpha^*_{ij} = H^*_i$, $\beta^*_{ij} = P^*_i \beta_{ij}$.

The characteristic equation will have $2n$ eigen values in n pairs, each pair having the form $\lambda = (\zeta + i\xi, -\zeta - i\xi)$. Therefore for each eigenvalue with $\mathrm{Re}\,\lambda > 0$, there is a counterpart $\mathrm{Re}\,\lambda < 0$, and the requirement for stability $\mathrm{Re}\,\lambda < 0$ is violated. Either all eigenvalues have $\mathrm{Re}\,\lambda = 0$ and the solutions are <u>neutrally stable</u> oscillations, or at least one eigenvalue has $\mathrm{Re}\,\lambda > 0$, and the system is unstable (May, 1974).

stable sol^{n}s for $n = 2$

Unstable soln for $n=2$



Complexity versus stability? in multispecies interactions:

It has been argued by ecologists that increased trophic web complexity leads to increased community stability. e.g. the rain forest, the paradigm of trophic web complexity, appears very stable, whereas cultivated or planted land with smaller web complexity may be unstable. Is this really true?

One example above, the 2n predator - prey system shows that while the single predator - single prey system has stable oscillations, the more Complex 2n system may be unstable!

There are various other examples of special cases, which show similar results, but often these models exemplify their unwholesome nature and yield results which border on the ridiculous (May, 1974). In fact there is no straightforward link between complexity and stability.

With regard to differences between natural systems and models, it can be said that there can be a great number of ways to make complex systems to be stable, by complicated forms of individual interactions, e.g. spatial heterogeneity, boundary effects, density dependent birth and death rates, damping by losses from the ecosystem (e.g. in chemical or precipitated form) etc. Thus, diversity alone is not the key mechanism which controls stability.

Qualitative stability criteria

The necessary and sufficient conditions for an m × m matrix $A = a_{ij}$ to be qualitatively stable are:

interpretation:

(i) $a_{ii} \leq 0$, all i — no positive feedback

(ii) $a_{ii} \neq$ at least one i — at least one self-stabilizing term

(iii) $a_{ij} a_{ji} \leq 0$ all $i \neq j$ — symbiotic or competitive relations are unstable

Symbiotic (+ +) and competitive (- -) imply similar instability characteristics, and they should be avoided, (+ -) and (- +) interactions are allowed

(iv) for any sequence of 3 or more indices $i, j, k, \dots q, r$, (with $i \neq j \neq k \neq \dots \neq q \neq r$) the product $a_{ij} a_{jk} \dots a_{qr} a_{ri} = 0$

Closed loops should yield ~~zero~~ net result

(v) $\det(A) \neq 0$

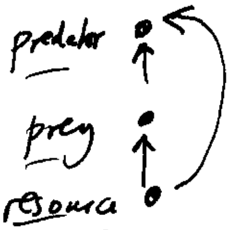
A is non-singular matrix, for system not to be underdetermined

Sometimes, only the signs of A is sufficient:

e.g.

$$A_1 = \begin{pmatrix} - & - & - \\ + & - & - \\ + & + & - \end{pmatrix}$$

for a three component system



is unstable, because it violates (iv)

$$a_{12}\,a_{23}\,a_{31} \neq 0$$

$$a_{13}\,a_{32}\,a_{21} \neq 0 \qquad \text{etc.}$$

if we remove one link,

$$A_2 = \begin{pmatrix} - & - & 0 \\ + & - & - \\ 0 & + & - \end{pmatrix}$$

Satisfies all criteria, so that a simpler web is more stable than a more complex web in this case.

PART II

A general multispecies form of Lotka-Volterra models

We can write a general form

$$\frac{dN_i(t)}{dt} = N_i(t)\left[a_i - \sum \alpha_{ij} N_j(t) \right] = F_i(t)$$

for the various simple forms of the multi-specie ecosystems, including, predator-prey, logistic and, competitive types of interactions in them, for m species, $i = 1, \dots m$.

e.g. we can set

(1) $a_i > 0$, $\alpha_{ij} > 0$ $i,j = 1, \dots n$ $i \neq j$

$a_i = -b_i < 0$, $\alpha_{ij} = -\beta_{ij} < 0$ $i,j = n+1, \dots 2n$ $i \neq j$

to recover the n-predator n-prey system used earlier.

