Interspecific competition, phase plane, eigenvalues & eigenvectors

Vincent Jansen

vincent.jansen@rhul.ac.uk

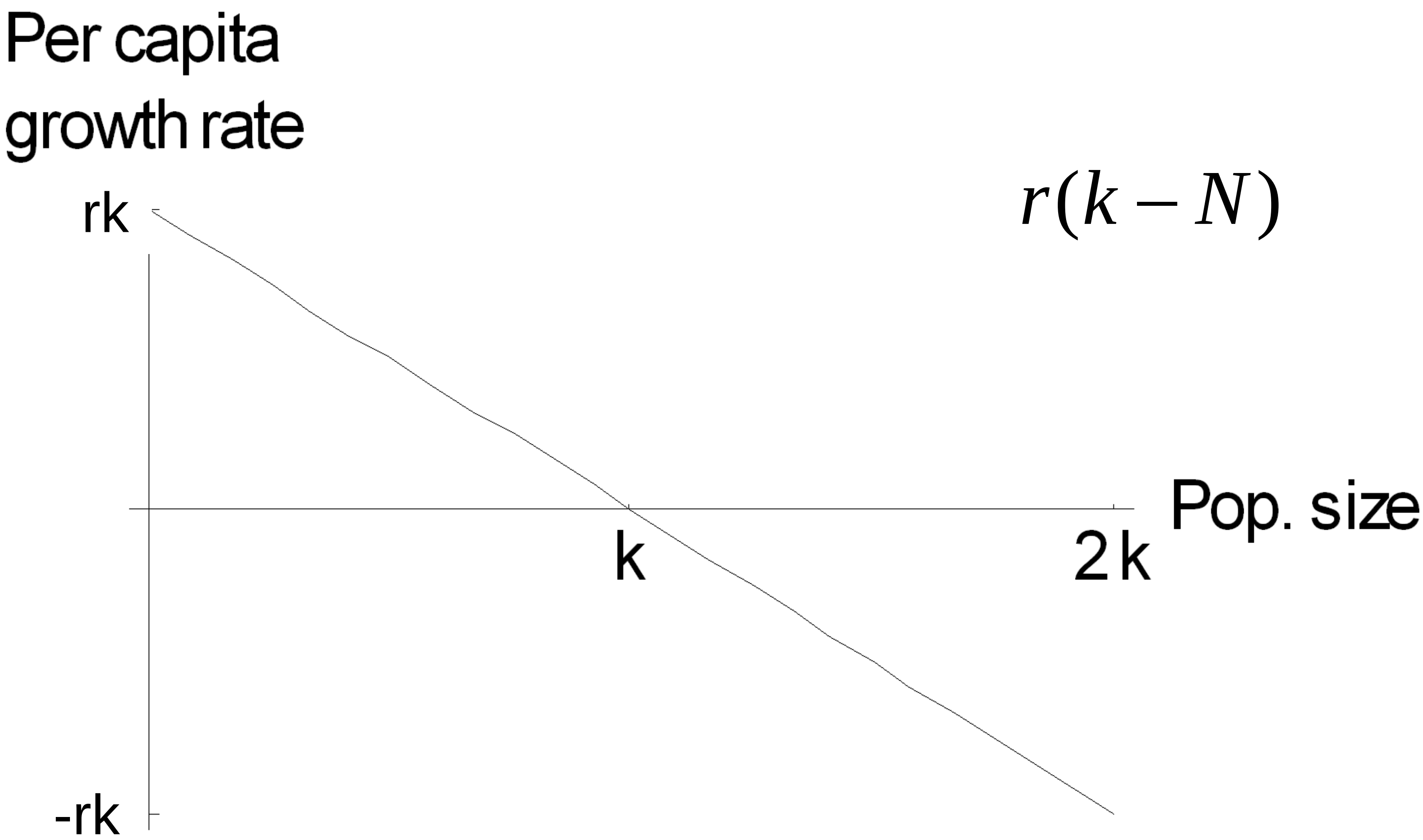
Outline

- Intraspecific and interspecific competition
- Gause’s experiments
- Generalised logistic growth
- The Lotka-Volterra interaction model
  - Competitive exclusion,
  - Coexistence,
  - Alternative stable states
- Apparent competition

Intraspecific competition

- Competition between individuals of the same species reduces the *per capita* growth rate
- This can be for various reasons
  - Competition for resources (exploitation competition)
  - Direct effects (e.g. fighting, allelopathy, interference competition)
- This motivated the logistic model for density dependent growth

Logistic Growth



Interspecific competition

- Competition between individuals of different species also has the potential to reduce the growth rate
- This can be for the same reasons
  - exploitation competition
  - interference competition

Interspecific competition

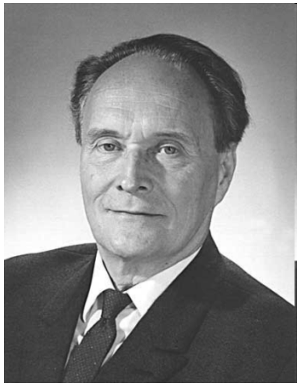
	Rodents removed	Ants removed	Rodents and ants removed	control
Ant colonies	543	-	-	318
Rodent nrs	-	144	-	122
Seed density relative to control	1.0	1.0	5.5	1.0

Competition between rodents and granivorous ants (After Brown and Davidson, 1977)

Interspecific competition

- Species coexist, but often do better in each other’s absence
- Conclusion: competition reduces the population size of the competitors

Gause’s experiments



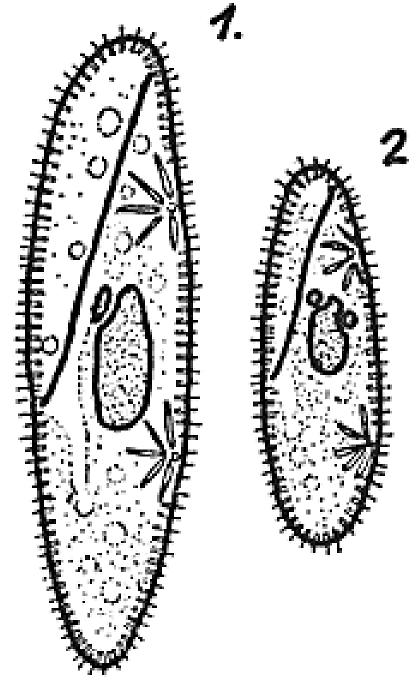
- G. F. Gause (1934) studied the competition between protozoans
- He asked ‘will one species … drive the other one out completely, or will a certain equilibrium become established between them? ‘

Gause’s experiments

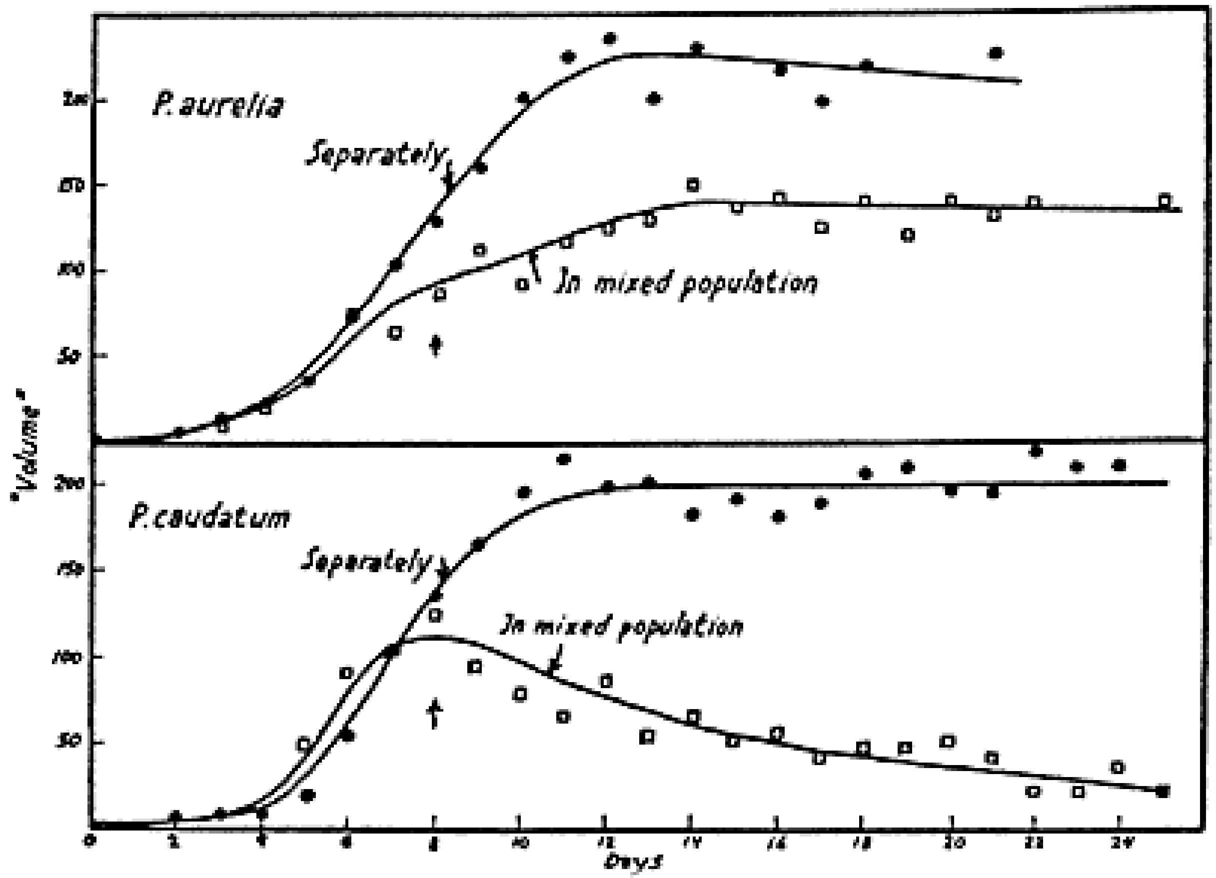
Gause’s experiments

- Next look at the competition between two very similar species:

1. *Paramecium caudatum*
2. *Paramecium aurelia*



Gause's experiments



- He found exclusion of one species by another

Logistic Growth

- Intraspecific competition can be described by the logistic model

$$\frac{dN}{dt} = r(k - N)N$$

- The per capita growth rate decreased with increasing population size:

$$r(k - N)$$

Generalised Logistic Growth

- To describe competition between two species we will use

  N_1: size of pop. of species 1

  N_2: size of pop. of species 2

- The max. per capita growth rate of species 1 is r_1, the carrying capacity of species 1 is k_1 (r_2, k_2 for species 2)

Generalised Logistic Growth

- We will assume that the *per capita* growth rate of species 1 will decrease with the density of species 1 and species 2:

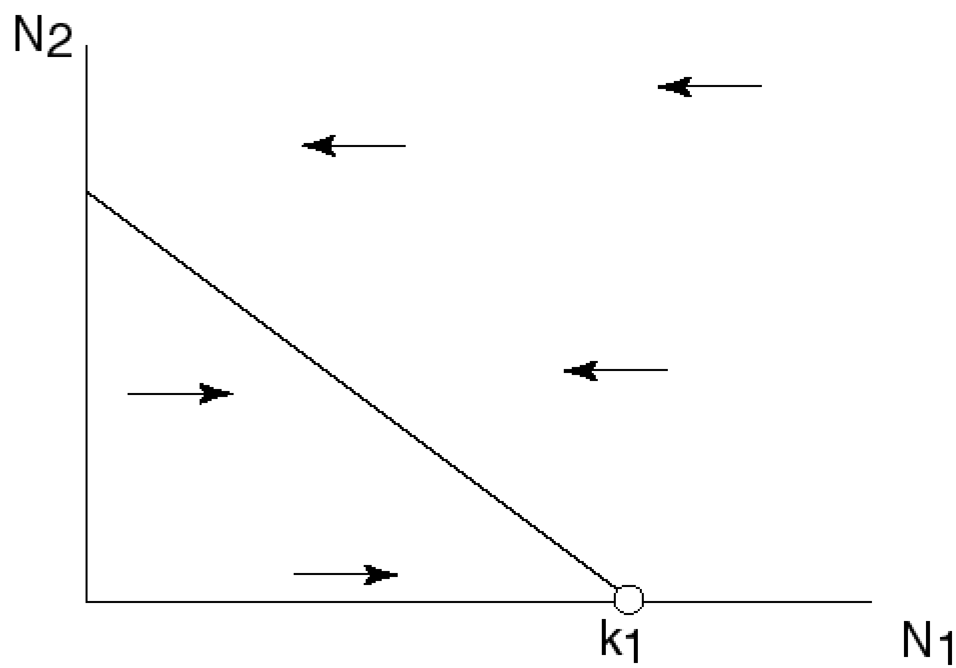
$$r_1(k_1 - N_1 - \alpha N_2)$$

- α is the competition coefficient (also called the equivalence number)
- Population growth of species 1:

$$\frac{dN_1}{dt} = r_1(k_1 - N_1 - \alpha N_2)N_1$$

Generalised Logistic Growth

- If the density of species 2 is constant, interspecific competition results in a reduction of the carrying capacity for species 1:



$$N_1 = k_1 - \alpha N_2$$

Generalised Logistic Growth

- Similarly, for the *per capita* growth rate of species 2 we assume:

