GATE ECOLOGY AND EVOLUTION

QUICK ACHIEVER COURSE

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GATE (Ecology and Evolution) 2016: AIR 08

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MATHEMATICAL MODELS FOR INTERACTIONS IN ECOLOGY

Lotka-Volterra Model for competition

- The model was independently proposed by Lotka (1925) and Volterra (1926).
- The model incorporates an additional competition term with the logistic growth equation.
- The model helps us to understand the conditions of competitive exclusion and stable coexistence.

Alfred J. Lotka
(1880-1949)

Vito Volterra
(1860-1940)

Lotka-Volterra Model for competition

- Logistic growth equation for a species:

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i - \boxed{N_i}}{K_i}\right)$$

Intraspecific competition term

- Inclusion of competition term:

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i - N_i - \boxed{\alpha N_j}}{K_i}\right)$$

Interspecific competition term

α is called competition coefficient.

Lotka-Volterra Model for competition

- **Logic of competition coefficient:**
  - It converts the number of one species to an equivalent number of another species in terms of competition.
  - $\alpha_{ij} < 1$ means that individuals of species j have a lesser inhibitory effect on individuals of species i than individuals of species i have on their own species.
  - $\alpha_{ij} > 1$ means that individuals of species j have a greater inhibitory effect on individuals of species i than individuals of species i have on their own species.

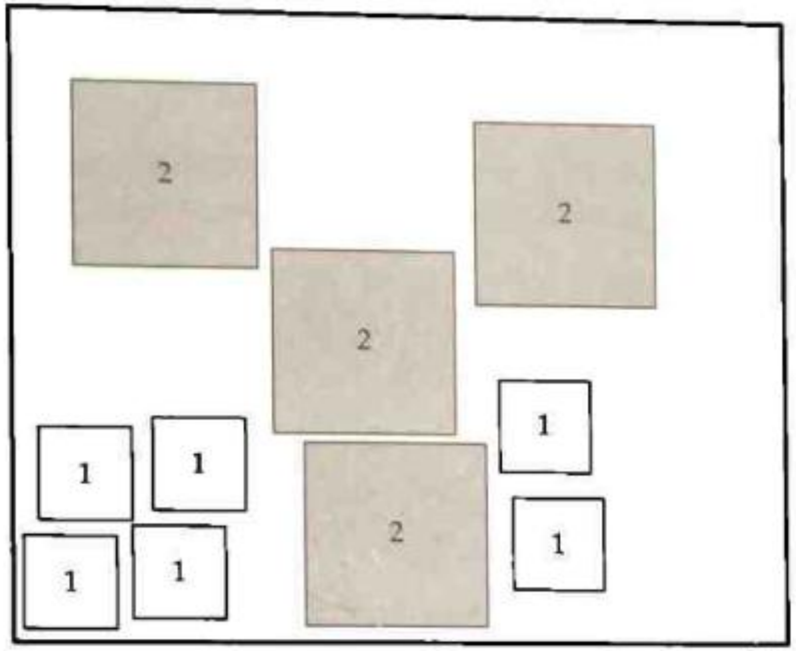


Figure 5.1 A graphical analogy for interspecific competition. The heavy square frame represents the carrying capacity for species 1 (K_1). Each individual consumes a portion of the limited resources available and is represented by a tile. Individuals of species 2 reduce the carrying capacity four times as much as individuals of species 1. Hence, the tiles for species 2 are four times larger than those for species 1, and $\alpha = 4.0$. (After Krebs 1985.)

Lotka-Volterra Model for competition

Parameters	Species 1	Species 2
Population density	N_1	N_2
Carrying capacity	K_1	K_2
Intrinsic rate of increase	r_1	r_2

Growth equation for species 1 will be:

$$\frac{dN_1}{dt} = r_1N_1\left(\frac{K_1 - N_1 - \alpha_{12}N_2}{K_1}\right)$$

Growth equation for species 2 will be:

$$\frac{dN_2}{dt} = r_2N_2(\frac{K_2 - N_2 - \alpha_{21}N_1}{K_2})$$

Lotka-Volterra Model for competition

- The equilibrium condition: $\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$
- Then for species 1:

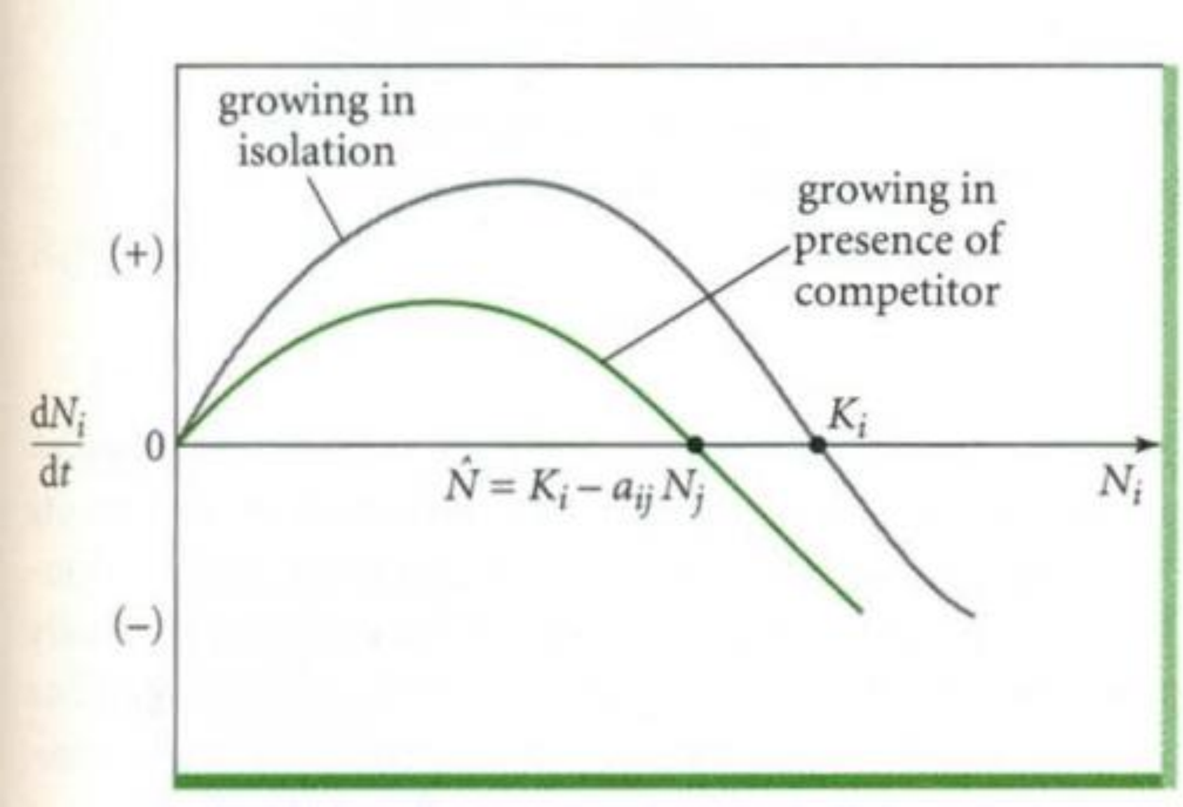
$\frac{dN_1}{dt} = 0$, or, $r_1 N_1 (K_1 - N_1 - \alpha_{12} N_2) = 0$, or,
$(K_1 - N_1 - \alpha_{12} N_2) = 0$,

or, $\boldsymbol{\widehat{N_1} = K_1 - \alpha_{12} N_2}$

- Similarly, for species 2:

$\frac{dN_2}{dt} = 0$, or, $r_2 N_2 (K_2 - N_2 - \alpha_{21} N_1) = 0$, or,
$(K_2 - N_2 - \alpha_{21} N_1) = 0$,

or, $\boldsymbol{\widehat{N_2} = K_2 - \alpha_{21} N_1}$



Lotka-Volterra Model for competition

- So, we can also write:

$\widehat{N_1} = K_1 - \alpha_{12}(K_2 - \alpha_{21}N_1)$, or, $N_1 = K_1 - \alpha_{12}K_2 + \alpha_{12}\alpha_{21}N_1$, or,
$N_1 - \alpha_{12}\alpha_{21}N_1 = K_1 - \alpha_{12}K_2$, or, $N_1(1 - \alpha_{12}\alpha_{21}) = K_1 - \alpha_{12}K_2$, or,
$\boldsymbol{\widehat{N_1}} = \frac{\boldsymbol{K_1 - \alpha_{12}K_2}}{\boldsymbol{1 - \alpha_{12}\alpha_{21}}}$

- Similarly for the $\widehat{N_2}$, we will get,

$$\boldsymbol{\widehat{N_2}} = \frac{\boldsymbol{K_2 - \alpha_{21}K_1}}{\boldsymbol{1 - \alpha_{12}\alpha_{21}}}$$