(2) set $\alpha_{ii} \neq 0$ to include logistic term

(3) $a_i > 0$, $\alpha_{ij} \gtrless 0$ $i, j = 1, \dots n$ including $i \neq j$

to model competitive systems

"Simple Ecosystem Models..."

E. OZSOY

(Hand-out)

to derive the community matrix, we note the equilibrium values are given by the solution of the matrix eqⁿ

$$\sum_j \alpha_{ij} N_j^* = a_i$$

and the community matrix $\underline{A} = a_{ij}$ is

$$\underline{A} = a_{ij} = \left.\frac{\partial F_i}{\partial N_j}\right|_*$$

$$= a_i \left.\frac{dN_i}{dN_j}\right|_* - \sum_j \alpha_{ij}\left(N_j \frac{dN_i}{dN_j} + N_i \frac{dN_j}{dN_j}\right)_*$$

$$= \underbrace{a_i}_{\cancel{\sum_j \alpha_{ij} N_j^*} \delta_{ij}} \delta_{ij} - \sum_j \cancel{\alpha_{ij} (N_j^*} \delta_{ij} + N_i^* \delta_{jj})$$

$$= -N_i^* \alpha_{ij}$$

the signs of the community matrix determines the interactions in the system:

		Effect of species j on i (sign of a_{ij})		
		+	0	−
Effect of species i on j (sign of a_{ji})	+	+ +	+ 0	+ −
	0	0 +	0 0	0 −
	−	− +	− 0	− −

+ +	symbiosis or mutualism
− −	competition
+ −	predator-prey / plant-herbivore / host-parasit phyto-zooplankton
0 +	commensalism
0 −	amensalism

Multispecies Models with special symmetries

A. Antisymmetric predator-prey equations

$$\frac{dN_i}{dt} = N_i \left[a_i - \sum_{j=1}^{m} \alpha_{ij} N_j(t) \right]$$

with $\alpha_{ii} = 0$ and $\alpha_{ij} = -\alpha_{ji}$

(similar to n-predator n-prey equations but this is more general, allowing one species to be predator and prey at the same time.

The equilibrium is given as $a_i = \sum_j \alpha_{ij} N_j^*$ and the $a_{ij} = -N_i^* \alpha_{ij}$, the community matrix which is a product of an antisymmetric matrix, has to have eigenvalues, which are all purely imaginary. This is then the pathological case which will only have periodic solutions (neutrally stable). It is also structurally unstable, because the solutions are set by initial conditions alone, and the trajectories will change with a slight change in parameters.

One can show that the quantity

$$\Phi = \sum_{i=1}^{m} \{N_i(t) - N_i^* \ln N_i(t)\}$$

is conserved in the system.

Differentiation yields

$$\frac{d\Phi}{dt} = \sum_i \frac{dN_i}{dt} - \frac{N_i^*}{N_i}\frac{dN_i}{dt}$$

$$= \sum_i \frac{1}{N_i}\frac{dN_i}{dt}(N_i - N_i^*)$$

$$= \sum_i (\underset{\underset{\sum_j \alpha_{ij} N_j^*}{\downarrow}}{a_i} - \sum_j \alpha_{ij} N_j)(N_i - N_i^*)$$

$$= -\sum_{i,j} (N_i - N_i^*)\alpha_{ij}(N_j - N_j^*)$$

$$= 0$$

which vanishes, because α_{ij} and hence the sum of symmetric products, i.e. the quadratic form sums up to zero.

Although elegant, these results are very fragile, because they rely on exact antisymmetry. The system has conservation laws, an equipartition theorem, etc. which are reminescent of classical mechanics conservative systems. This is similar to the 2n predator-prey system because they are both pathological.

B. Competition Equations with Symmetry
(single trophic level)

$$\frac{dN_i}{dt} = N_i \left[a_i - \sum_j \alpha_{ij} N_j \right]$$

$$a_i > 0 \quad , \quad \alpha_{ij} \geqslant 0 \qquad \alpha_{ii} \neq 0 .$$

Because of symmetry, the quadratic form

$$Q(t) = \sum_{i,j} (N_i - N_i^*) \, \alpha_{ij} \, (N_j - N_j^*)$$

is minimized by competition, i.e

$$\frac{dQ}{dt} \leq 0 .$$

N_j^* are the equilibrium values $a_i = \sum_j \alpha_{ij} N_j^*$.