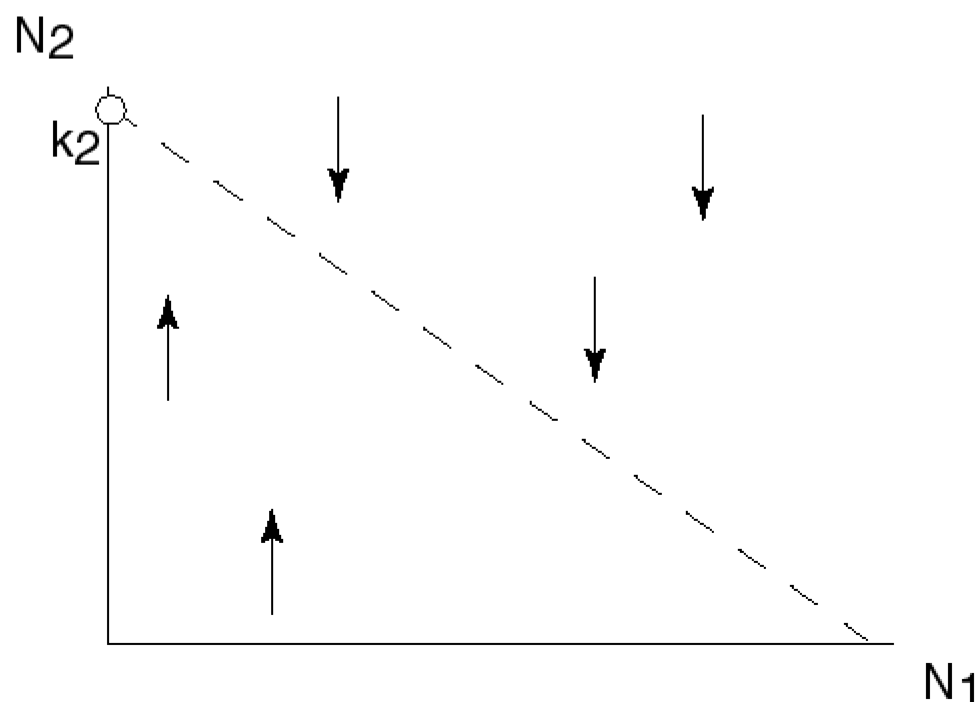
$$r_2(k_2 - \beta N_1 - N_2)$$

- β is the competition coefficient (also called the equivalence number)
- Population growth of species 2:

$$\frac{dN_2}{dt} = r_2(k_2 - \beta N_1 - N_2)N_2$$

Generalised Logistic Growth

- If the density of species 1 were constant, interspecific competition results in a reduction of the carrying capacity for species 2:



$$N_2 = k_2 - \beta N_1$$

Lotka-Volterra interaction model

- The densities of the two species change simultaneously
- This is described by a system of 2 differential equations:

$$\frac{dN_1}{dt} = r_1(k_1 - N_1 - \alpha N_2)N_1$$

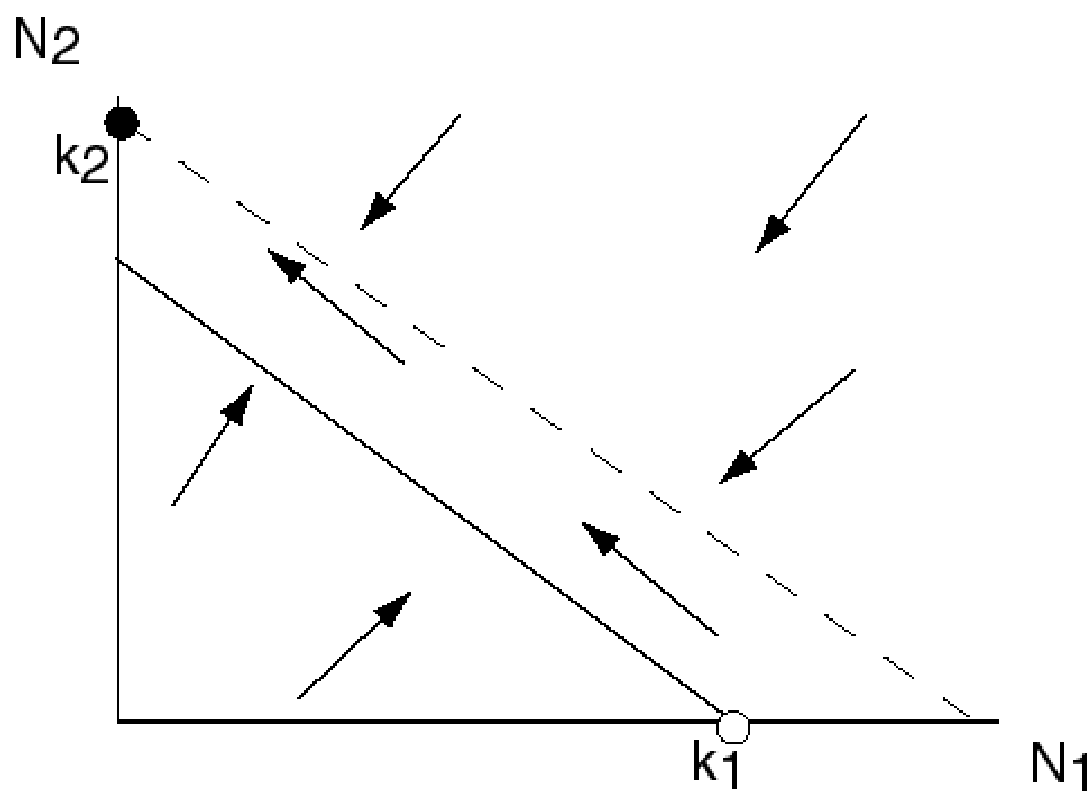
$$\frac{dN_2}{dt} = r_2(k_2 - \beta N_1 - N_2)N_2$$

- This model is known as the Lotka-Volterra interaction model

Lotka-Volterra interaction model

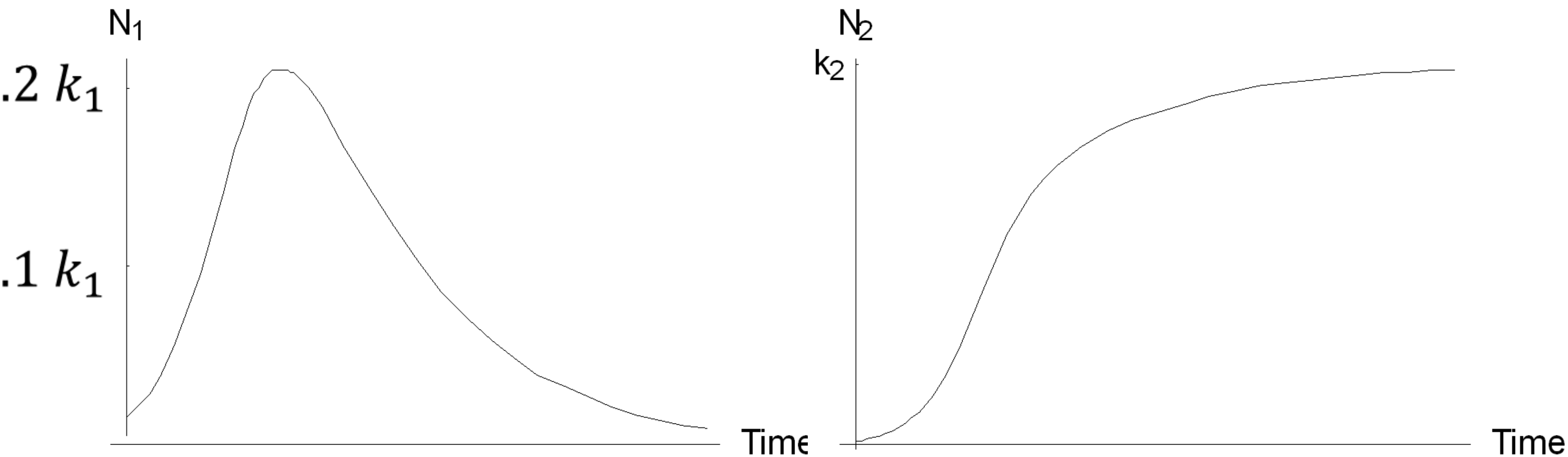
- The curves on which either species does not grow are called isoclines
- The isoclines delimit the parts of the state space for which the density of that species increases or decreases in number
- By combining the isoclines for the two species we can get an idea of the population dynamics

Lotka-Volterra interaction model: exclusion



Lotka-Volterra interaction model: exclusion

- Species 2 outcompetes and excludes species 1

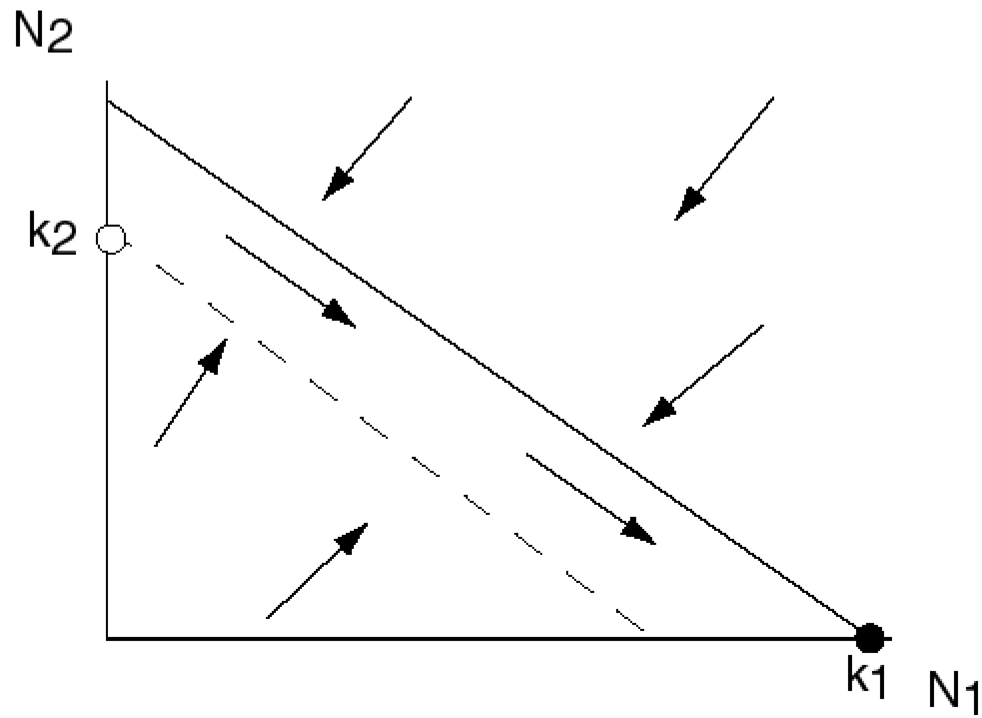


- This looks similar to Gause's results

Lotka-Volterra interaction model: exclusion

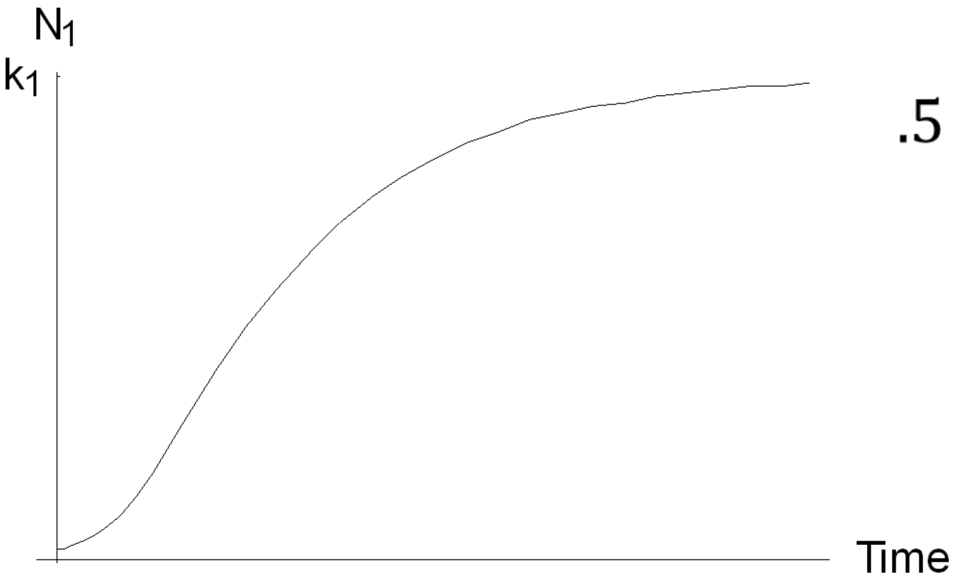
Other outcomes of the model:

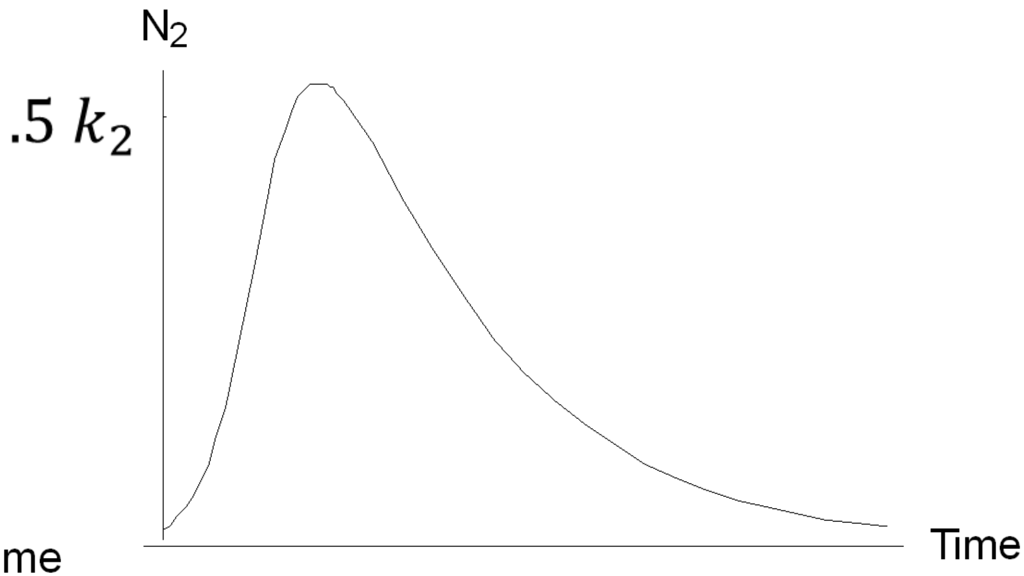
Species 1 can outcompete species 2



Lotka-Volterra interaction model: exclusion

- This happens for different parameters



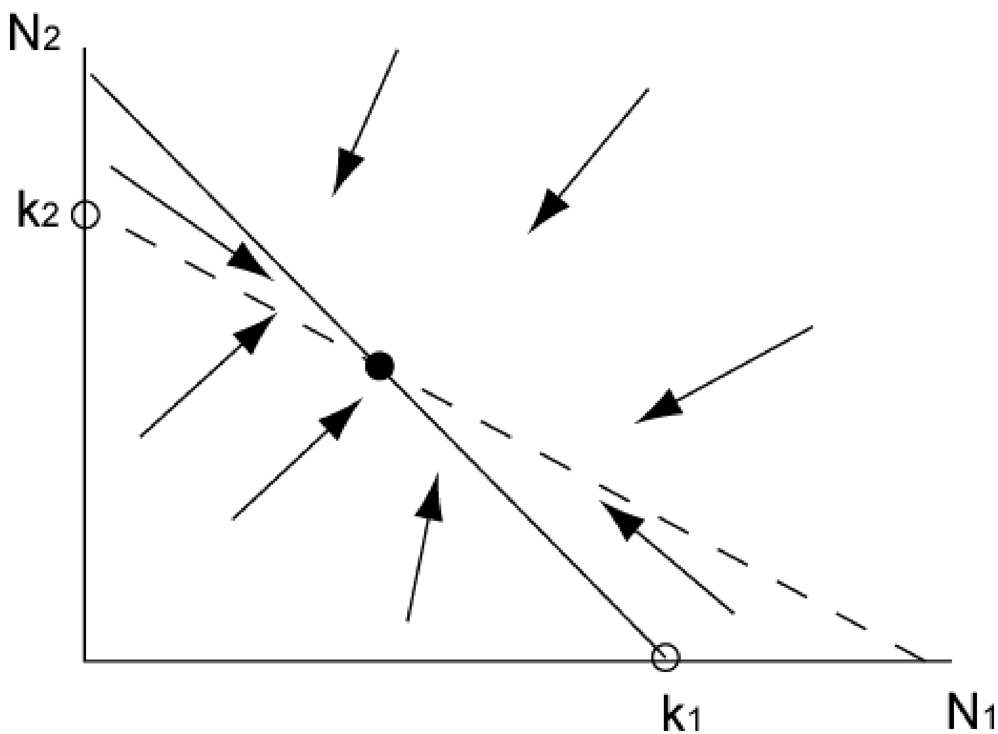


- This is not all that surprising since the labelling (species 1, 2) is arbitrary

Lotka-Volterra interaction model: coexistence

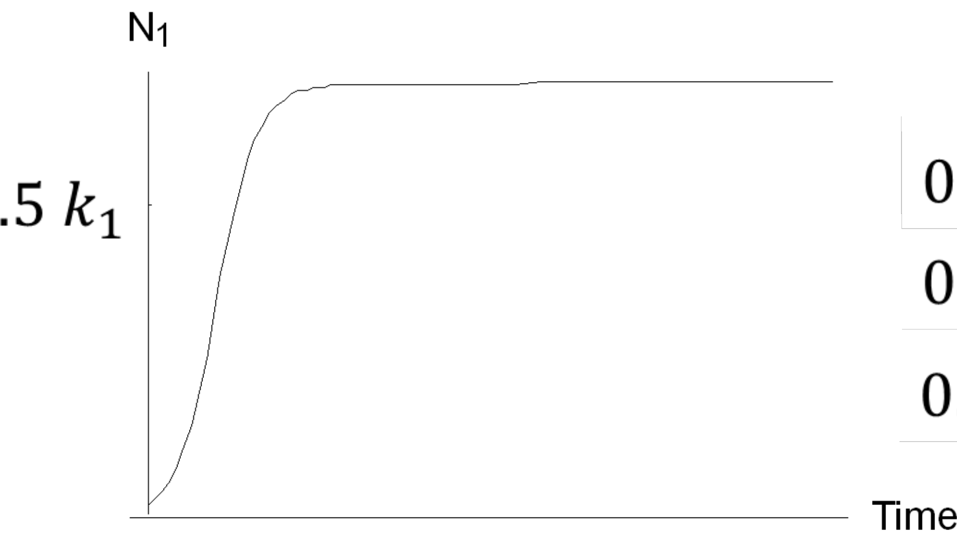
Other outcomes of the model:

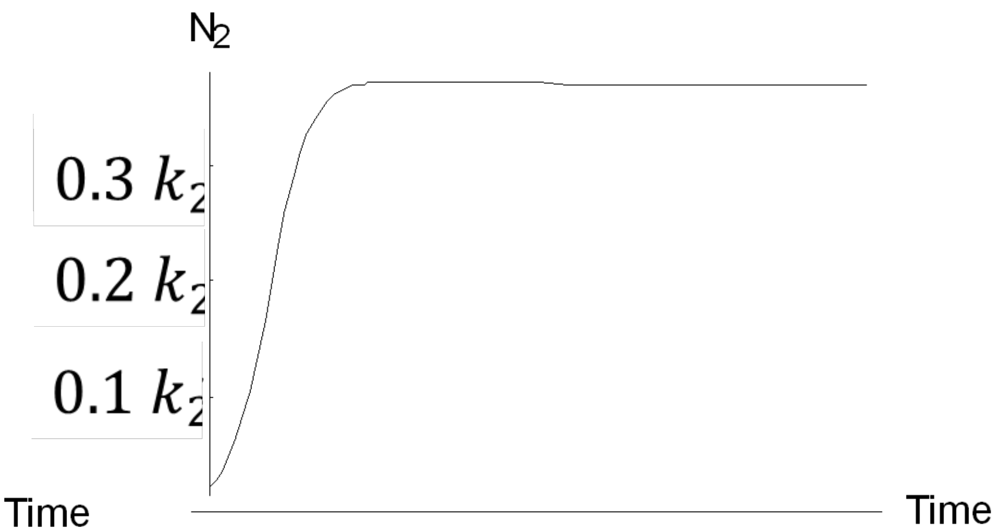
Species 1 and 2 can coexist



Lotka-Volterra interaction model: coexistence

- This for different parameters



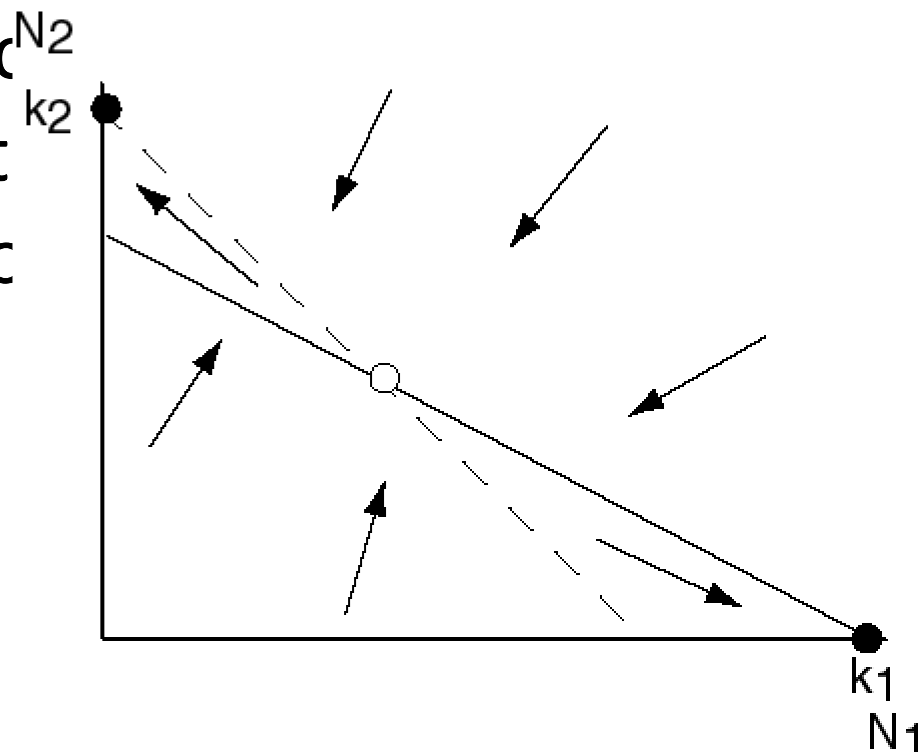


- Gause also found coexistence

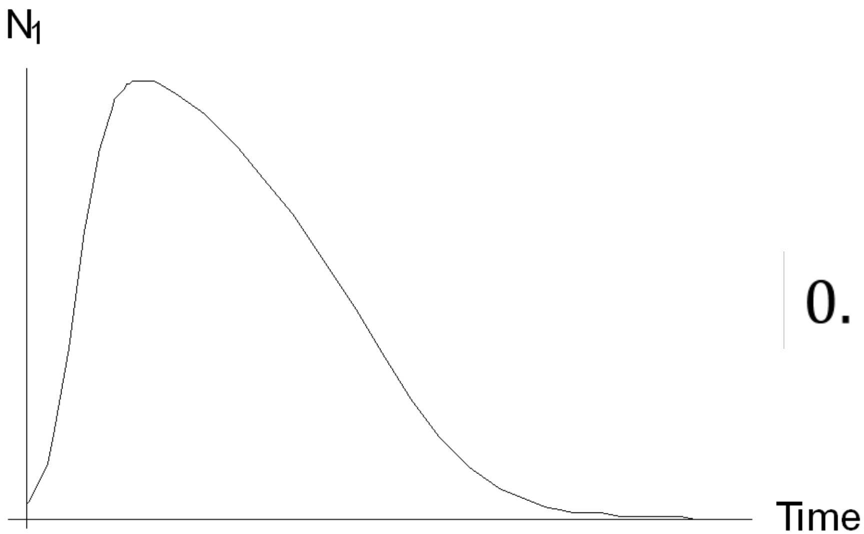
L-V interaction model: alternative stable states