Lotka-Volterra Model for competition

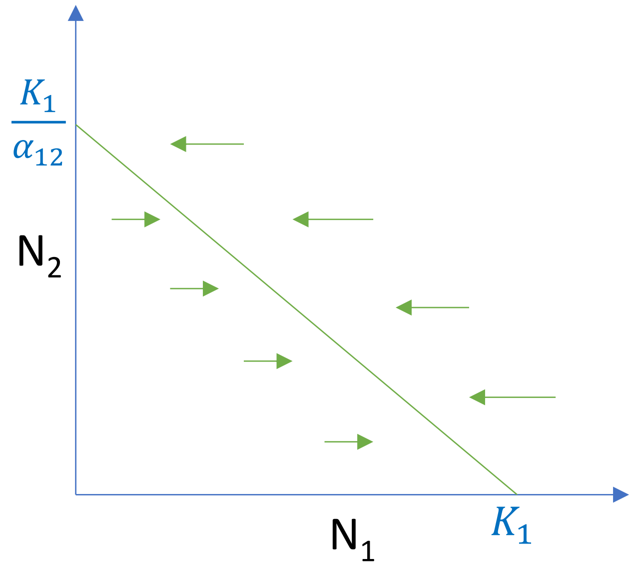
- If, $\alpha_{12}\alpha_{21} < 1$, then both $\widehat{N_1}$ and $\widehat{N_2}$ will be positive.
- The values of $\widehat{N_1}$ and $\widehat{N_2}$ depends on the carrying capacities of the two populations and competition coefficients, rather than the actual population size
- The coexistence will not be possible if carrying capacity of one population far exceeds the carrying capacities of the other populations. $\widehat{N_1} < 0$, when $K_1 < \alpha_{12}K_2$ or, $K_1/\alpha_{12} < K_2$. Likewise, $\widehat{N_2} < 0$, when $K_2 < \alpha_{21}K_1$ or, $K_2/\alpha_{21} < K_1$.

$$\boldsymbol{\widehat{N_1} = \frac{K_1 - \alpha_{12}K_2}{1 - \alpha_{12}\alpha_{21}}}$$

$$\boldsymbol{\widehat{N_2} = \frac{K_2 - \alpha_{21}K_1}{1 - \alpha_{12}\alpha_{21}}}$$

Lotka-Volterra Model for competition

- **State space:**
  - It is a graph of two variables, N_1 at x-axis and N_2 at y-axis.
  - At equilibrium condition, $N_1 = K_1 - \alpha_{12}N_2$, it follows a linear relationship with negative slope.
  - Now, when, N_1=0, then, $K_1 - \alpha_{12}N_2 = 0$, or, $N_2 = K_1/\alpha_{12}$
  - When N_2=0, then, $N_1 = K_1$
  - If we join the point of N_1=0 and N_2=0 in N_1-N_2 plot, then the resulting straight line will follow the equilibrium state equation.
  - The straight line is called *zero growth isocline* and for any values of species 1 and 2 on the straight line in N_1-N_2 plot will satisfy the equilibrium condition.
  - If the values of N_1 exceeds the values of isocline on the plot population will decrease towards the isocline and *vice versa*.



Lotka-Volterra Model for competition

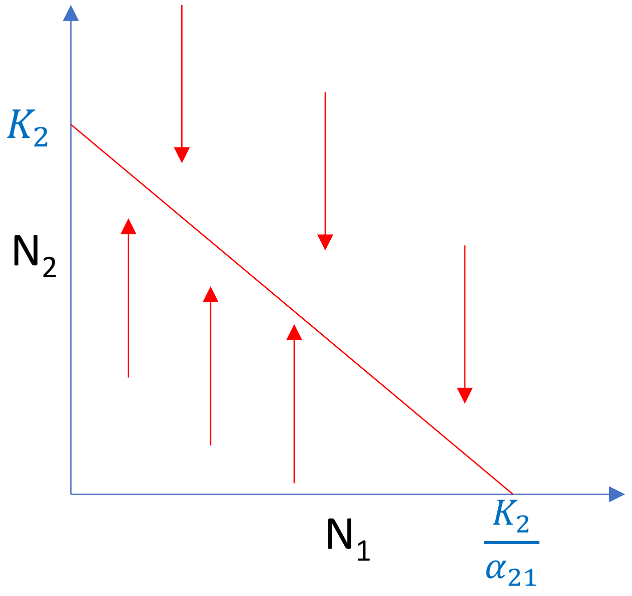
- **Plotting N_2 in state space:**
  - Likewise, the equilibrium equation for N_2 also follows a linear relationship with negative slop like N_1:

$$N_2 = K_2 - \alpha_{21} N_1$$

When, N_1=0, then, $N_2 = K_2$

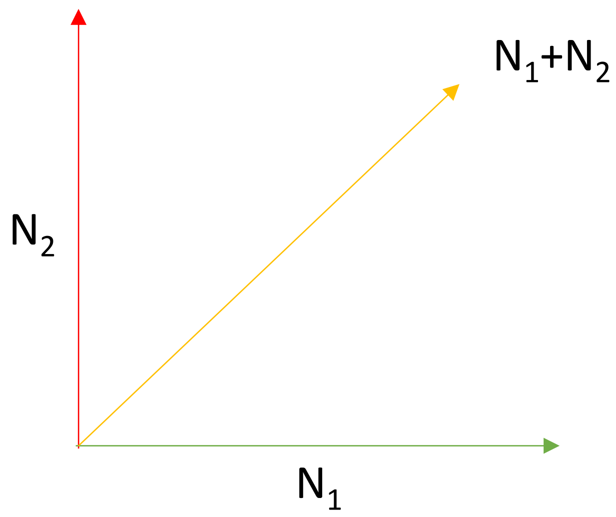
When, N_2=0, then, $N_1 = K_2/\alpha_{21}$

  - Notice that the direction of the arrow is vertical here. Why?