Differentiating Q,

$$\frac{dQ}{dt} = \sum_{i,j} \left(\frac{dN_i}{dt} \alpha_{ij} (N_j - N_j^*) + (N_i - N_i^*) \alpha_{ij} \frac{dN_j}{dt} \right)$$

$$= \sum_{i,j} N_i \Big[\underbrace{a_k}_{\sum_k \alpha_{ik} N_k^*} - \sum_k \alpha_{ik} N_k \Big] \alpha_{ij} (N_j - N_j^*) + (N_i - N_i^*) \alpha_{ij} N_j \Big[\underbrace{a_k} - \sum \alpha_{ik} N_k \Big]$$

$$= - \sum_{ijk} \Big[N_i \alpha_{ik} (N_k - N_k^*) \alpha_{ij} (N_j - N_j^*) + (N_i - N_i^*) \alpha_{ij} N_j \alpha_{jk} (N_k - N_k^*) \Big]$$

because $\alpha_{ij} = \alpha_{ji}$, we can rewrite

$$\frac{dQ}{dt} = -2 \sum_{i=1}^{m} N_i(t) \left[J_i(t) \right]^2$$

where $J_i(t) = \sum_k \alpha_{ik} \left(N_k(t) - N_k^* \right)$

Since $N_i(t) > 0$, $J_i^2(t) \geq 0$,

$$\frac{dQ(t)}{dt} \leq 0$$

Further, if the competition coefficients α_{ij} make up a positive-definite matrix, i.e. all eigenvalues are necessarily real because α_{ij} is symmetric, are also positive. Then the quadratic form $Q(t)$ is also positive definite

$$Q(t) > 0$$

for all population values, except in the equilibrium point where $Q = 0$. This is the definition of a Lyapunov function (~ Hamiltonian in classical mechanics). Consequently the full nonlinear global stability analysis of the system is legitimately described by the local equilibrium linearized analysis. The landscape in $N_1 \dots N_m$ coordinates is a simple valley, and system trajectories minimize Q to reach the stable point where $Q = 0$ (minimize 'energy').

Note that as α_{ij} is symmetric all the eigenvalues of $a_{ij} = -N_i^* \alpha_{ij}$ are real and negative $(\lambda_i < 0)$, so that the solutions are exponentially decaying.

Although very specific, This case is less fragile than the antisymmetric case, because a small variation from perfect symmetry seems to be tolerated well,

If $\alpha_{ij} = \alpha_{ij} + \epsilon_{ij}$ where ϵ_{ij} are small, then the eigenvalues of $A' = A + \epsilon B$ differ from the original eigenvalues by $O(\epsilon)$, where ϵ is small.

Further if a single species is added by augmenting the system to $m+1$ equations the smallest eigenvalue, which characterises system stability decreases, making the system less stable. i.e. the more species we have the less stable is the system.

Competition between two species

Lotka - Volterra eq^n s

$$\frac{dN_1}{dt} = N_1\,(a - bN_1 - cN_2)$$

$$\frac{dN_2}{dt} = N_2\,(\underbrace{e - fN_2}_{\substack{\text{logistic}\\ \text{control}}} - \underbrace{gN_1}_{\text{competition}})$$

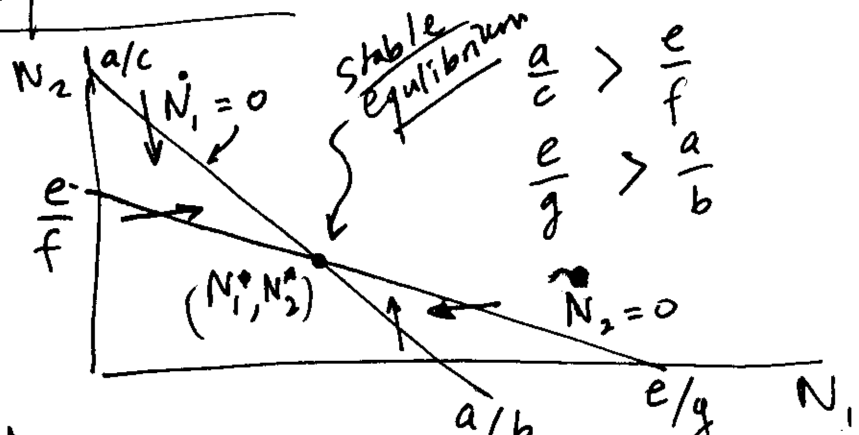
$$\frac{dN_1}{dt} = 0 \quad \Rightarrow \quad bN_1 + cN_2 - a = 0$$

$$\frac{dN_2}{dt} = 0 \quad \Rightarrow \quad fN_2 + gN_1 - e = 0$$

Two types of equilibria :

Type A.