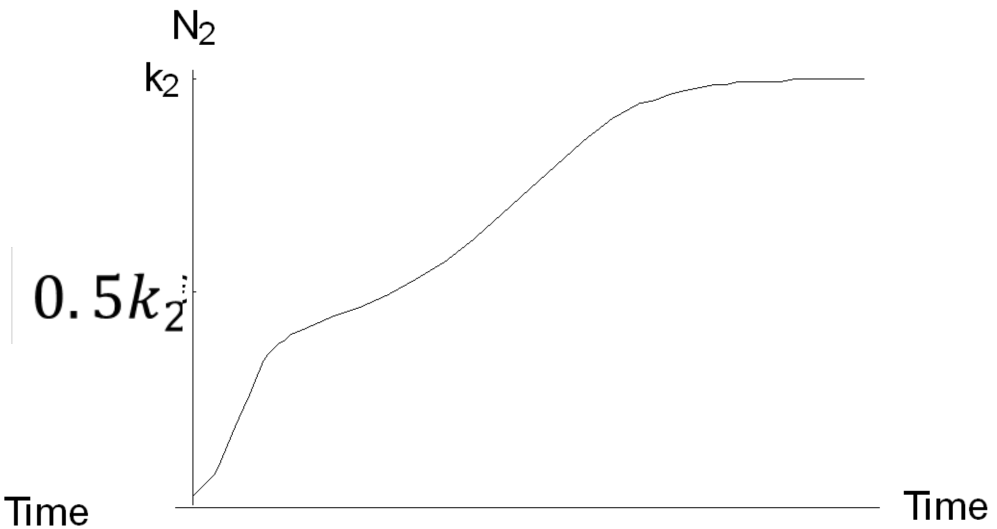
Other outcomes of the model:

An unstable equilibrium exists, yet there is no lasting c the compet l conditic

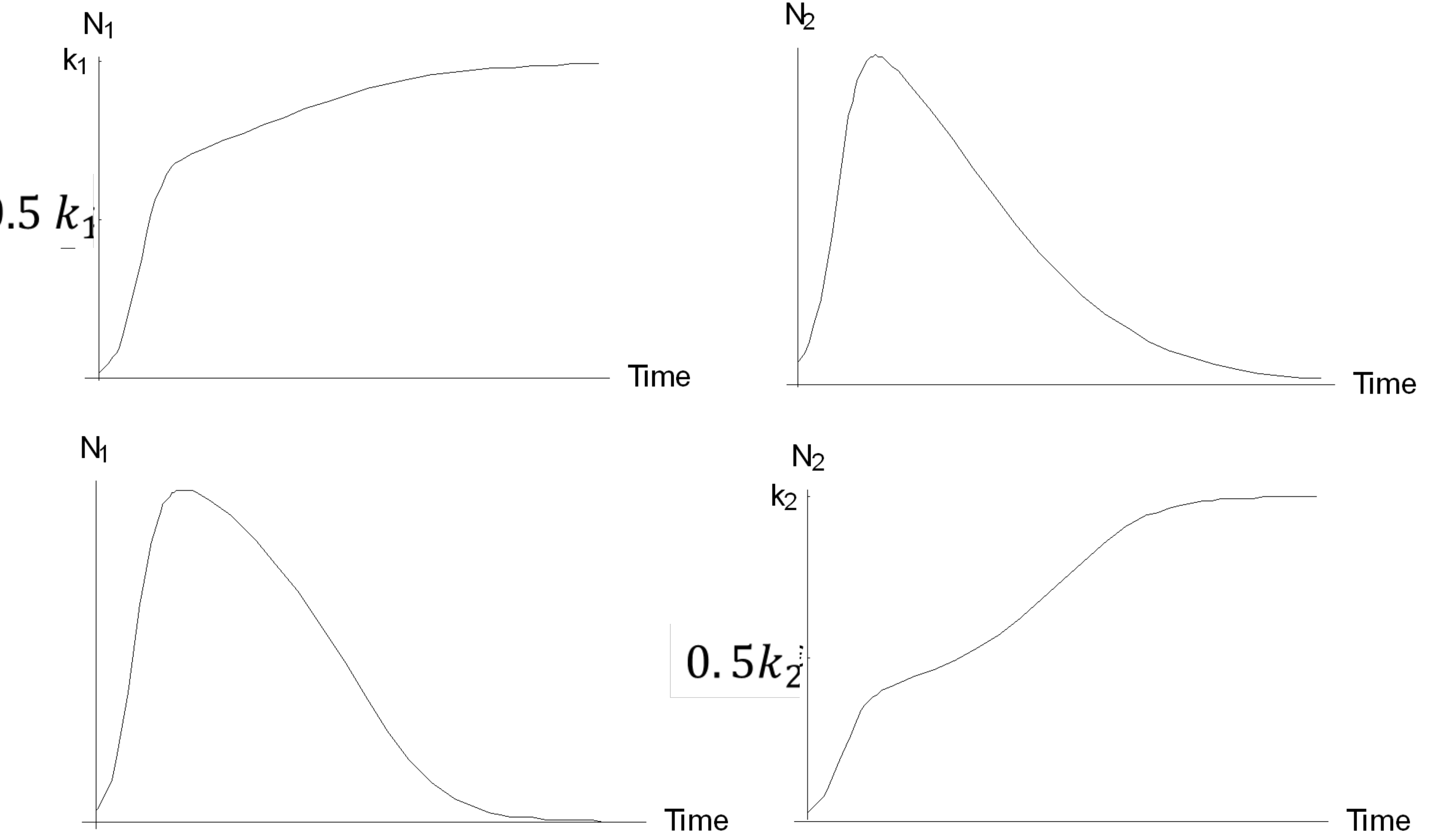


Alternative stable states

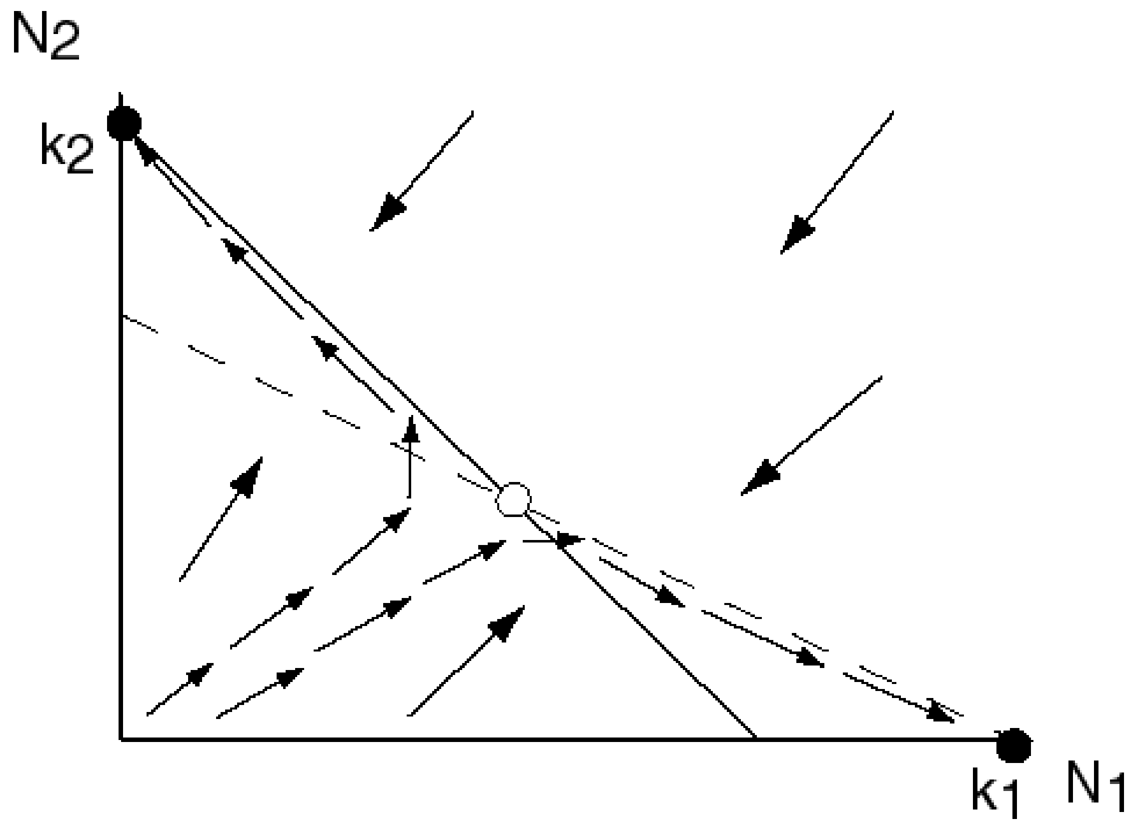




Alternative stable states



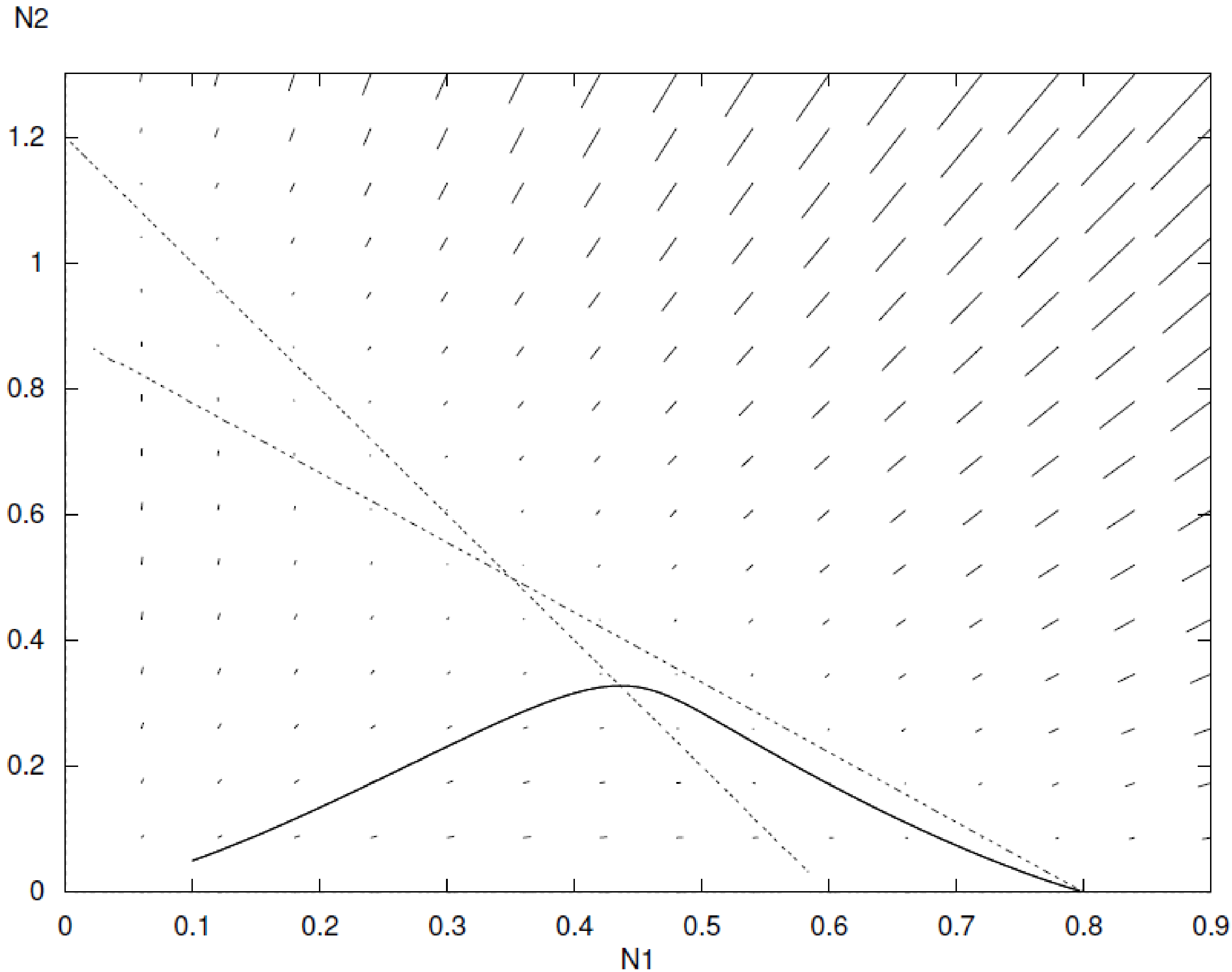
Alternative stable states



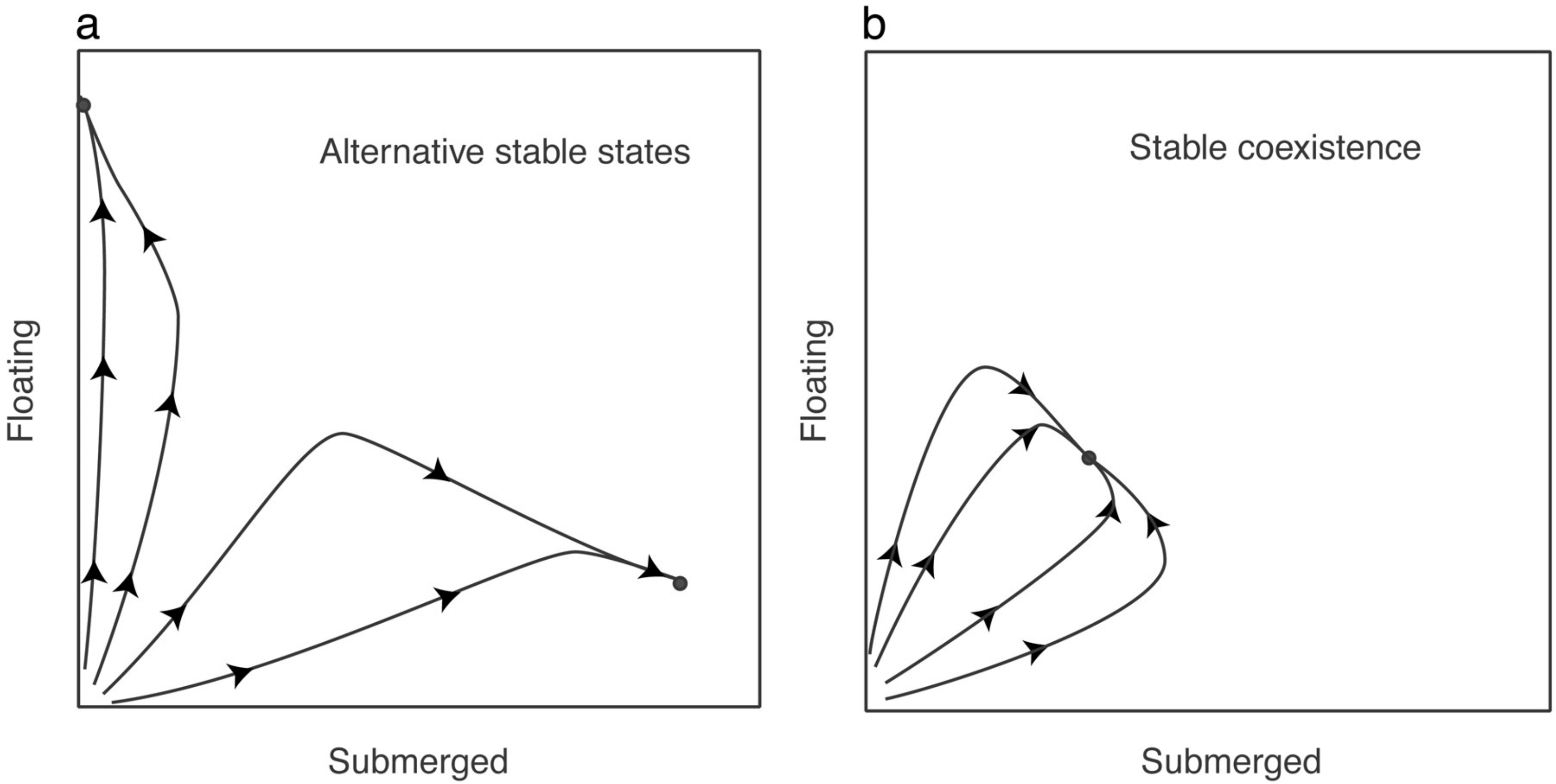
The phase plane

- The previous plot captures the information about the solution in a very convenient way
- Rather than plotting N_1 and N_2 versus time, we have plotted the values of N_1 and N_2 at various time points
- The solution traverses the N_1, N_2 plane over time, the path it covers is called an orbit
- The N_1, N_2 plane is the phase plane
- All orbits together give you the phase portrait

The phase plane

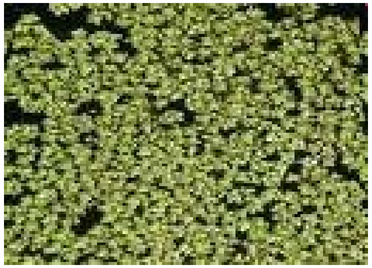


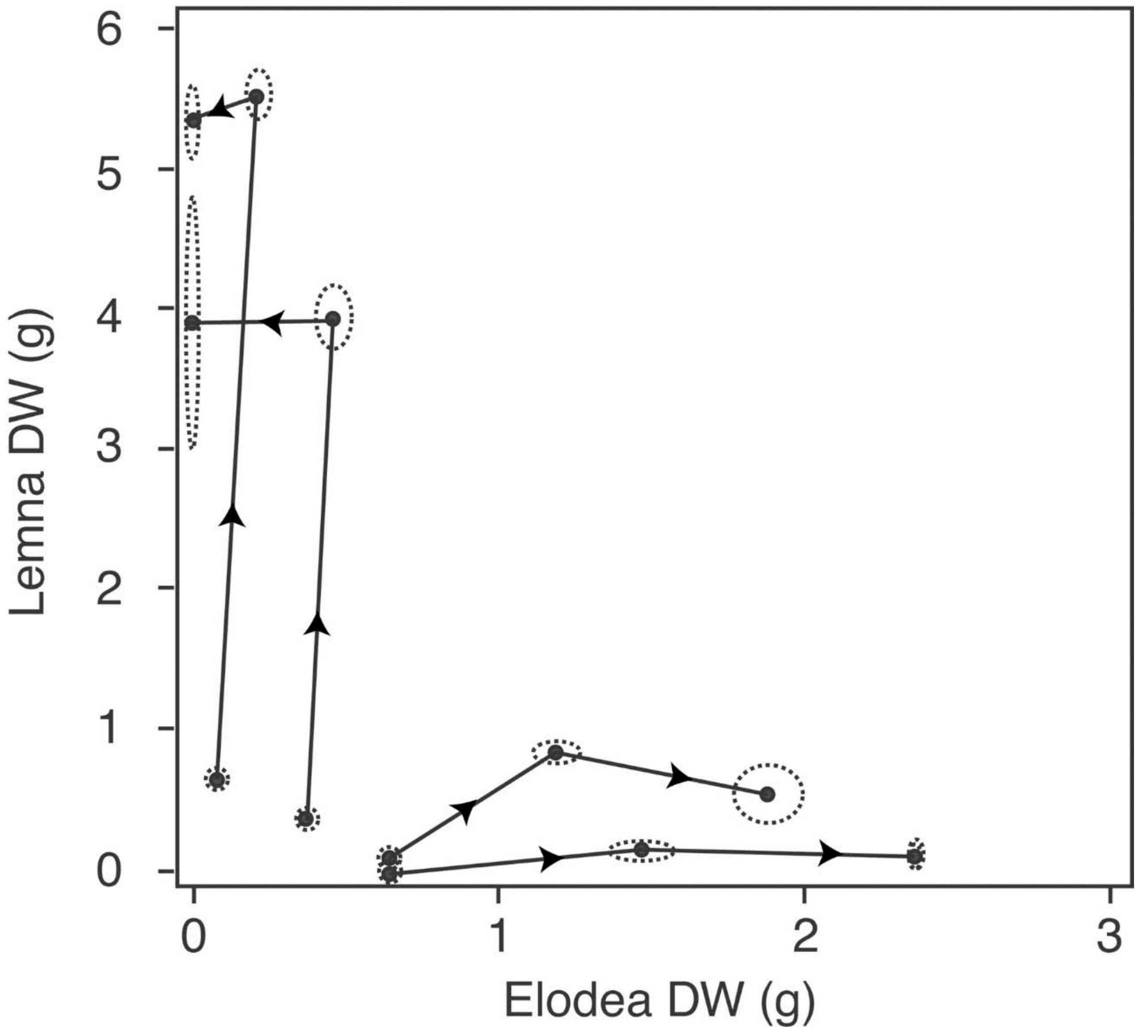
Theoretical growth trajectories in competition experiments of a submerged plant and a floating plant



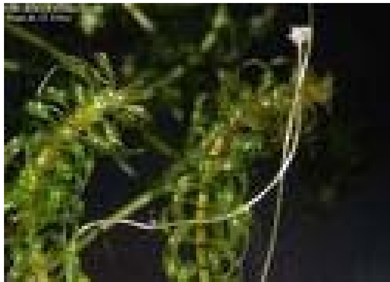
Scheffer M et al. PNAS 2003;100:4040-4045

Observed growth trajectories in competition experiments of a submerged plant (Elodea) and a floating plant (Lemna) tend to different final states, depending on the initial plant densities