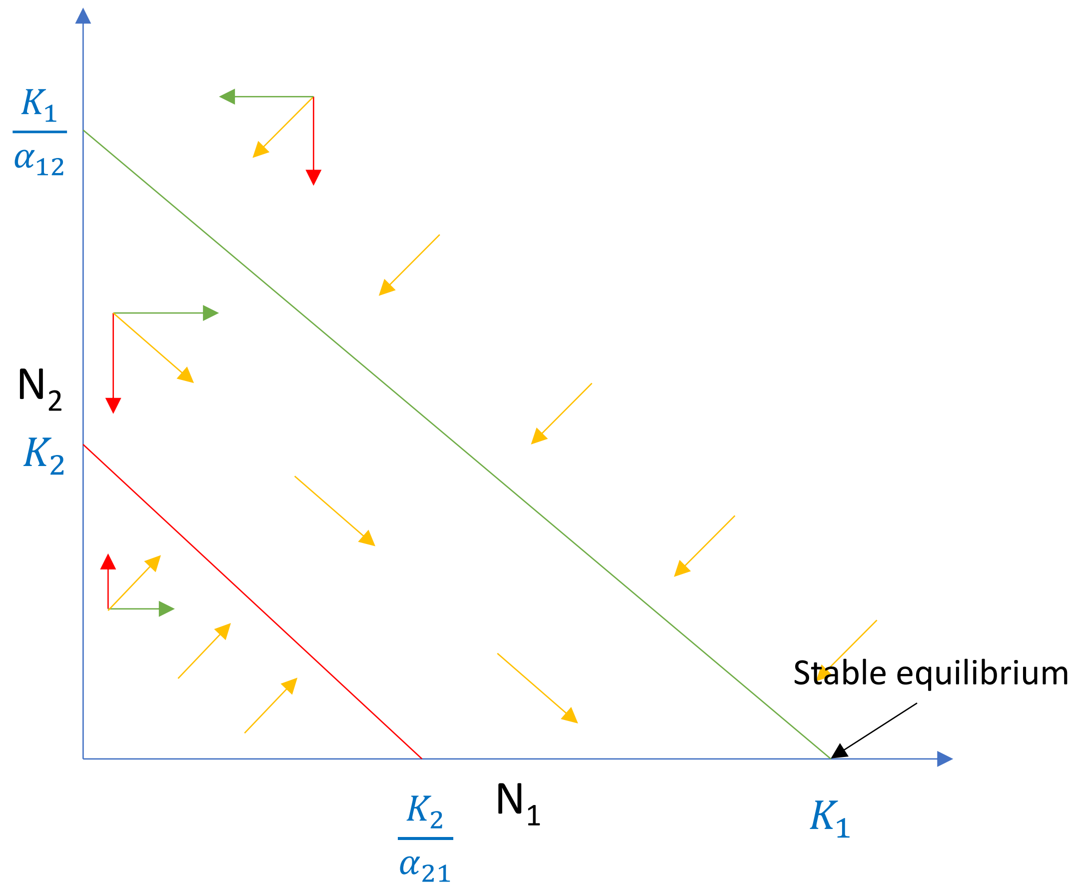
Lotka-Volterra Model for competition

- To understand the effect of one species on another in the *state space* the two plot must be merged and should be interpreted together.
- The *arrows* indicating the increase and decrease of the population have both magnitude and direction. So, if two graphs superimposed, the resulting arrow will follow the rule of vector addition.
- There can be four cases:
  - $\frac{K_1}{\alpha_{12}} > K_2$ and $K_1 > \frac{K_2}{\alpha_{21}}$ or $K_1 > K_2\alpha_{12}$and $K_1\alpha_{21} > K_2$
  - $K_2 > \frac{K_1}{\alpha_{12}}$ and $\frac{K_2}{\alpha_{21}} > K_1$ or $K_2\alpha_{12} > K_1$ and $K_2 > K_1\alpha_{21}$
  - $K_1 > \frac{K_2}{\alpha_{21}}$ and $K_2 > \frac{K_1}{\alpha_{12}}$ or $K_1\alpha_{21} > K_2$ and $K_2\alpha_{12} > K_1$
  - $\frac{K_1}{\alpha_{12}} > K_2$ and $\frac{K_2}{\alpha_{21}} > K_1$ or $K_1 > K_2\alpha_{12}$ and $K_2 > K_1\alpha_{21}$



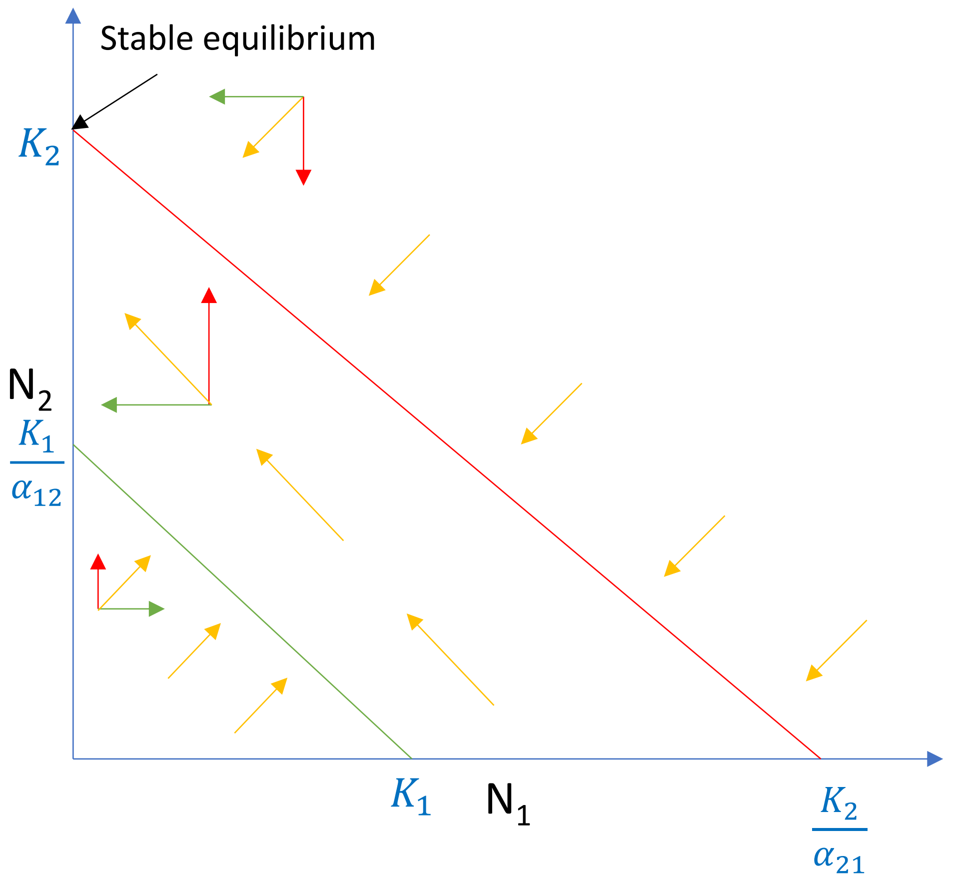
Lotka-Volterra Model for competition

- **Case I:** $\boldsymbol{\frac{K_1}{\alpha_{12}} > K_2}$ **and** $\boldsymbol{K_1 > \frac{K_2}{\alpha_{21}}}$ **or** $\boldsymbol{K_1 > K_2\alpha_{12}}$**and** $\boldsymbol{K_1\alpha_{21} > K_2}$
  - $K_1 > K_2\alpha_{12}$ indicates that intraspecific competition between the individuals of species 1 is greater than interspecific competition effect exerted by species 2.
  - $K_1\alpha_{21} > K_2$ indicates that interspecific competition effect exerted by species 1 is more than intraspecific competition between the individuals of species 2.
  - *Species 1 will attain its maximum carrying capacity and will drive species 2 to extinction.*