'peaceful coexistence'



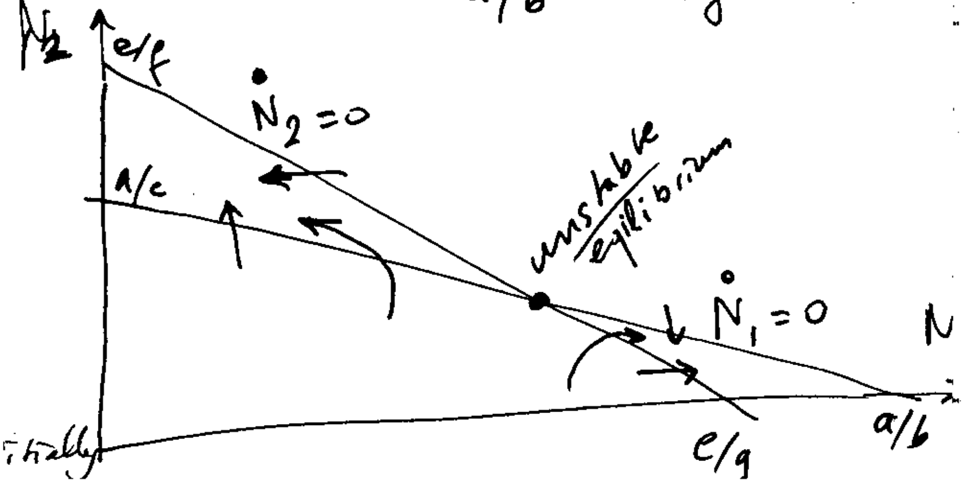
$\frac{a}{c} > \frac{e}{f}$

$\frac{e}{g} > \frac{a}{b}$

Type B

$\frac{e}{f} > \frac{a}{c}$

$\frac{a}{b} > \frac{e}{g}$



[illegible] species initially

can write

$$\frac{dN_1}{dt} = aN_1\left(1 - \frac{b}{a}N_1 - \frac{c}{a}N_2\right)$$

$$\frac{dN_2}{dt} = eN_2\left(1 - \frac{f}{e}N_2 - \frac{g}{e}N_1\right)$$

Condition for stability:

$$\frac{b}{a} > \frac{g}{e}$$

$$\frac{f}{e} > \frac{c}{a}$$

means that either species has to inhibit its own growth more than it inhibits its competitor.

If ~~that~~ two species are limited by different resources, this is more likely to hold, i.e. they are stable; if they use the same resources one of the two species is likely to be more efficient and will eliminate its competitor (unstable).

Gause's exclusion principle: two species with identical requirements cannot co-exist in a habitat.

balowma

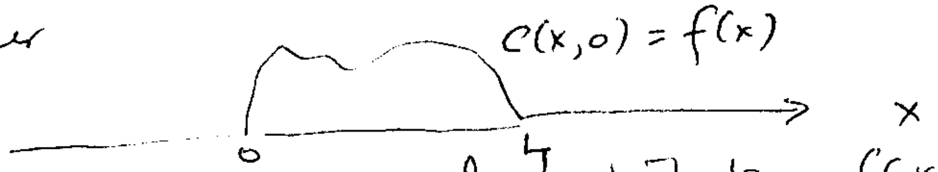
Diffusion takes place over the surface S, and growth takes place within the volume V contained in it. Then

$$\frac{\left(D \frac{\partial c}{\partial n}\right) \cdot S}{(\alpha) . V} \propto \frac{S}{V} \sim \frac{1}{r}$$

diffusion plays an increasing role for a smaller water mass, and there is a minimum size below which production can not compensate diffusion, and the plankton population can not increase; it has to decay. This size $L_c = [L]$ depends on two parameters $\alpha = [T^{-1}]$ and $D = [L^2 T^{-1}]$ and dimensional analysis leads to

$$L_c = c\left(\frac{D}{\alpha}\right)^{1/2} \quad \text{where } c \text{ is a constant}$$

Consider



an initial one-dimensional distribution $f(x)$ of plankton confined to $(0, L)$, whose development is determined by

$$\frac{dc}{dt} = D \frac{\partial^2 c}{\partial x^2} + \alpha S$$

with b.c. $c(0) = c(L) = 0$.