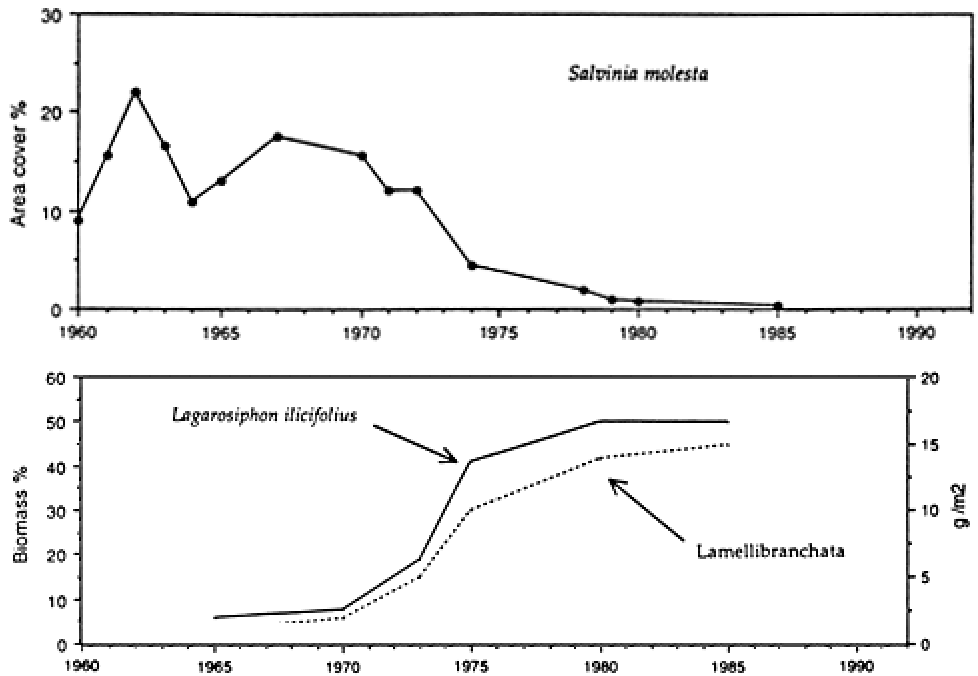


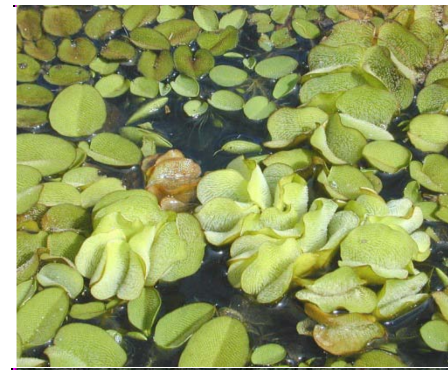


Scheffer M et al. PNAS 2003;100:4040-4045



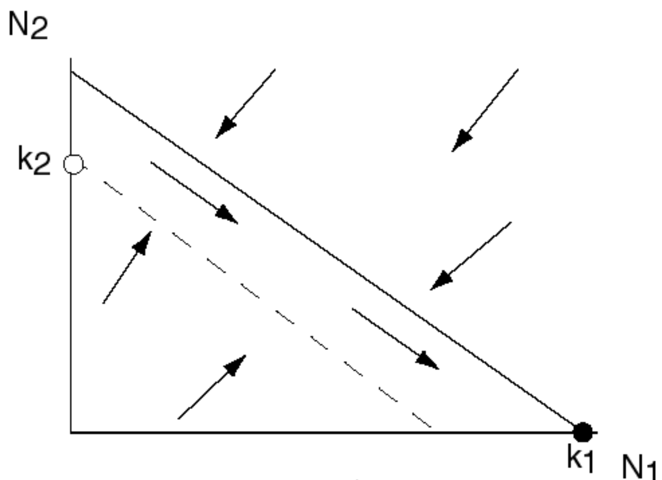
Changes in vegetation on Lake Kariba



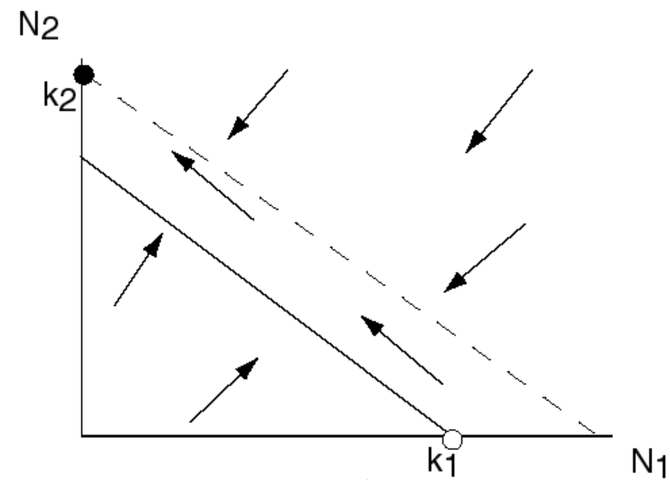


Lake Kariba: monthly and mean annual lake levels, mean annual lake level fluctuations, coverage of *Salvinia molesta*, changes in the benthic (Lamellibranchiata) and aquatic macrophyte biomass (*Lagarosiphon*). (From Karenge and Kolding, 1995).

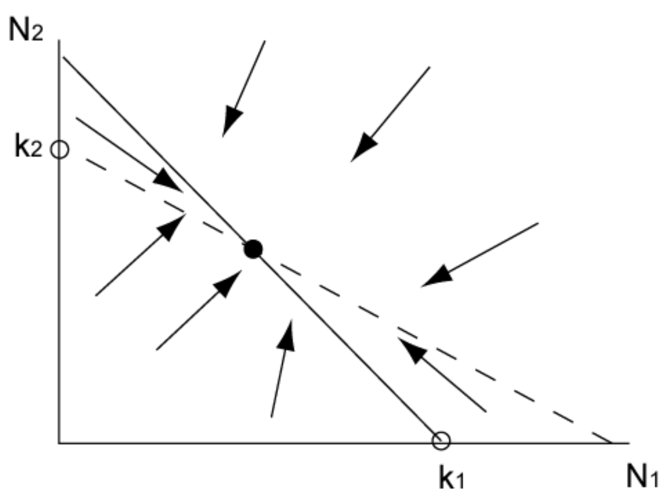
The outcomes of competition



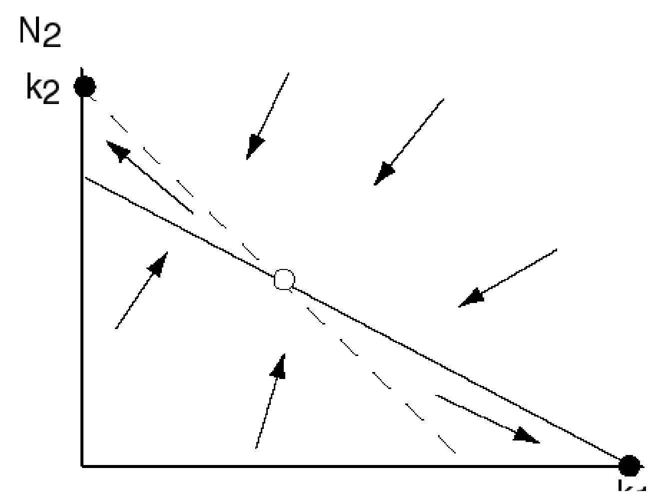
Species 1 excludes 2



Species 2 excludes 1



Coexistence



Alternative stable states

Equilibria and stability

- The L-V competition model can have 4 different equilbria
- We can find these by solving:

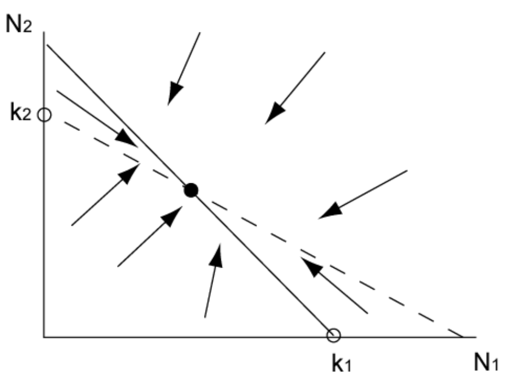
$$0 = r_1(k_1 - N_1^* - \alpha N_2^*)N_1^*$$

$$0 = r_2(k_2 - \beta N_1^* - N_2^*)N_2^*$$

- Which gives

$$0 = (k_1 - N_1^* - \alpha N_2^*) \text{ or } N_1^* = 0$$

$$0 = (k_2 - \beta N_1^* - N_2^*) \text{ or } N_2^* = 0$$



Equilibria and stability

- 3 equilibria are:

$$(N_1^*, N_2^*) = (0,0)$$

$$(N_1^*, N_2^*) = (k_1,0)$$

$$(N_1^*, N_2^*) = (0,k_2)$$

- The 4th one you can find by solving:

$$\begin{cases} 0 = k_1 - N_1^* - \alpha N_2^* \\ 0 = k_2 - \beta N_1^* - N_2^* \end{cases}$$

- Which gives

$$(N_1^*, N_2^*) = (k_1 \frac{1-\alpha k_2 / k_1}{1-\alpha\beta}, k_2 \frac{1-\beta k_1 / k_2}{1-\alpha\beta})$$

Linearised dynamics

- We study the dynamics close to the equilibrium(N_1^*, N_2^*)
- Let the dynamics be given by

$$\frac{dN_1}{dt} = F(N_1, N_2)$$

$$\frac{dN_2}{dt} = G(N_1, N_2)$$

- Equilibrium can be found from:

$$0 = F(N_1^*, N_2^*)$$

$$0 = G(N_1^*, N_2^*)$$

Linearised dynamics

We will now linearise the dynamics around the equilibrium

To do so Taylor expand in (N_1^*, N_2^*)

$$F(N_1,N_2) = F(N_1^*,N_2^*) + (N_1 - N_1^*)\left.\frac{\partial F(N_1,N_2)}{\partial N_1}\right|_{\substack{N_1=N_1^* \\ N_2=N_1^*}} + (N_2 - N_2^*)\left.\frac{\partial F(N_1,N_2)}{\partial N_2}\right|_{\substack{N_1=N_1^* \\ N_2=N_1^*}}$$

$$G(N_1,N_2) = G(N_1^*,N_2^*) + (N_1 - N_1^*)\left.\frac{\partial G(N_1,N_2)}{\partial N_1}\right|_{\substack{N_1=N_1^* \\ N_2=N_1^*}} + (N_2 - N_2^*)\left.\frac{\partial G(N_1,N_2)}{\partial N_2}\right|_{\substack{N_1=N_1^* \\ N_2=N_1^*}}$$

+h.o.t

Linearised dynamics

At equilibrium this simplifies to

$$F(N_1, N_2) = (N_1 - N_1^*)\left.\frac{\partial F(N_1, N_2)}{\partial N_1}\right|_{\substack{N_1 = N_1^* \\ N_2 = N_1^*}} + (N_2 - N_2^*)\left.\frac{\partial F(N_1, N_2)}{\partial N_2}\right|_{\substack{N_1 = N_1^* \\ N_2 = N_1^*}}$$

$$G(N_1, N_2) = (N_1 - N_1^*)\left.\frac{\partial G(N_1, N_2)}{\partial N_1}\right|_{\substack{N_1 = N_1^* \\ N_2 = N_1^*}} + (N_2 - N_2^*)\left.\frac{\partial G(N_1, N_2)}{\partial N_2}\right|_{\substack{N_1 = N_1^* \\ N_2 = N_1^*}}$$

+h.o.t

Linearised dynamics

By using $x = N_1 - N_1^*$ and $y = N_2 - N_2^*$

We can write the linearised dynamics as:

$$\begin{pmatrix} \dfrac{dx}{dt} \\ \dfrac{dy}{dt} \end{pmatrix} = \left[\begin{matrix} \dfrac{\partial F(N_1, N_2)}{\partial N_1} & \dfrac{\partial F(N_1, N_2)}{\partial N_2} \\ \dfrac{\partial G(N_1, N_2)}{\partial N_1} & \dfrac{\partial G(N_1, N_2)}{\partial N_2} \end{matrix} \right]_{\substack{N_1 = N_1^* \\ N_2 = N_1^*}} \cdot \begin{pmatrix} x \\ y \end{pmatrix}$$

$$\begin{pmatrix} \dfrac{dx}{dt} \\ \dfrac{dy}{dt} \end{pmatrix} = J \cdot \begin{pmatrix} x \\ y \end{pmatrix}$$

Equilibria and stability

- Now apply this to the Lotka-Volterra interaction model
- Let $x = N_1 - N_1^*$ and $y = N_2 - N_2^*$
- The dynamics close to an equilibrium are approximately:

$$\frac{dx}{dt} = r_1(k_1 - 2N_1^* - \alpha N_2^*)x - r_1\alpha N_1^* y$$

$$\frac{dy}{dt} = -r_2\beta N_2^* x + r_2(k_2 - \beta N_1^* - 2N_2^*)y$$

Equilibria and stability

- Or using vector notation

$$\begin{pmatrix} \dfrac{dx}{dt} \\ \dfrac{dy}{dt} \end{pmatrix} = \begin{pmatrix} r_1(k_1 - 2N_1^* - \alpha N_2^*) & -r_1\alpha N_1^* \\ -r_2\beta N_2^* & r_2(k_2 - \beta N_1^* - 2N_2^*) \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

- Next we will look at the 4 equilibria and study their stability

Stability of $(N_1^*, N_2^*) = (k_1, 0)$

- The Jacobian matrix is

$$J = \begin{pmatrix} -r_1 k_1 & \alpha r_1 k_1 \\ 0 & r_2 k_2 (1 - \beta k_1 / k_2) \end{pmatrix}$$

- One eigenvalue is $-r_1 k_1$ (same as the logistic model), the other one is $r_2 k_2$ $(1-\beta k_1/k_2)$
- If $r_2 k_2 > 0$ and $1-\beta k_1/k_2 < 0$ y moves towards $y=0$ and
  if $r_2 k_2 > 0$ and $1-\beta k_1/k_2 > 0$ y moves away from $y=0$ (equilibrium unstable)
- This allows the interpretation that if $1/\beta > k_1/k_2$ then N_2 can invade in $(N_1^*, N_2^*) = (k_1, 0)$

Stability of $(N_1^*, N_2^*) = (0, k_2)$

- The dynamics close to equilibrium are approximately:

$$\frac{dx}{dt} = r_1(k_1 - \alpha k_2)x = r_1 k_1(1 - \alpha k_2 / k_1)x$$

$$\frac{dy}{dt} = -r_2 \beta k_2 x - r_2 k_2 y = -r_2 k_2(\beta x + y)$$

Stability of $(N_1^*, N_2^*) = (0, k_2)$

- The Jacobian matrix is

$$J = \begin{pmatrix} r_1 k_1 (1 - \alpha k_2 / k_1) & 0 \\ -r_2 k_2 \beta & -r_2 k_2 \end{pmatrix}$$

- One eigenvalue is $-r_2 k_2$ (same as the logistic model) the other one is $r_1 k_1$ $(1-\alpha k_2/k_1)$
- If $r_1 k_1 > 0$ and $1-\alpha k_2/k_1 < 0$ x moves towards x=0 and
  if $r_1 k_1 > 0$ and $1-\alpha k_2/k_1 > 0$ x moves away from x=0 (equilibrium unstable)
- Interpretation: if $\alpha < k_1/k_2$ then N_1 can invade in $(N_1^*, N_2^*) = (0, k_2)$

Formal criteria

- The following inequalities predict the outcome of competition (if all *r*s and *k*s +ive)

	$1/\beta < k_1/k_2$	$1/\beta > k_1/k_2$
$\alpha < k_1/k_2$	N_1 invades, N_2 doesnot	Both invade
$\alpha > k_1/k_2$	Neither can invade	N_1 no invasion, N_2 invades

Formal criteria to predict the outcome of the LV model

- The following inequalities predict the outcome of competition (if all *r*s and *k*s +ive)

	$1/\beta < k_1/k_2$	$1/\beta > k_1/k_2$
$\alpha < k_1/k_2$	Species 1 excludes 2	Coexistence
$\alpha > k_1/k_2$	Alternative stable states	Species 2 excludes 1

But how about the stability of the 4th equilibrium?

