Interspecific competition, phase plane, eigenvalues & eigenvectors

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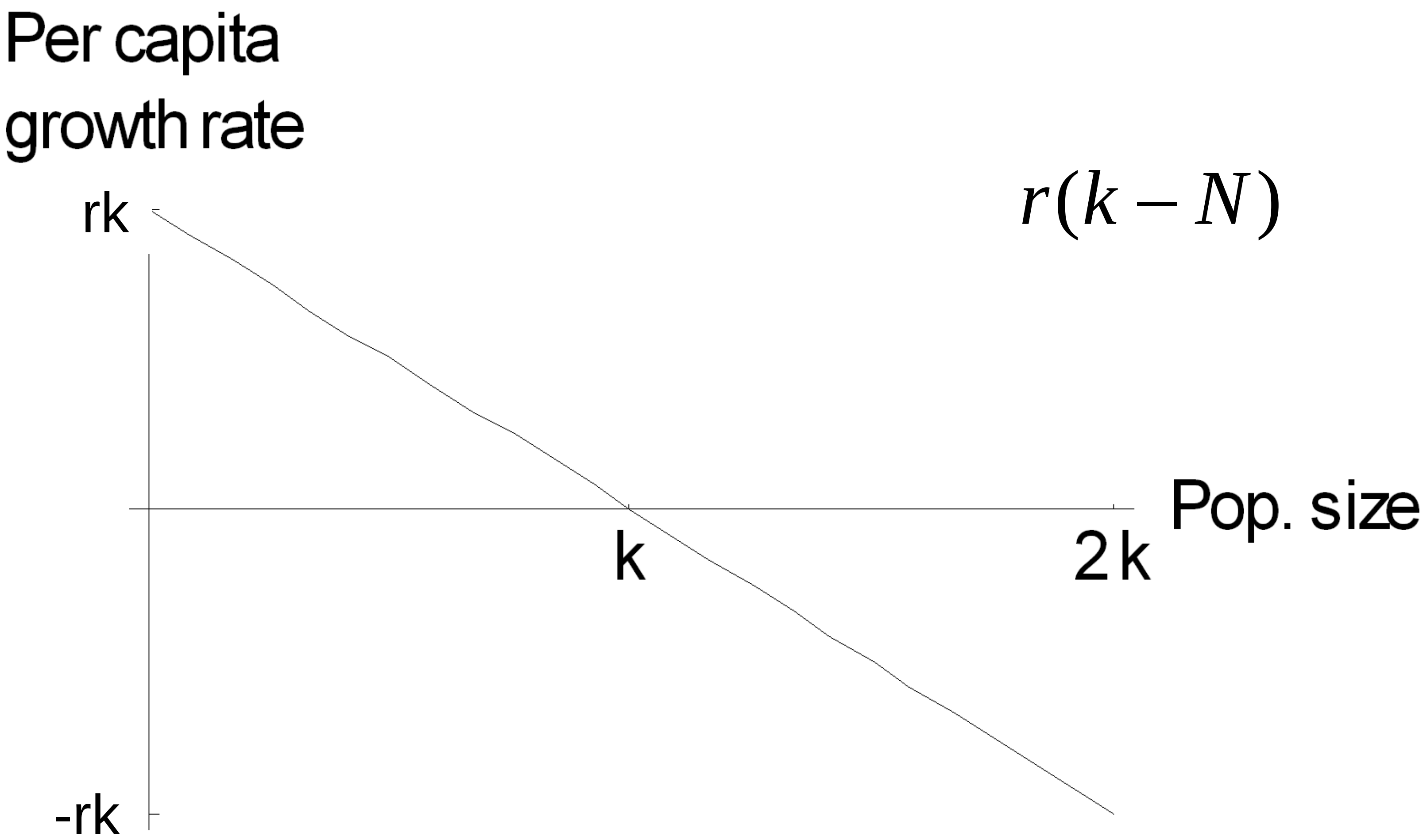
Outline

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

Intr<u>a</u>specific 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



$$r(k - N)$$

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

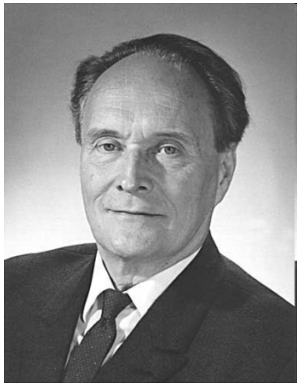
	Rodents removed	Ants removed	Rodents and ants removed	control
Ant colonies	543	-	-	318
Rodent nrs	-	144	-	122
Seed density relative to control	1.0	1.0	5.5	1.0

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



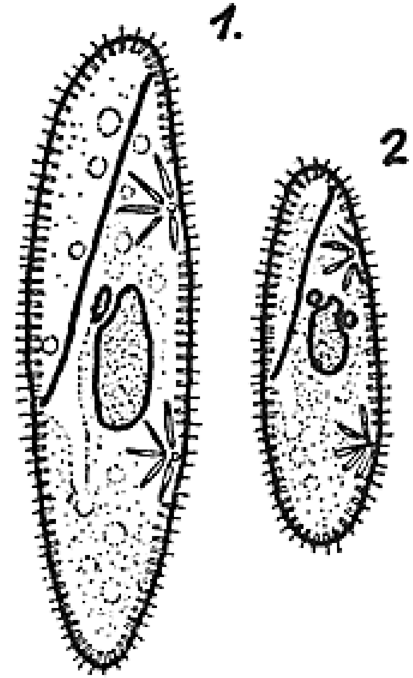
- G. F. Gause (1934) studied the competition between protozoans
- He asked ‘will one species … drive the other one out completely, or will a certain equilibrium become established between them? ‘

Gause’s experiments

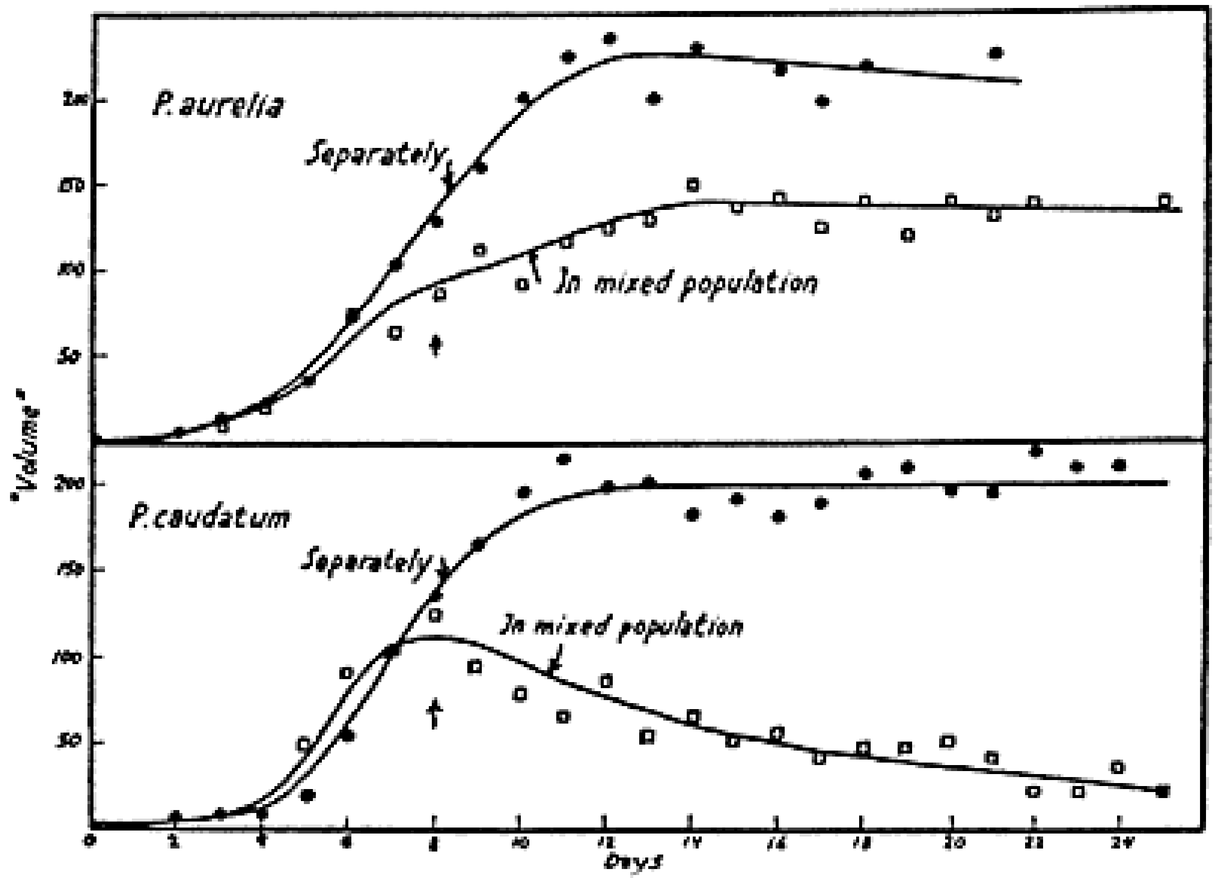
Gause’s experiments

- 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:

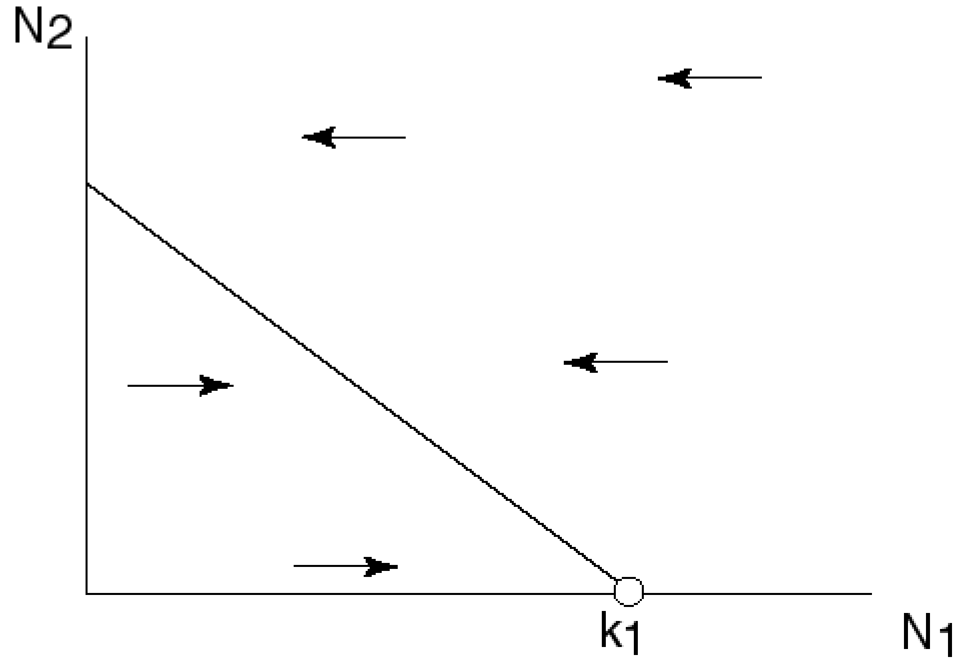
$$r_1(k_1 - N_1 - \alpha N_2)$$

- 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:

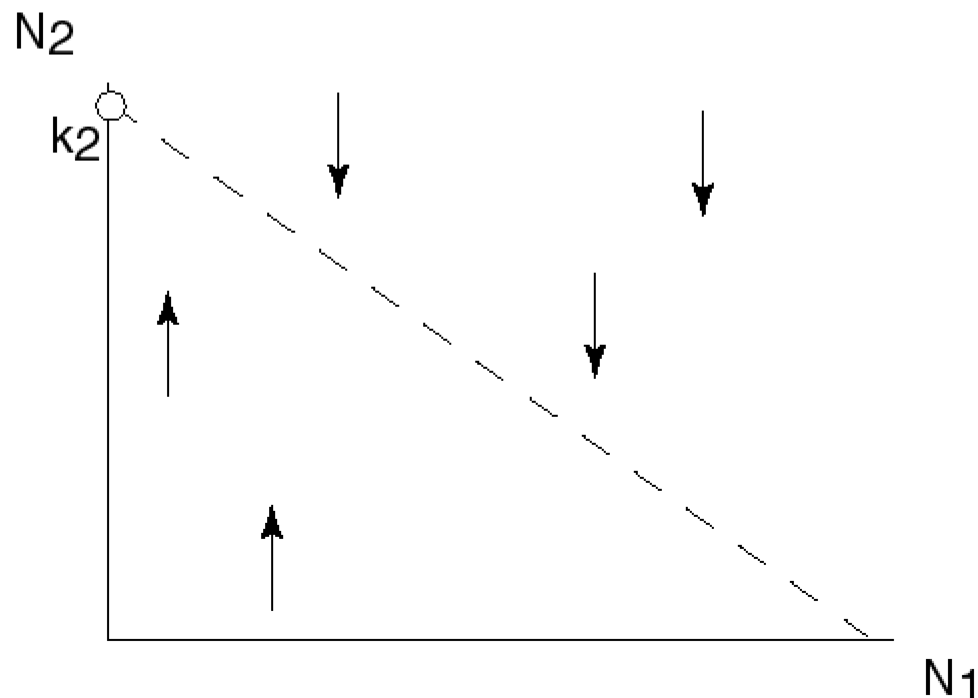
$$r_2(k_2 - \beta N_1 - N_2)$$

- 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:

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

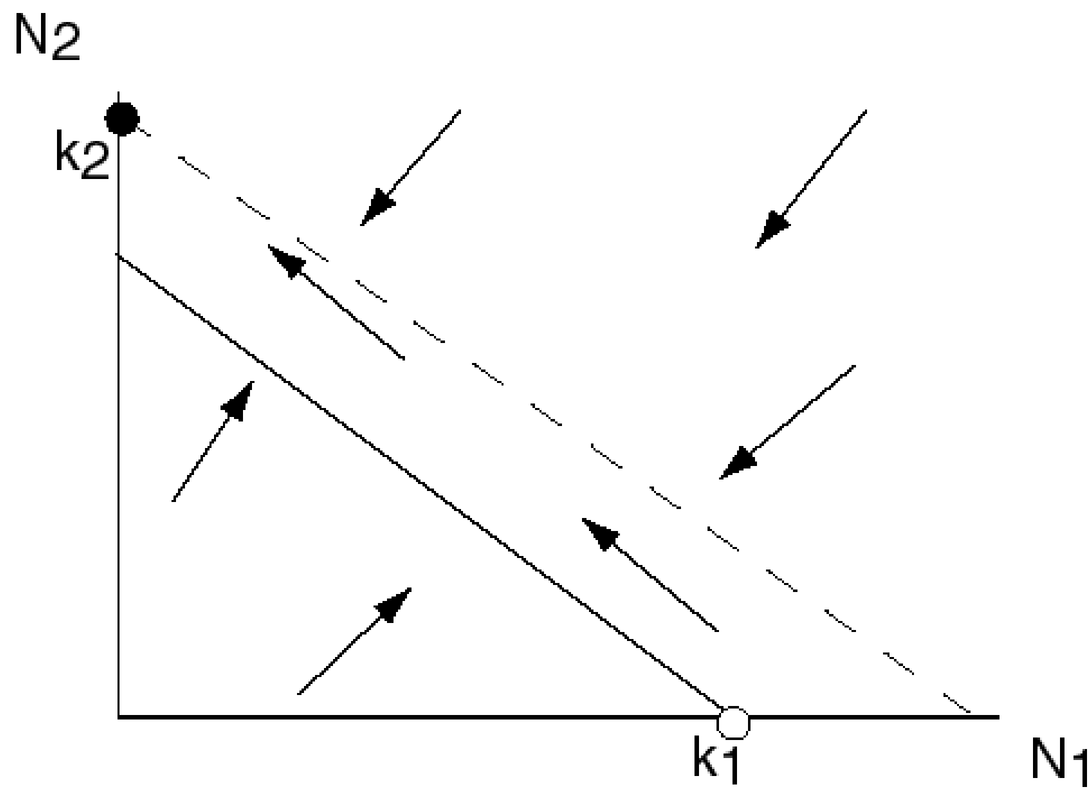
$$\frac{dN_2}{dt} = r_2(k_2 - \beta N_1 - N_2)N_2$$

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

Lotka-Volterra interaction model

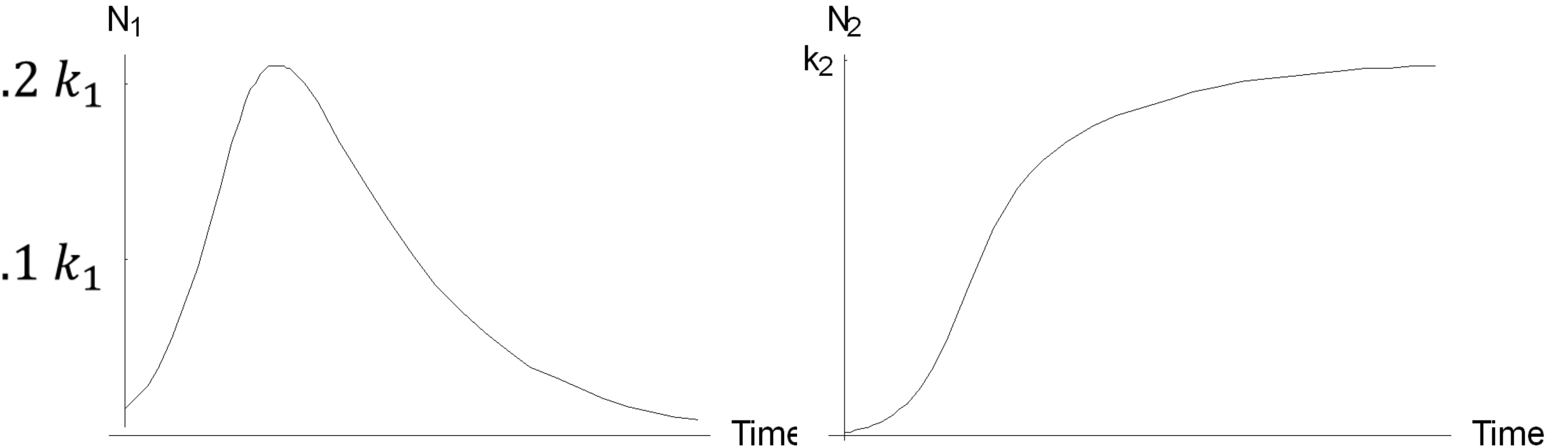
- The curves on which either species does not grow are called isoclines
- The isoclines delimit the parts of the state space for which the density of that species increases or decreases in number
- By combining the isoclines for the two species we can get an idea of the population dynamics