Diffusive effects,

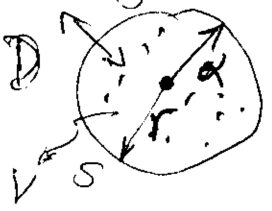
Plankton Patchiness:

Most distributions of biological organisms are 'patchy', i.e. form aggregates, rather than being uniform or random.

Mechanisms
- reaction to medium properties
- circulation cells (e.g. Langmuir cells)
- exclusion of certain zooplankton by phytoplankton
- food chain associations; predator-prey relationships
- swarming and schooling behaviour

However the basic mechanism opposing patchiness is the same: patchiness is destroyed by diffusion; and some of the above mechanisms could balance it.

The simplest model is a balance of growth (production) versus diffusion.



Consider a water mass within which plankton growth at rate α takes place. Assume that the population is confined to this water mass and does not exist outside. Then diffusion (with diffusivity D) would try to smooth out what is produced.

The time dependent solution is

$$c(x,t) = \sum_{n=1}^{\infty} A_n \sin\frac{n\pi x}{L}\, e^{\left(\alpha - \frac{Dn^2\pi^2}{L^2}\right)t}$$

where $A_n = \frac{2}{L}\int_0^L f(x)\sin\frac{n\pi x}{L}\,dx$.

Note that terms with $\alpha > \frac{Dn^2\pi^2}{L^2}$ will increase indefinitely with time, resulting in a bloom. On the other hand if $\alpha < \frac{D\pi^2}{L^2}$ then all terms will decay. Thus the balance for at least one term to survive requires $L > L_c$ such that

$$L_c = \pi (D/\alpha)^{1/2}$$

More general Advection - Diffusion problems for passive organisms :

In general, the distribution of passive material is determined by

$$\frac{\partial c_i}{\partial t} + \vec{u}\cdot\nabla c_i = \nabla\vec{D}\cdot\nabla c_i + \underbrace{F(c_i,t,x,y,z)}_{\text{source function}}$$

where 'passive' means material that does not display aggregative or swimming behaviour.

One-dimensional examples:

Single Species with logistic growth.

$$\frac{\partial c}{\partial t} = D\frac{\partial^2 c}{\partial x^2} + \alpha S - \beta S^2$$

Can have travelling fronts $c(x,t) = c(x-ut)$

$$u \geqslant 2(\alpha D)^{1/2} = 2\alpha^{\text{[illegible]}} L_c$$

or steady-state can be obtained

$$D\frac{\partial^2 c}{\partial x^2} + \alpha S - \beta S^2 = 0$$

Grazing

$$\frac{\partial c}{\partial t} = D\frac{\partial^2 c}{\partial x^2} + \alpha c - \underbrace{R_m\left[1 - e^{-\lambda(c-c_0)}\right]}_{\text{Ivlev function}}$$

$$L_c = \pi\left(\frac{D}{\alpha - R_m\lambda}\right)^{1/2} \quad \text{for} \quad c_0 = 0, \ \alpha > R_m\lambda$$

Predator-Prey system

$$\frac{\partial c_1}{\partial t} = D_1\frac{\partial^2 S_1}{\partial x^2} + a_1 S_1 - b_1 S_1 S_2$$

$$\frac{\partial c_2}{\partial t} = D_2\frac{\partial^2 S_2}{\partial x^2} \text{[illegible]} a_2 S_2 + b_2 S_1 S_2$$

Equilibrium pts $c_1 = c_1^* = a_2/b_2 \quad c_2 = c_2^* = a_1/b_1$

Linearize about equilibrium points

$$c_1 = a_2/b_2 + c_1'$$

$$c_2 = a_1/b_2 + c_2'$$

$$\frac{\partial c_1'}{\partial t} = D_1 \frac{\partial^2 c_1'}{\partial x^2} - \frac{a_2 b_1}{b_2} c_2'$$

$$\frac{\partial c_2'}{\partial t} = D_2 \frac{\partial^2 c_2'}{\partial x^2} + \frac{a_1 b_2}{b_1} c_1'$$

b.c.