Equilibrium is given by

$$(N_1^*, N_2^*) = (k_1 \frac{1-\alpha k_2 / k_1}{1-\alpha\beta}, k_2 \frac{1-\beta k_1 / k_2}{1-\alpha\beta})$$

- The dynamics close to equilibrium are approximately:

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = \begin{pmatrix} -r_1 N_1^* & -r_1 \alpha N_1^* \\ -r_2 \beta N_2^* & -r_2 N_2^* \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

- And from this we can calculate the eigenvalues and eigenvectors

But how about the stability of the 4^{th} equilibrium?

- We are not going to determine the eigenvalues, as it is cumbersome. There are criteria to determine if the eigenvalues are all smaller than 0.
- They are called the Routh-Hurwitz criteria
- The eigenvalues of a 2x2 matrix are all negative iff
  - The trace (sum over the diagonal) is negative
  - The determinant is positive

But how about the stability of the 4th equilibrium?

- The matrix $J = \begin{pmatrix} -r_1 N_1^* & -r_1 \alpha N_1^* \\ -r_2 \beta N_2^* & -r_2 N_2^* \end{pmatrix}$
- Has as trace $-r_1 N_1^* - r_2 N_2^*$
- And as determinant

$$r_1 r_2 N_1^* N_2^* - r_1 r_2 \alpha\beta N_1^* N_2^* = r_1 r_2 N_1^* N_2^* (1 - \alpha\beta)$$

- So if $N_1^*, N_2^* > 0$ the trace is always negative and the determinant is positive if $1 - \alpha\beta > 0$

Formal criteria

- The following inequalities predict the outcome of competition (if all *r*s and *k*s +ive)

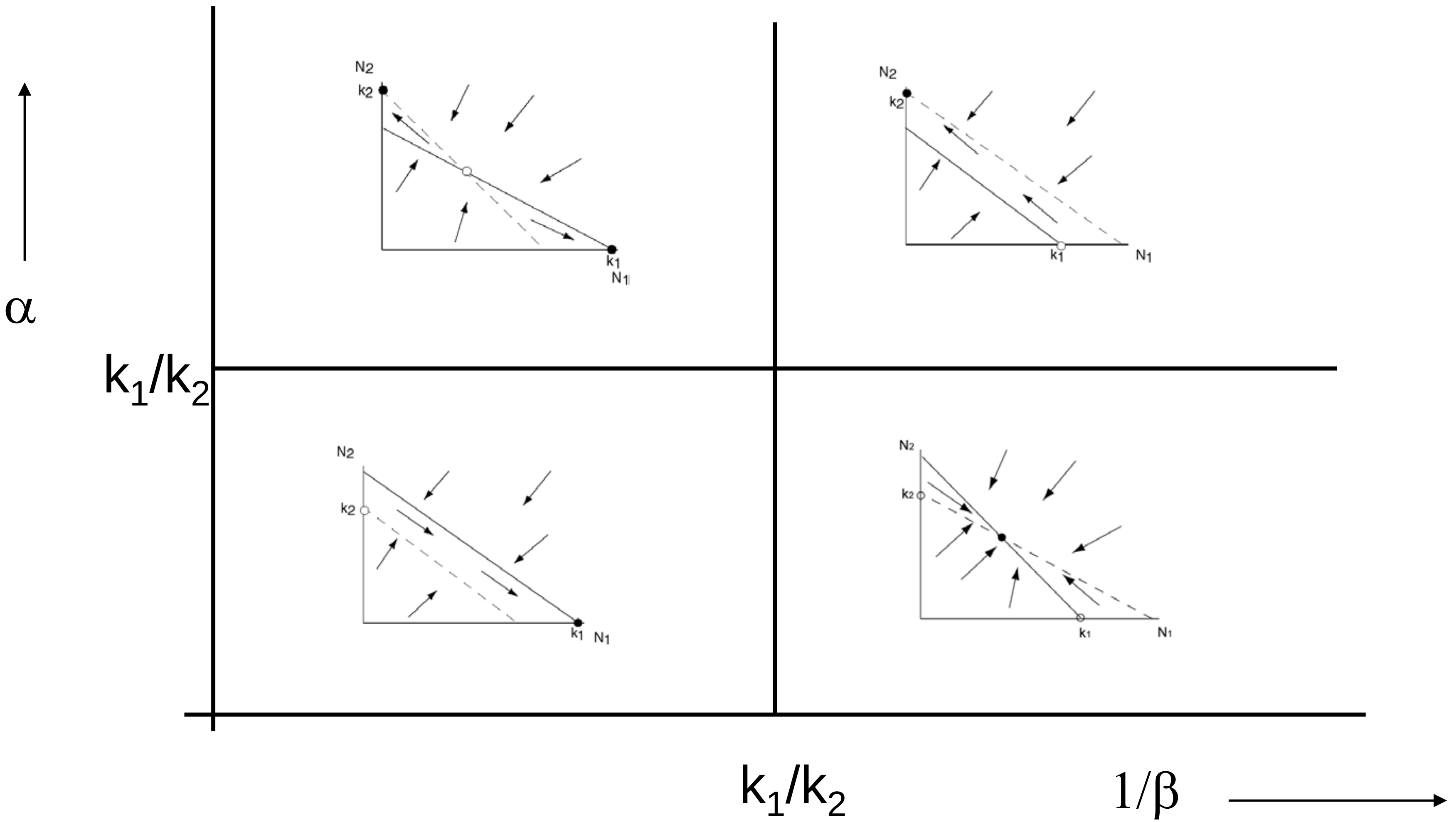
	$1/\beta < k_1/k_2$	$1/\beta > k_1/k_2$
$\alpha < k_1/k_2$	N_1 invades, N_2 no invasion Eq. 4 not +ive	Both invade Eq. 4 stable
$\alpha > k_1/k_2$	Neither can invade Eq. 4 unstable	N_1 no invasion, N_2 invades Eq. 4 not +ive

Formal criteria to predict the outcome of the LV model

- The following inequalities predict the outcome of competition (if all *r*s and *k*s +ive)

	$1/\beta < k_1/k_2$	$1/\beta > k_1/k_2$
$\alpha < k_1/k_2$	Species 1 excludes 2	Coexistence
$\alpha > k_1/k_2$	Alternative stable states	Species 2 excludes 1

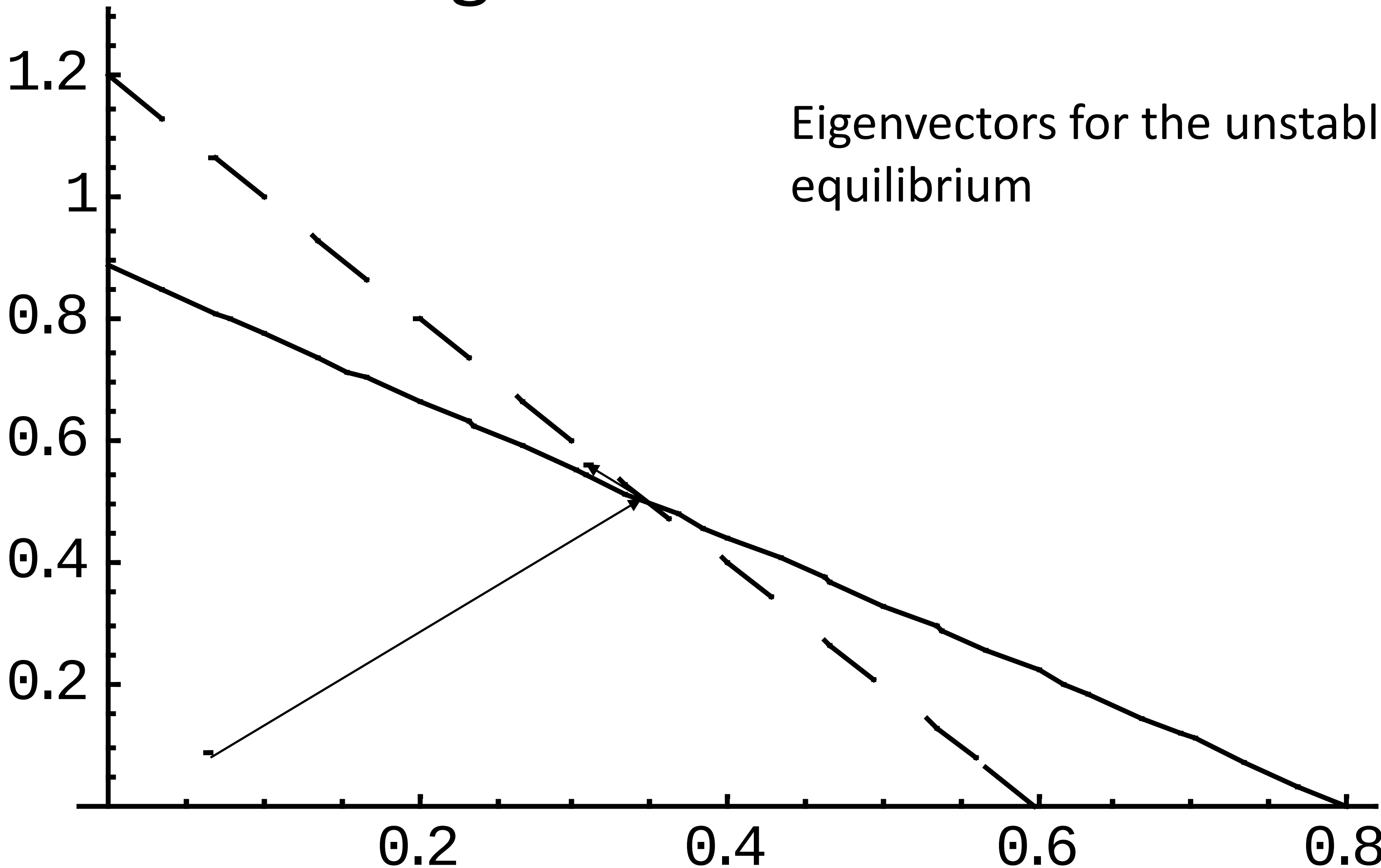
Classification as bifurcations



What do the eigenvalues and eigenvectors mean?

- In the phase plane, eigenvectors are directions over which you can move away from, or towards, an equilibrium (close to the equilibrium)
- The eigenvalues are the speed with which you move towards, or away from the equilibrium over these eigenvectors
- In the vicinity of the equilibrium the directions are the weighted vector sums of the eigenvectors

What do the eigenvalues and eigenvectors mean?



Eigenvectors for the unstable equilibrium

What do the eigenvalues and eigenvectors mean?

- If one of the eigenvalues is positive, the equilibrium point is unstable, you will move away from it
- If some eigenvalues are positive whilst others are negative, the point is a saddle: you can move towards it from certain directions, but move away from it once you get closer
- The eigenvalues are the speed with which you move towards, or away from the equilibrium over these eigenvectors

Competitive exclusion principle

- For coexistence we require $1/\beta > k_1/k_2$ and $\alpha < k_1/k_2$ (hence $1/\beta > \alpha$)
- In words this means:

for coexistence we require that

the interspecific competition should be weaker than the intraspecific competition.