Lotka-Volterra interaction model: exclusion



Lotka-Volterra interaction model: exclusion

- Species 2 outcompetes and excludes species 1

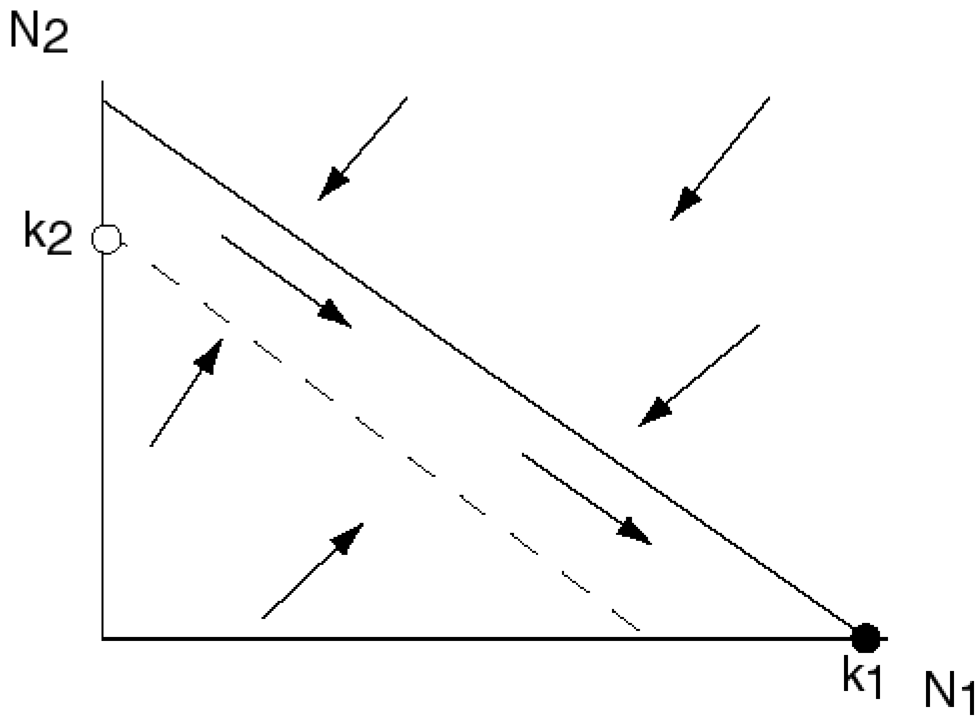


- This looks similar to Gause’s results

Lotka-Volterra interaction model: exclusion

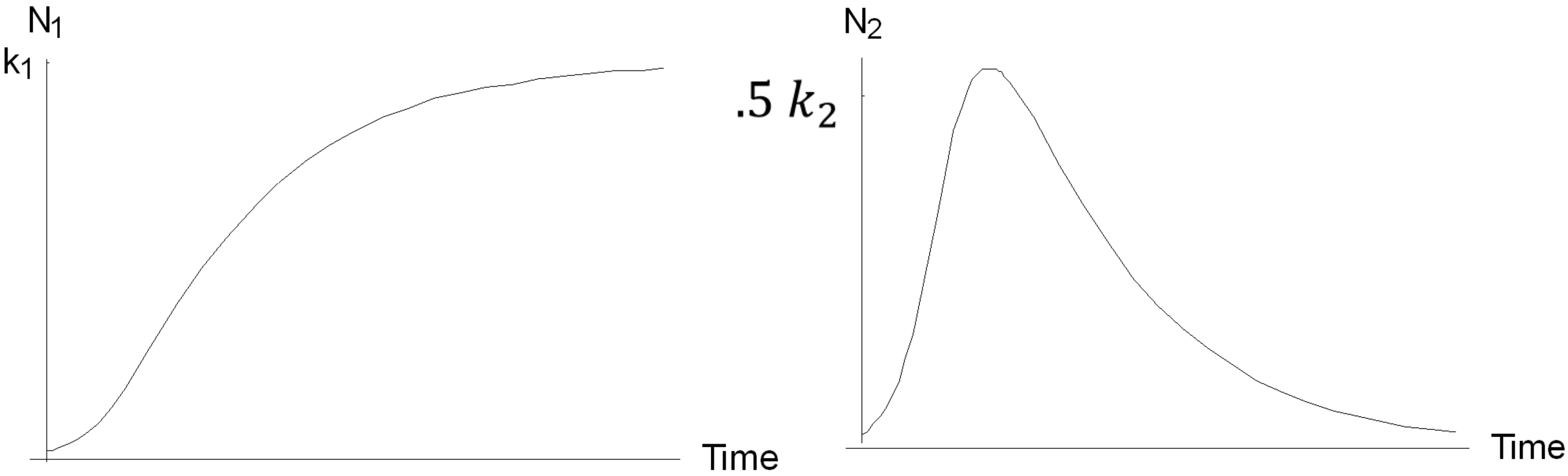
Other outcomes of the model:

Species 1 can outcompete species 2



Lotka-Volterra interaction model: exclusion

- This happens for different parameters

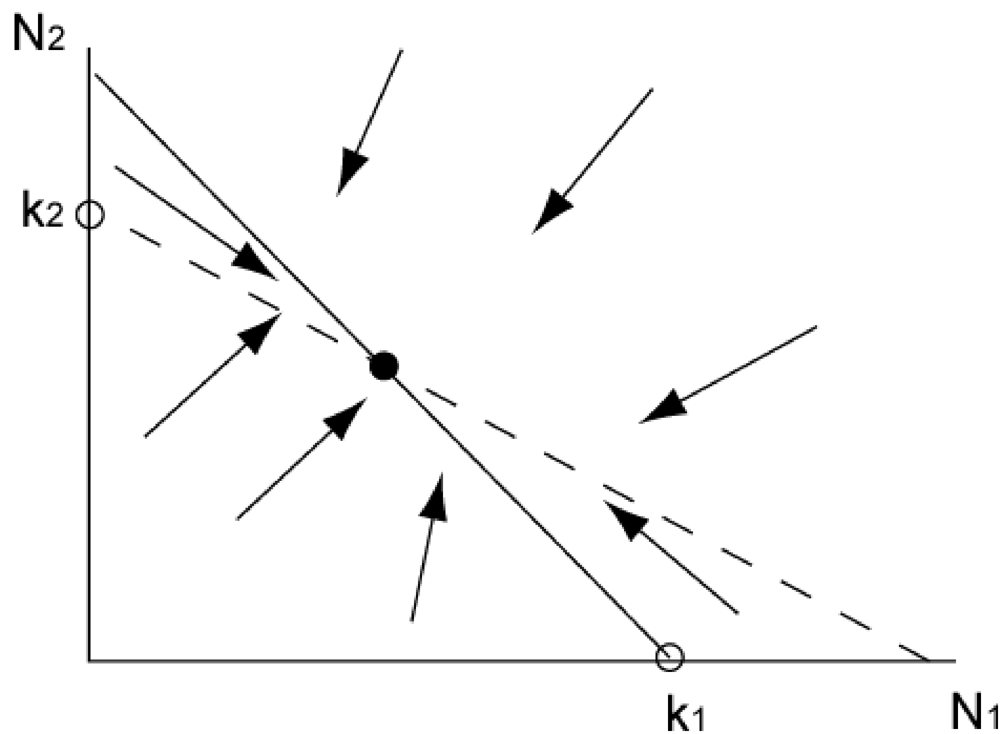


- This is not all that surprising since the labelling (species 1, 2) is arbitrary

Lotka-Volterra interaction model: coexistence

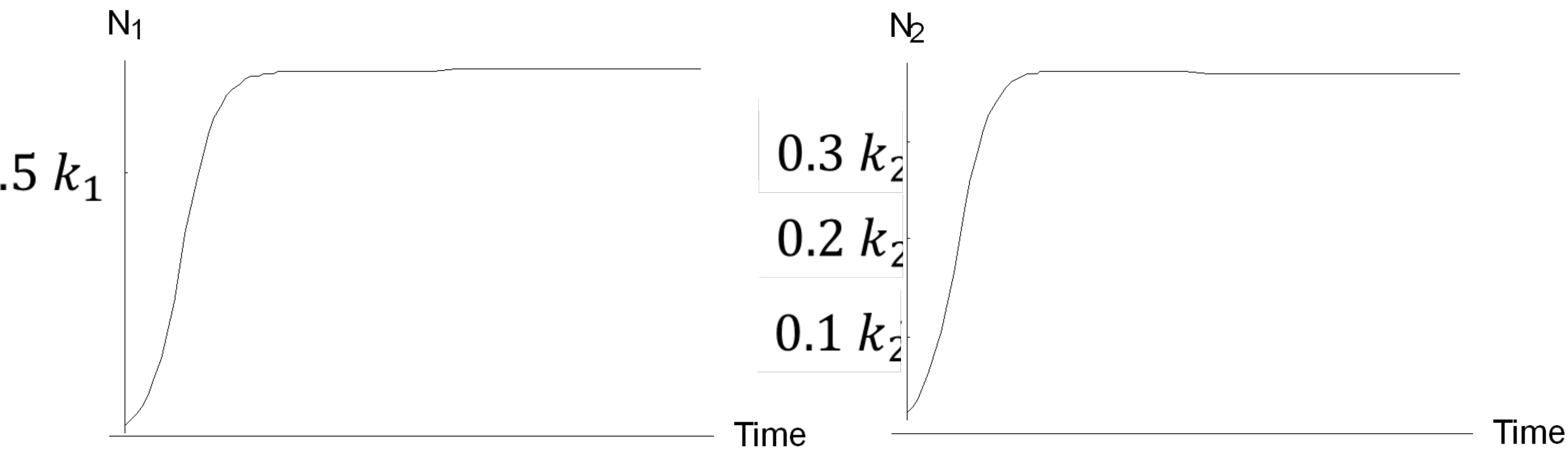
Other outcomes of the model:

Species 1 and 2 can coexist



Lotka-Volterra interaction model: coexistence

- This for different parameters

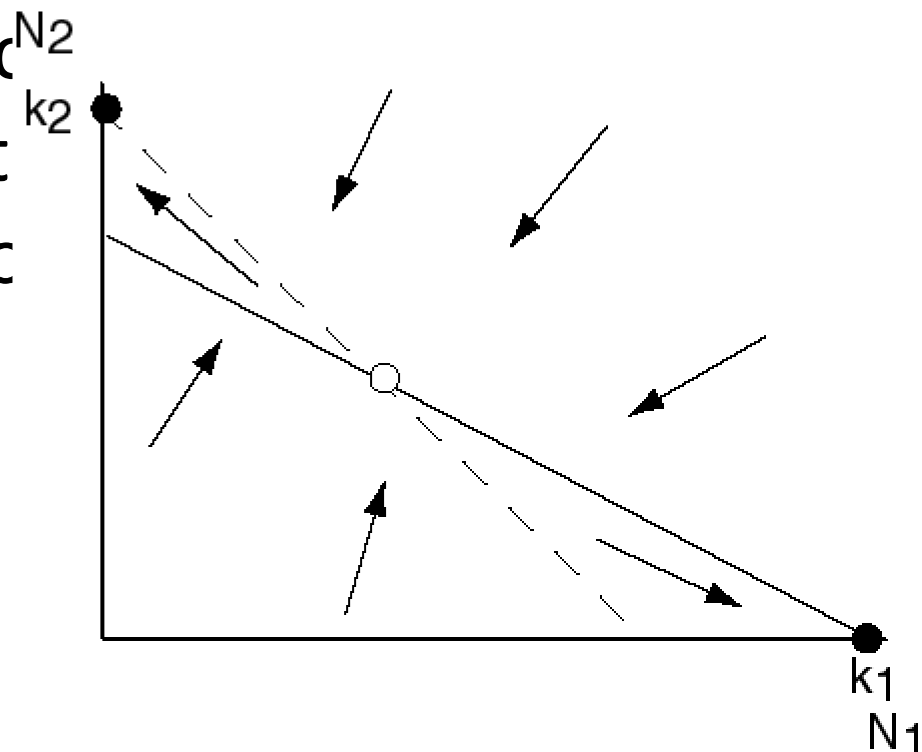


- Gause also found coexistence

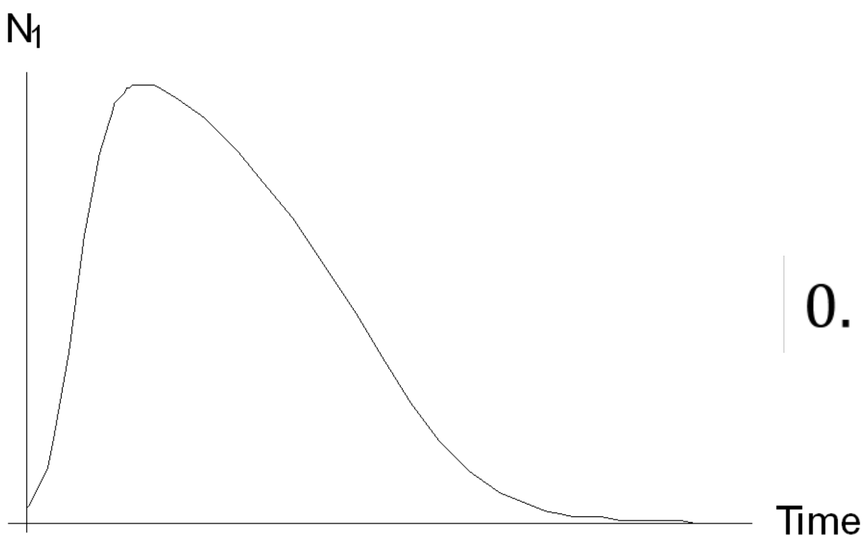
L-V interaction model: alternative stable states

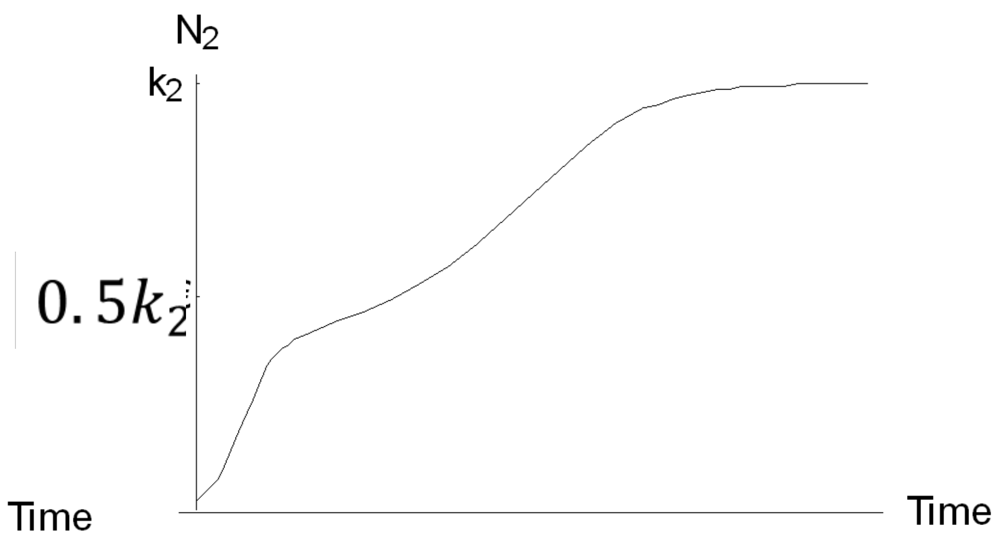
Other outcomes of the model:

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

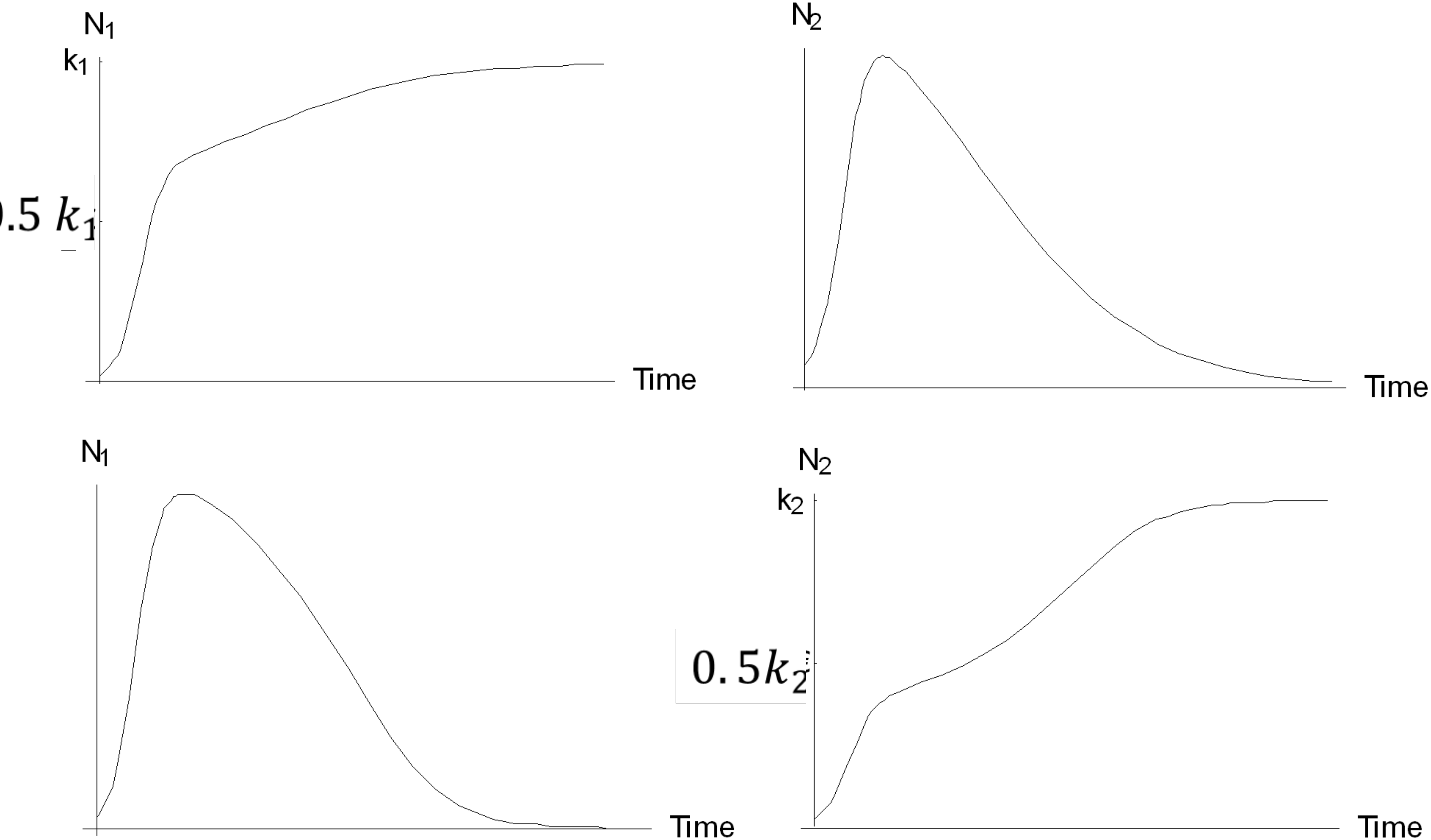


Alternative stable states

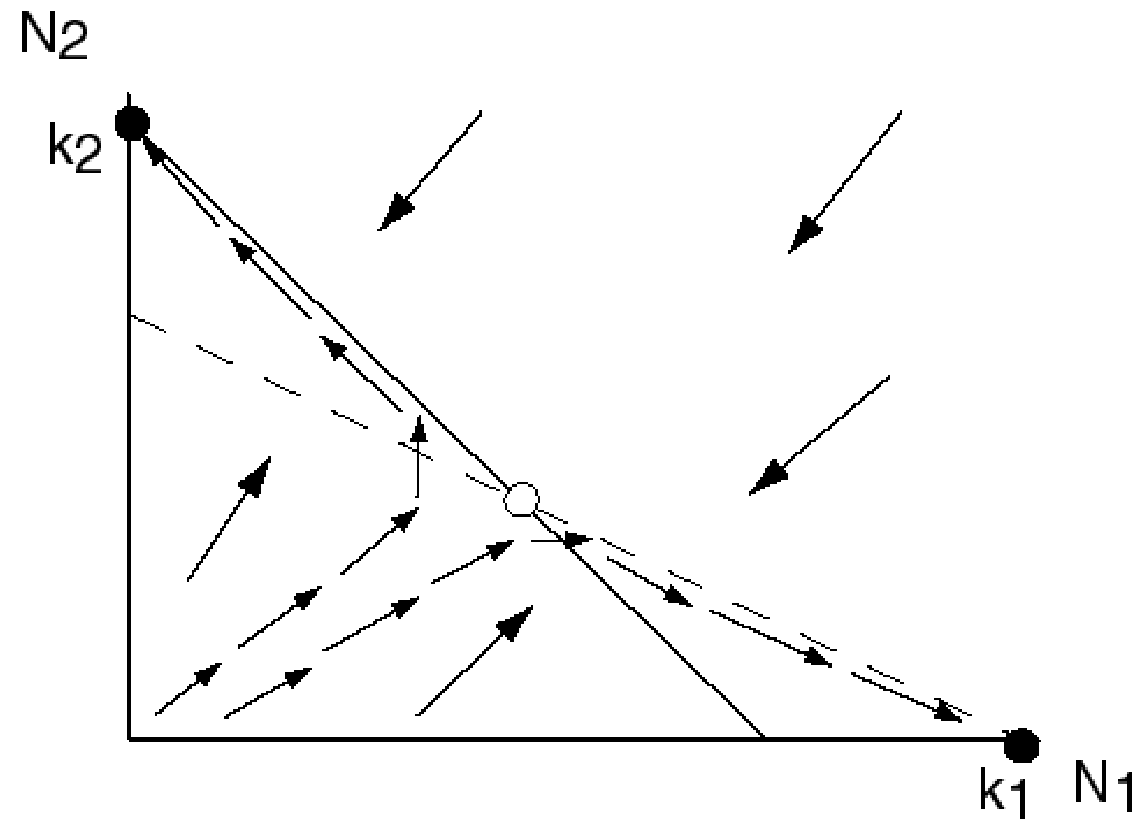




Alternative stable states



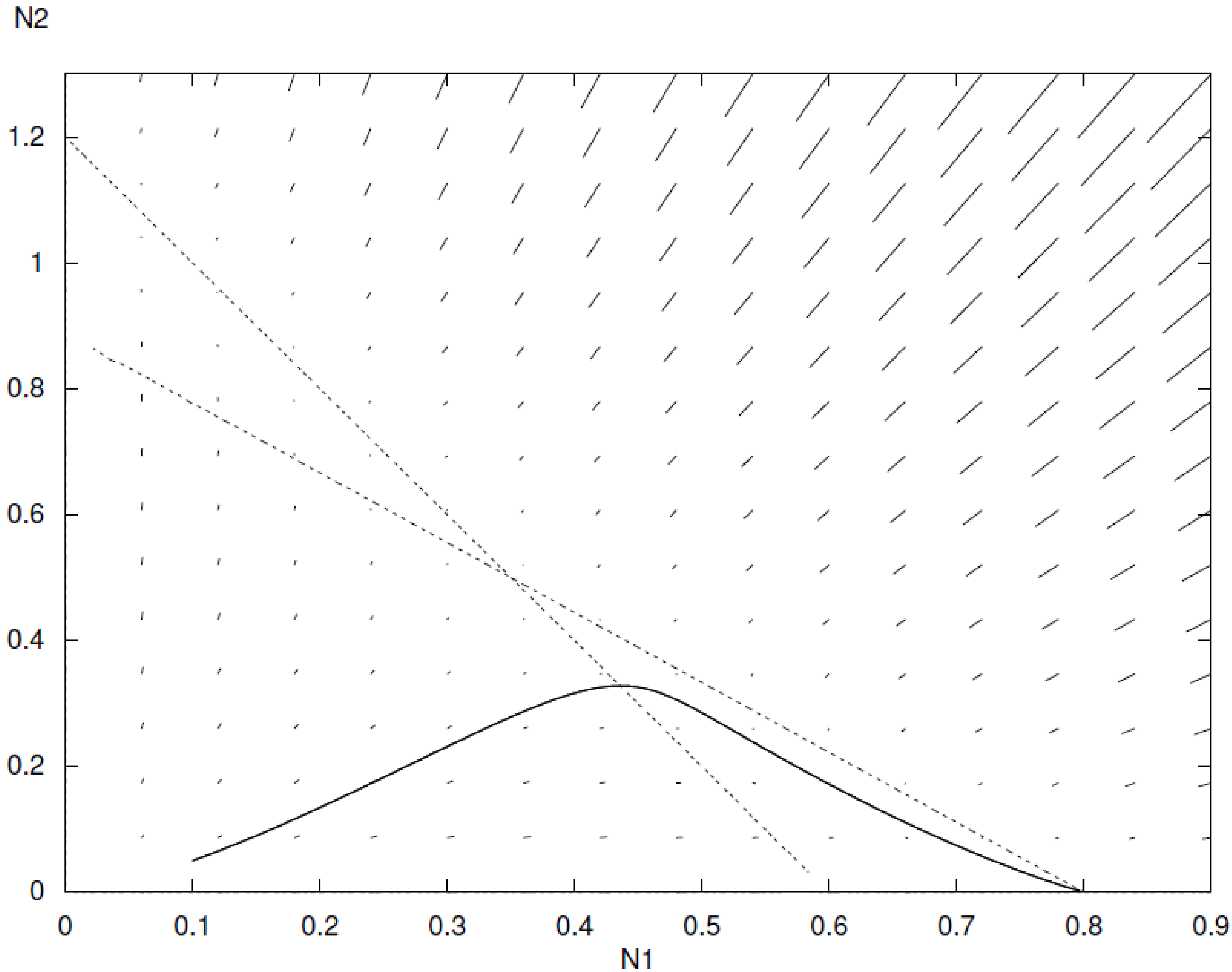
Alternative stable states



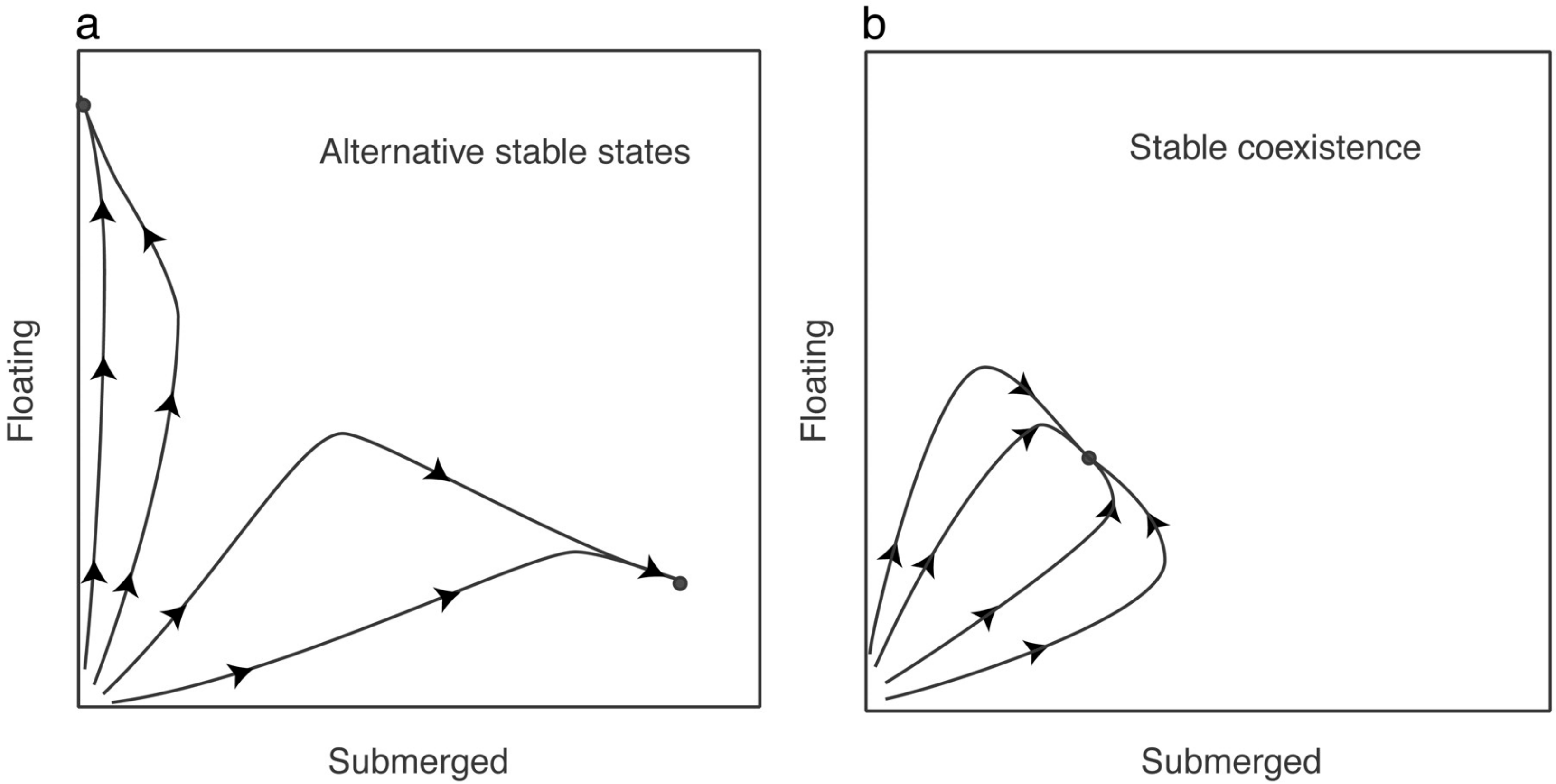
The phase plane

- 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

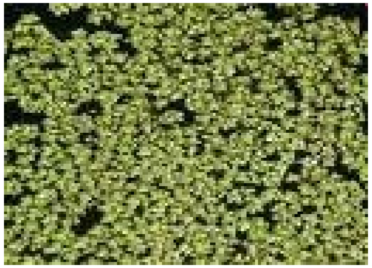


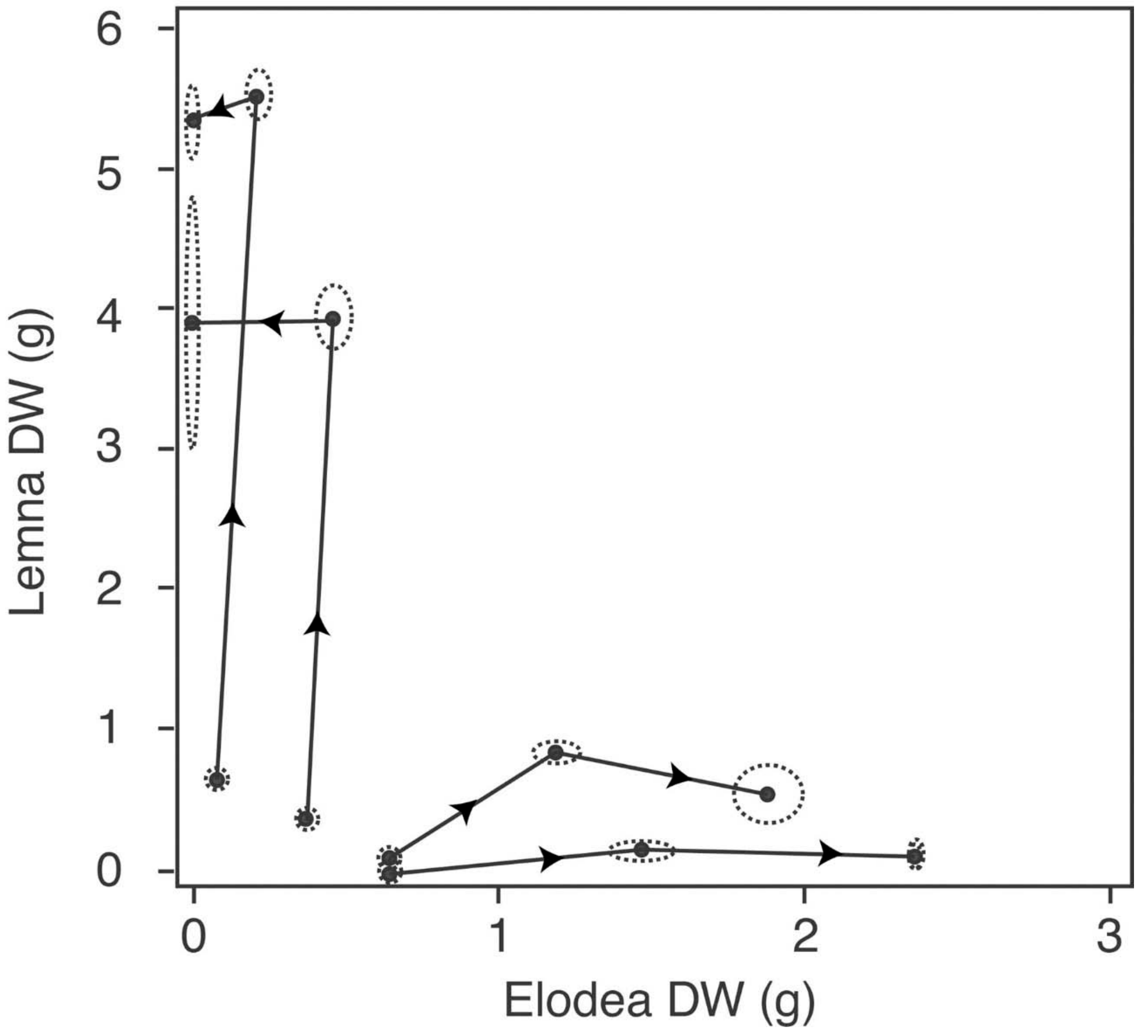
Theoretical growth trajectories in competition experiments of a submerged plant and a floating plant