① $c_1' = c_2' = 0$ on $x = 0, L$

or ② $D_1 \frac{\partial c_1'}{\partial x} = D_2 \frac{\partial c_2'}{\partial x} = 0$ on $x = 0, L$

for ①: sine transforms

$$\Gamma_i = \int_0^L c_i' \sin \frac{m\pi x}{L} \, dx \qquad i = 1, 2; \quad m = 1, 2 \ldots$$

then

$$\frac{\partial \Gamma_1}{\partial t} = -\frac{m^2\pi^2}{L^2} D_1 \Gamma_1 - \frac{a_2 b_1}{b_2} \Gamma_2$$

$$\frac{\partial \Gamma_2}{\partial t} = -\frac{m^2\pi^2}{L^2} D_2 \Gamma_2 + \frac{a_1 b_2}{b_1} \Gamma_1$$

let $\Gamma_i = A_i e^{\lambda t}$,

then

$$\lambda = \frac{1}{2}\Big[\underbrace{-\frac{m^2\pi^2 (D_1 + D_2)}{L^2}}_{\text{negative real part decaying sol}^n} \pm \underbrace{\Big\{ \frac{m^4\pi^4 (D_1 - D_2)^2}{L^4} - 4a_1a_2 \Big\}^{1/2}}_{\text{imaginary for large } a_1, \text{ oscillatory}} \Big]$$

Sol^n is stable, going to c_1^*, c_2^* as $t \to \infty$.

with ②: cosine series will get same equations, but including $m = 0$, so that the smallest λ will be $\lambda = \pm i\sqrt{a_1a_2}$, pure oscillatory: neutral stability. other modes will

no patchiness

Travelling solutions

- let $D_1 = 0$, then

$$c_1(t,x) = \underbrace{f_1(x)}_{\text{initial prey distribution}} e^{\{a_1 t - b_1 \int_0^t c_2(t',x)\,dt'\}}$$

and

$$\frac{\partial c_2}{\partial t} = D_2 \frac{\partial^2 c_2}{\partial x^2} - a_2 c_2 \left[1 - \frac{b_2}{a_2} f_1(x)\, e^{\{a_1 t - b_1 \int c_2(t',x)dt'\}} \right.$$

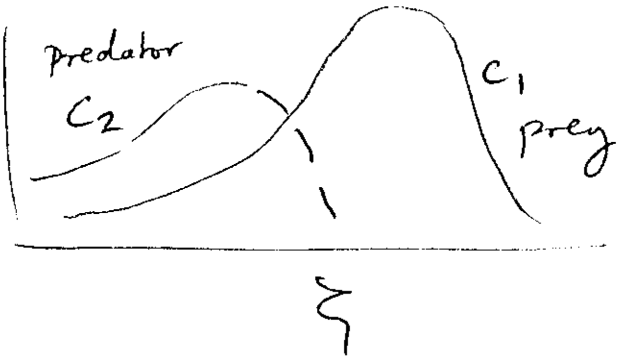
let $f_1(x) = A e^{-k|x|}$, $A, k > 0$

Assymptotic solution for large $\xi = x - ut$,

$$c_1(\xi) \sim A e^{-\xi}$$

$$c_2(\xi) \sim \frac{1}{\Gamma(\nu+1)} \left(\frac{A b_2}{k^2 \nu^2}\right)^{\nu/2} e^{-\left(\frac{a_2}{D_2}\right)^{1/2} \xi}$$

travelling wave solutions



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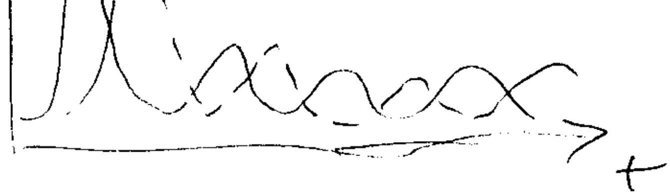
* Oscillatory wave-like solutions

with $D_1 = D_2$, $a_2 = 0$



Spread of epidemics – Black Death in Europe