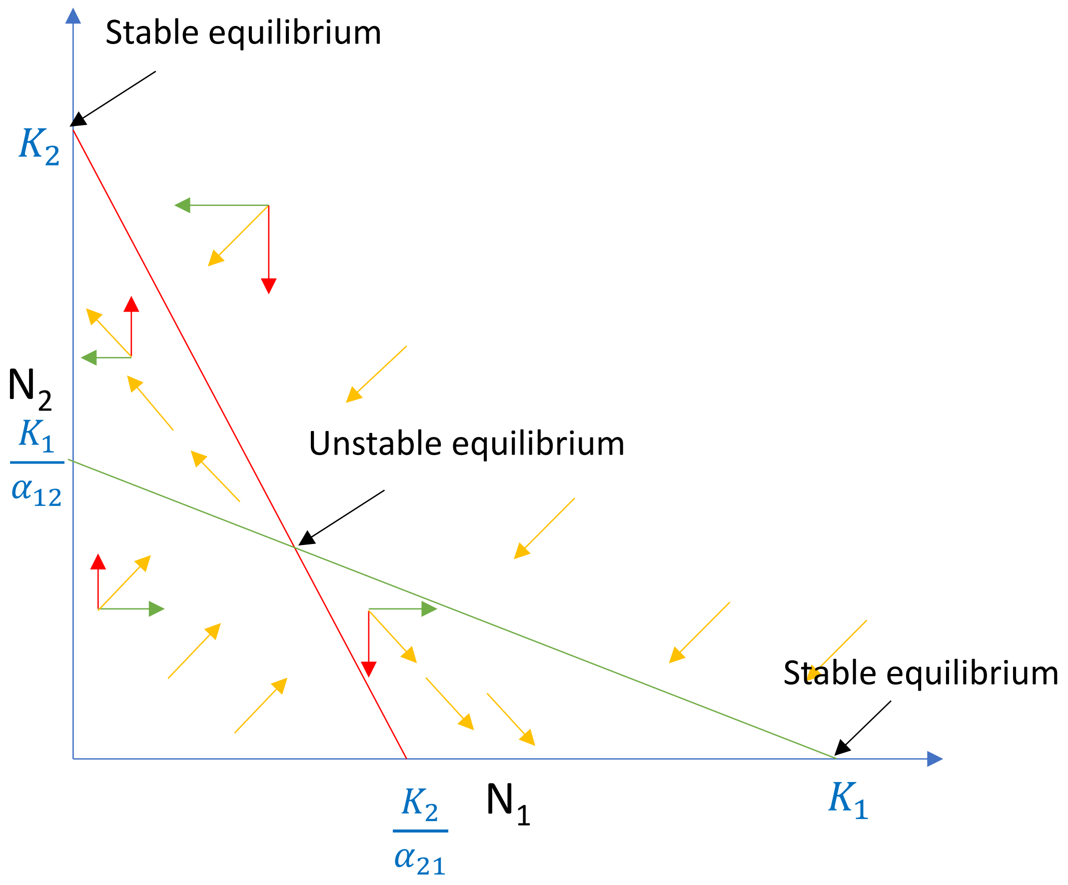
Lotka-Volterra Model for competition

- **Case II:** $\boldsymbol{K_2 > \frac{K_1}{\alpha_{12}}}$ **and** $\boldsymbol{\frac{K_2}{\alpha_{21}} > K_1}$ **or** $\boldsymbol{K_2\alpha_{12} > K_1}$ **and** $\boldsymbol{K_2 > K_1\alpha_{21}}$
  - $K_2\alpha_{12} > K_1$ indicates that interspecific competition effect exerted by species 2 is more than intraspecific competition between the individuals of species 1.
  - $K_2 > K_1\alpha_{21}$ indicates that intraspecific competition between the individuals of species 2 is greater than interspecific competition effect exerted by species 1.
  - *Species 2 will attain its maximum carrying capacity and will drive species 1 to extinction.*