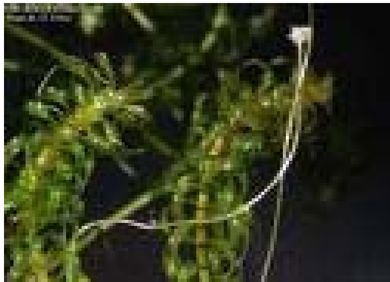


Scheffer M et al. PNAS 2003;100:4040-4045

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







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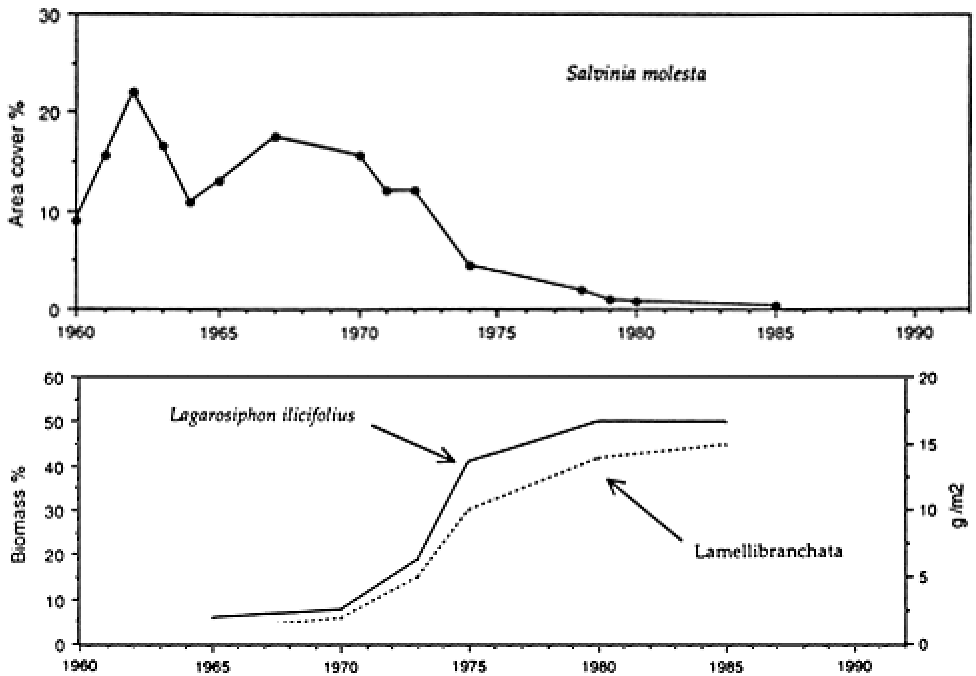
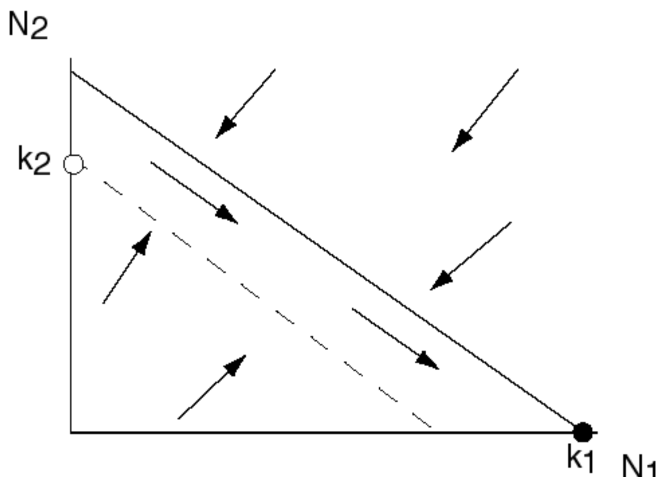
Changes in vegetation on Lake Kariba

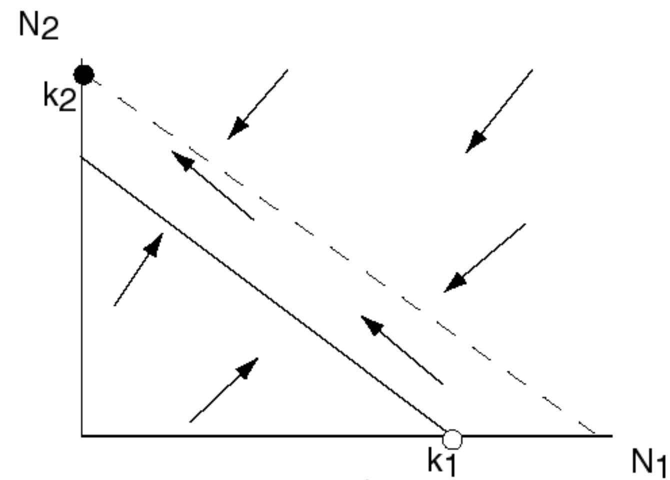


Lake Kariba: monthly and mean annual lake levels, mean annual lake level fluctuations, coverage of *Salvinia molesta*, changes in the benthic (Lamellibranchiata) and aquatic macrophyte biomass (*Lagarosiphon*). (From Karenge and Kolding, 1995).