Competitive exclusion principle

- For coexistence we require $\alpha > 1/\beta$
- If two species use resources in exactly the same way $\alpha = 1/\beta$ (isoclines are parallel)
- If $\alpha \approx 1/\beta$ the two species are very similar in their resource use (isoclines almost parallel)
- In that case there is only a narrow range of carrying capacities for which coexistence is possible

Limitations of the L-V model

- The model assumes constant competition coefficients. It might well be that the effects of competition depend in some complicated way on the densities.
- It is quite possible that the populations are structured so that this description is not correct (e.g. age structure, spatial structure, etc.). (You would then need more than 2 equations to describe this)

Limitations of the L-V model

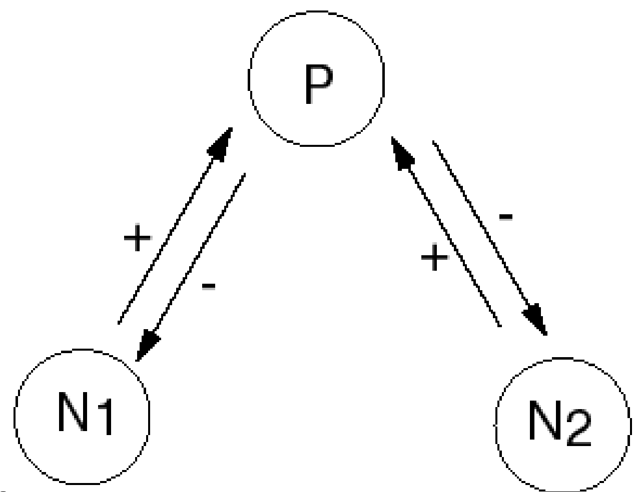
- The model only considers competition and no effects of any other parts of the ecosystem are taken into account (e.g. depletion of resources, shared predators or pathogens)
- All effects of competition are assumed to be immediate. No delays are taken into account

Apparent Competition

- We have so far implicitly assumed that competition has a direct effect on the other species
- This need not always be the case. Indirect effects occur when the effect of species 1 on species 2 is transmitted through a third species

Apparent Competition

- For instance, a shared predator can mediate an indirect effect between two species, even if there is no direct contact between them



- This is called apparent competition

Apparent Competition

a Lotka-Volterra type model could read:

$$\frac{dN_1}{dt} = r_1(k_1 - N_1)N_1 - \gamma_1 P N_1$$

$$\frac{dN_2}{dt} = r_2(k_2 - N_2)N_2 - \gamma_2 P N_2$$

and the predator density changes as:

$$\frac{dP}{dt} = \gamma_1 N_1 P + \gamma_2 N_2 P - \mu(m + P)P$$

Apparent Competition

We can bring this back to a 2 species model by assuming that the predator responds much faster, and is at quasi-equilbrium

$$P^* = \frac{\gamma_1}{\mu} N_1 + \frac{\gamma_2}{\mu} N_2 - m$$

So that the model reads

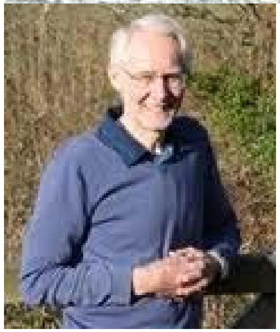
$$\frac{dN_1}{dt} = r_1(k_1 - N_1 - \gamma_1 P^*) N_1$$

$$\frac{dN_2}{dt} = r_2(k_2 - N_2 - \gamma_2 P^*) N_2$$

Apparent Competition

- It can be shown that for large carrying capacities one species of prey always outcompetes the other.
- The species that wins the competition is the one that can withstand the highest predator density

Apparent Competition

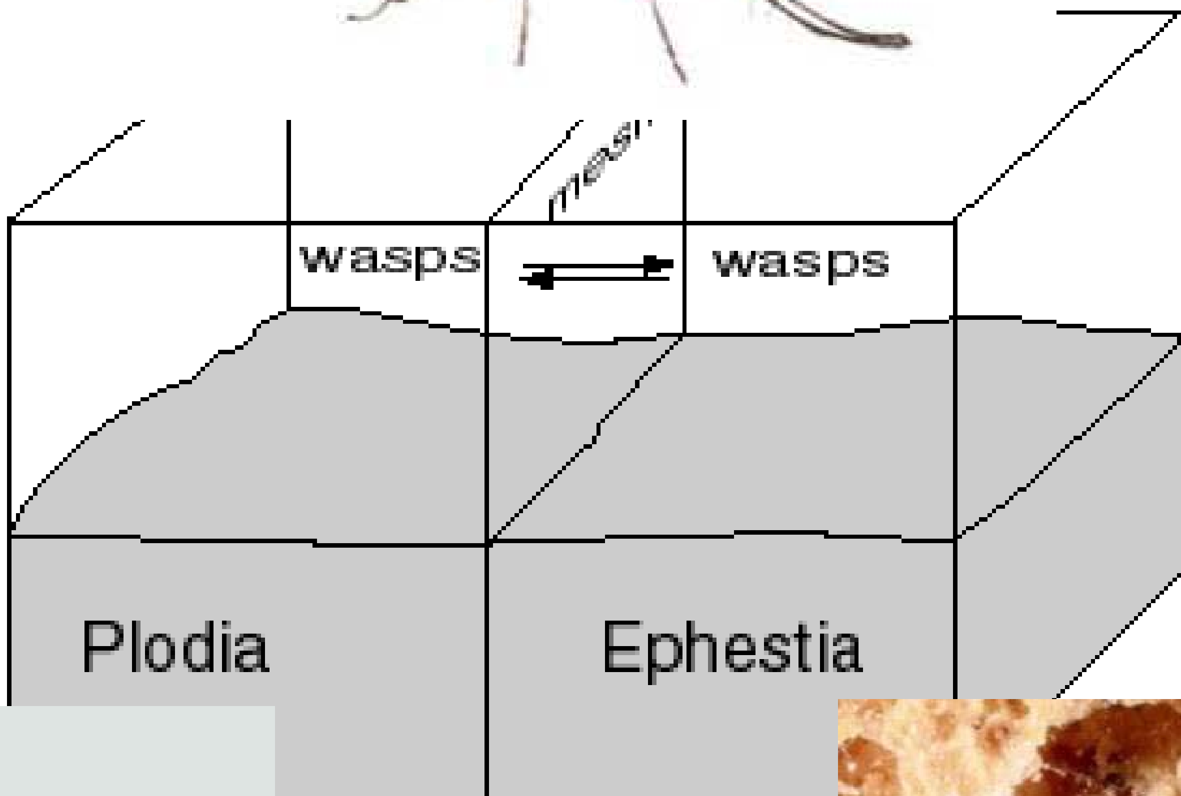


- Bonsall and Hassell (1997) performed an experiment in which to study apparent competition
- The studied 2 species of moths. Each species on its own could support a parasitic wasp which attacks the larvae

Apparent Competition

- Next they let the species compete in an arena in which the moths had no direct interaction, but in which the wasp mediated an indirect interaction

A n



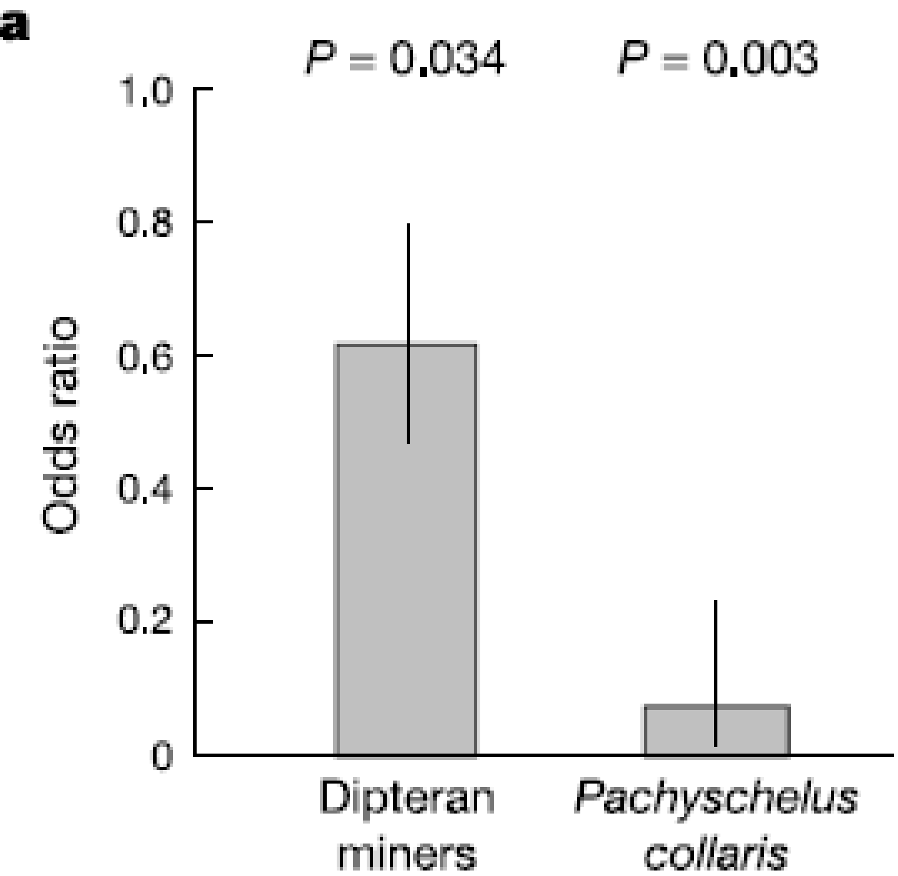
Apparent Competition

- They found that one of the moths, *Ephestia kuehniella*, was repeatedly eliminated in this experiment.
- Because *Ephestia kuehniella* on its own can persist in the presence of the parasitic wasp, this is due to apparent competition

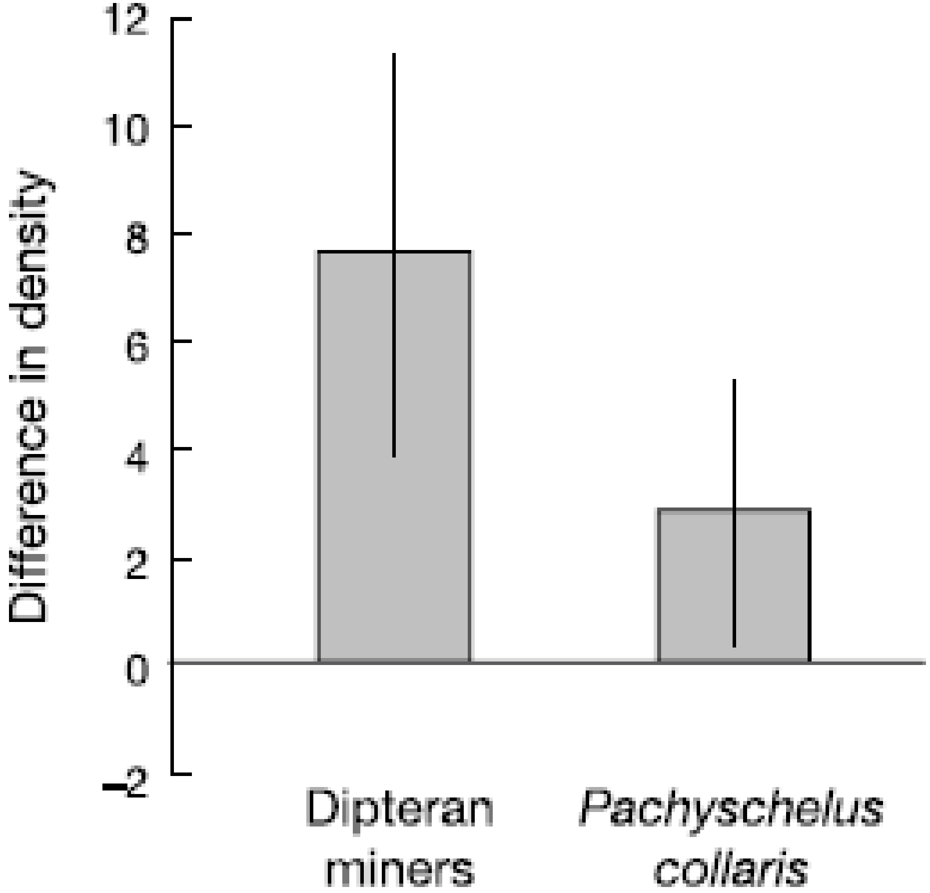
Apparent Competition

- This confirmed the theoretical prediction.
- It is also illustrates the limitations of the Lotka-Volterra competition model.
- It has also been shown that apparent competition occurs in the field: by removing a herbivore species from enclosures in a rainforest Morris et al. (2004) provided experimental evidence for competitive exclusion.

Effect on parasitism



Effect on abundance



Learning outcomes

- Understand the rationale behind the Lotka-Volterra interaction model
- Know the 3 possible outcomes of competition
- Understand isoclines and phase plots
- Have an appreciation of the limitations of the LV model
- Understand what eigenvalues and eigenvectors mean in the context of the LV model