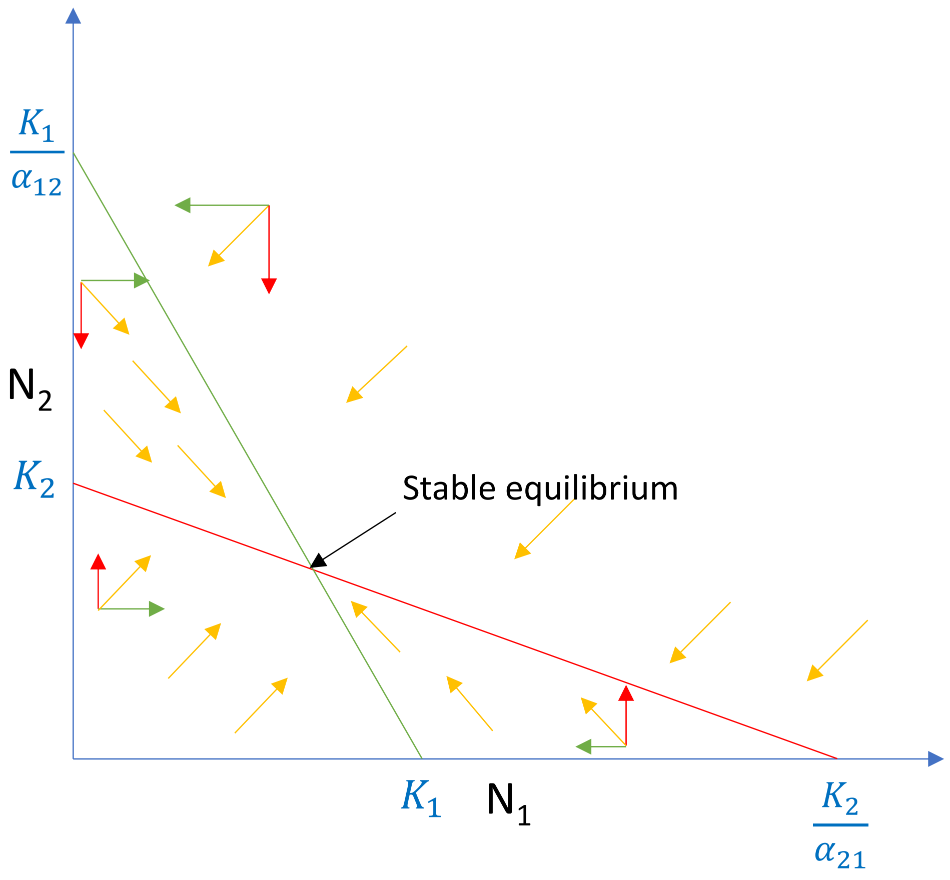
Lotka-Volterra Model for competition

- **Case III: $K_1 > \frac{K_2}{\alpha_{21}}$ and $K_2 > \frac{K_1}{\alpha_{12}}$ or $K_1\alpha_{21} > K_2$ and $K_2\alpha_{12} > K_1$**
  - $K_1\alpha_{21} > K_2$ indicates that interspecific competition effect exerted by species 1 is more than intraspecific competition between the individuals of species 2.
  - $K_2\alpha_{12} > K_1$ indicates that interspecific competition effect exerted by species 2 is more than intraspecific competition between the individuals of species 1.
  - *The consequence, as the figure shows, is an unstable equilibrium combination of N_1 and N_2 (where the isoclines cross), and two stable points. At the first of these stable points, species 1 reaches its carrying capacity with species 2 extinct; whilst at the second, species 2 reaches its carrying capacity with species 1 extinct.*
  - *Which of these two outcomes is actually attained is determined by the initial densities: the species which has the initial advantage will drive the other species to extinction.*



Lotka-Volterra Model for competition

- **Case IV:** $\boldsymbol{\frac{K_1}{\alpha_{12}} > K_2}$ **and** $\boldsymbol{\frac{K_2}{\alpha_{21}} > K_1}$ **or** $\boldsymbol{K_1 > K_2\alpha_{12}}$ **and** $\boldsymbol{K_2 > K_1\alpha_{21}}$
    - $K_1 > K_2\alpha_{12}$ indicates that intraspecific competition between the individuals of species 1 is greater than interspecific competition effect exerted by species 2.
    - $K_2 > K_1\alpha_{21}$ indicates that intraspecific competition between the individuals of species 2 is greater than interspecific competition effect exerted by species 1.
    - *Hence, intraspecific competition is greater than the interspecific competition, a stable coexistence of both species will result at the stable equilibrium point, where 2 isocline intersects.*