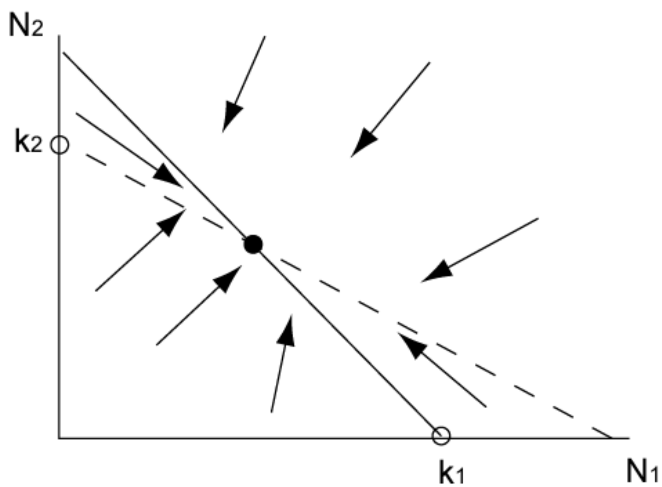
The outcomes of competition



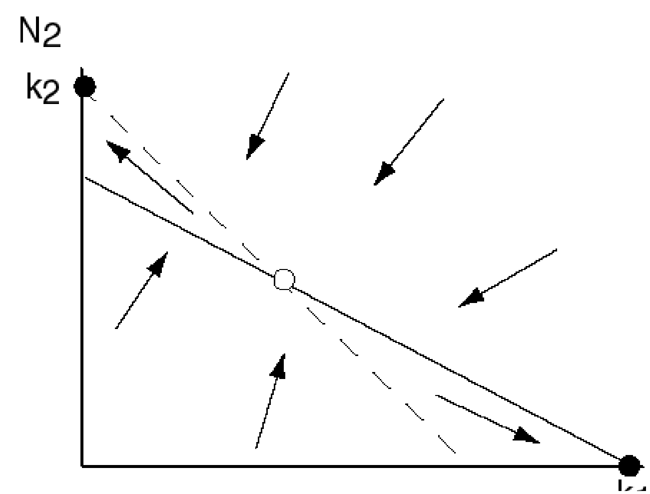
Species 1 excludes 2



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:

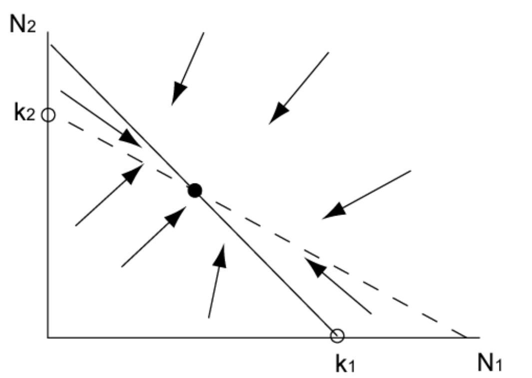
$$0 = r_1(k_1 - N_1^* - \alpha N_2^*)N_1^*$$

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

- 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 4th 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)

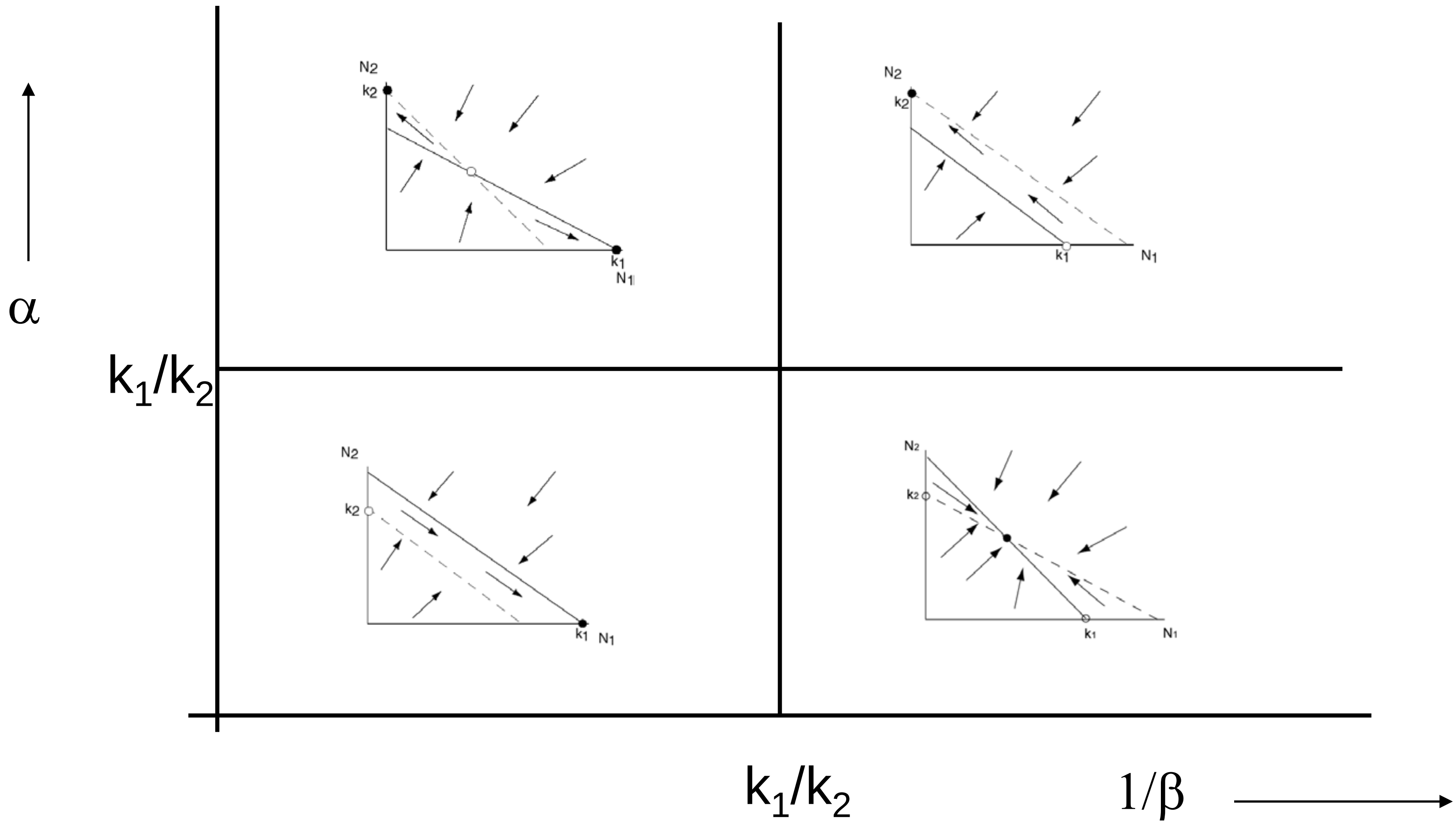
	$1/\beta < k_1/k_2$	$1/\beta > k_1/k_2$
$\alpha < k_1/k_2$	N_1 invades, N_2 no invasion Eq. 4 not +ive	Both invade Eq. 4 stable
$\alpha > k_1/k_2$	Neither can invade Eq. 4 unstable	N_1 no invasion, N_2 invades Eq. 4 not +ive

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

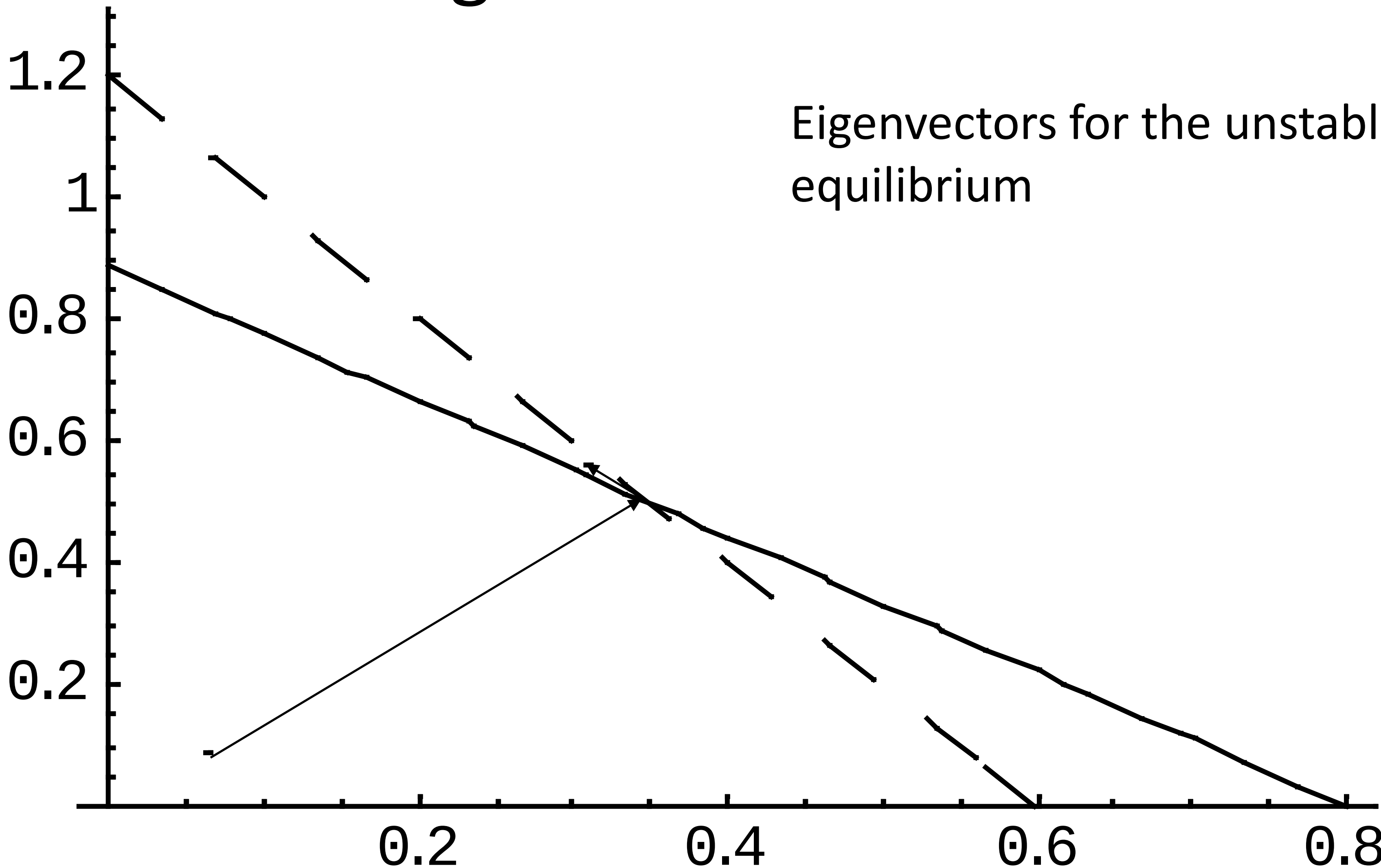
Classification as bifurcations



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?



What do the eigenvalues and eigenvectors mean?

- If one of the eigenvalues is positive, the equilibrium 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

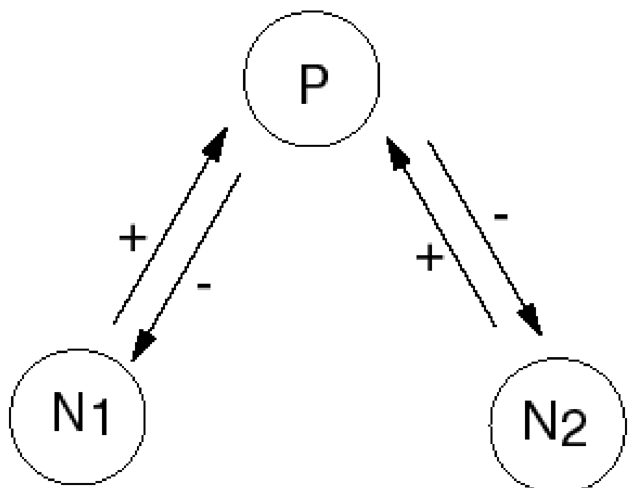
- The model only considers competition and no effects of any other parts of the ecosystem are taken into account (e.g. depletion of resources, shared predators or pathogens)
- All effects of competition are assumed to be immediate. No delays are taken into account

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

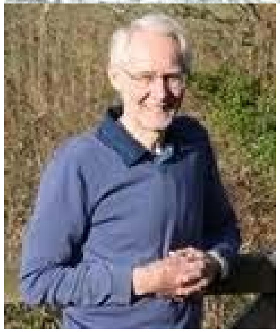
$$\frac{dN_1}{dt} = r_1(k_1 - N_1 - \gamma_1 P^*) N_1$$

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

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

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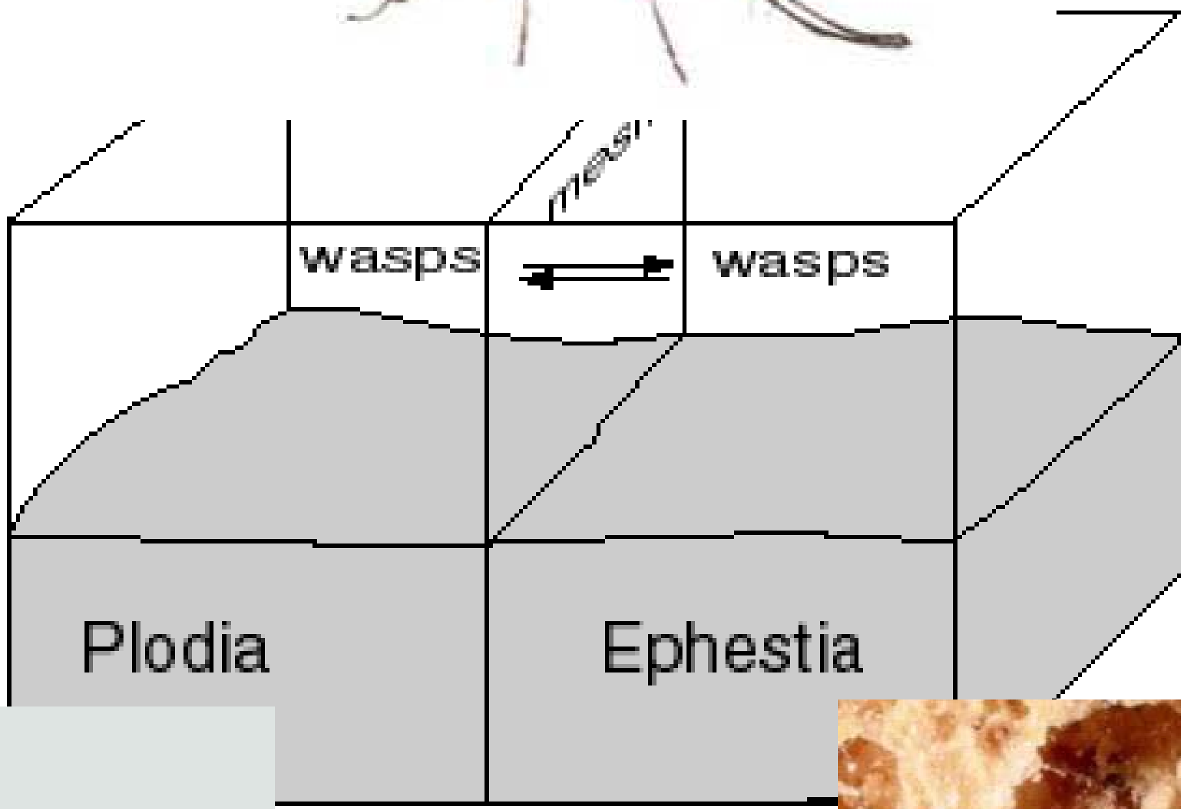


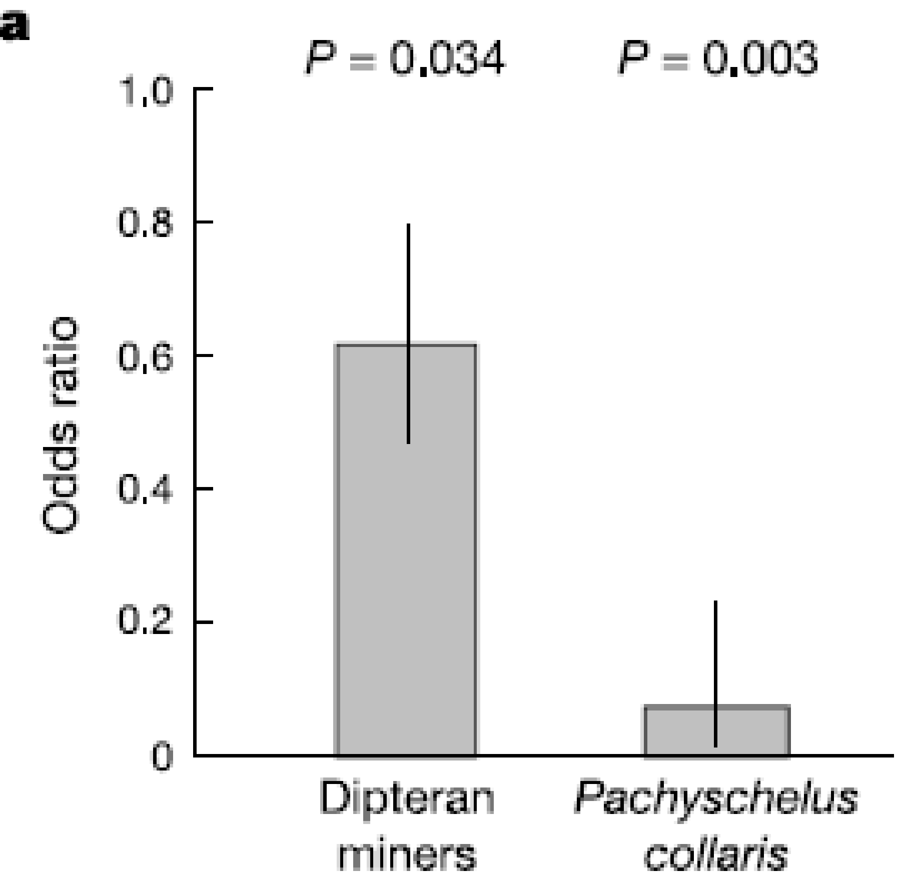
Apparent Competition

- 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

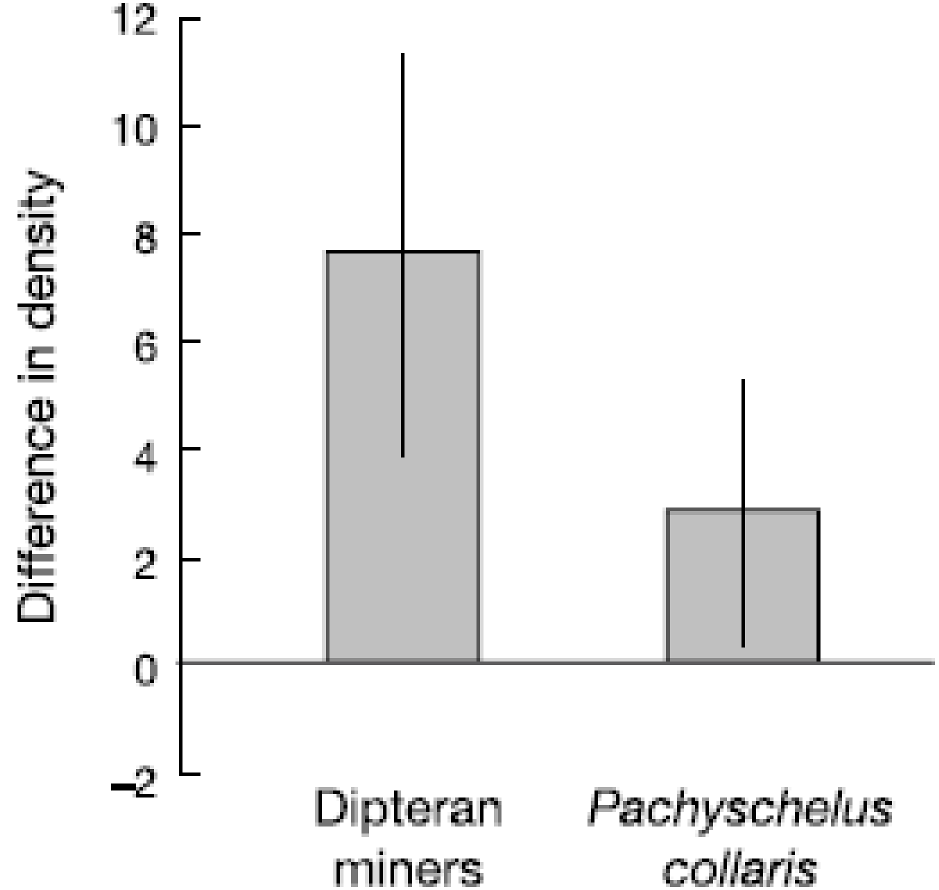
Apparent Competition

- 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