Lotka-Volterra Model for competition

- Gause's experiment follows Lotka-Volterra model

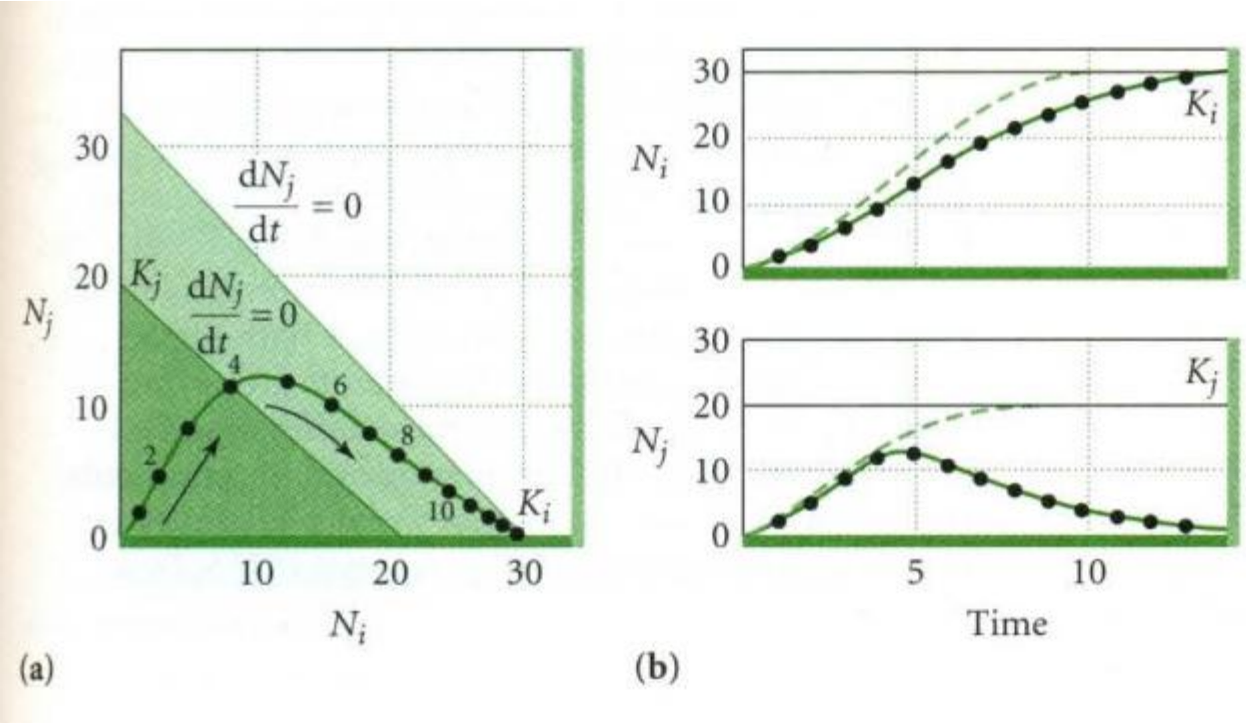


FIGURE 21-6 The course of competition between two populations portrayed (a) on a competition graph and (b) as changes in population size over time. The time intervals are indicated on the competition graph by numerals next to the sample points. Dashed lines indicate population increases when the species are grown separately.

Lotka-Volterra Model for competition

- Competitive exclusion principle:

  If the species 1 have to invade from very worst condition (where $N_1 \approx 0$, and $N_2 \approx K_2$), then per capita growth rate of the species must be greater than 1. It leads to following condition:

  $$\frac{dN_1}{N_1 dt} > 0\ or, r_1\left(\frac{K_1 - 0 - \alpha_{12}K_2}{K_1}\right) > 0, or, K_1 > \alpha_{12}K_2, or\ \boldsymbol{\frac{K_1}{K_2} > \alpha_{12}}$$

  If similar conditions is applied for species 2, it will result: $\frac{K_2}{K_1} > \alpha_{21}$

  or $\boldsymbol{\frac{K_1}{K_2} > \frac{1}{\alpha_{21}}}$

Inequalities	Outcome
$\frac{K_1}{K_2} > \alpha_{12}$	Species 1 invades
$\frac{K_1}{K_2} < \alpha_{12}$	Species 1 cannot invade
$\frac{K_1}{K_2} < \frac{1}{\alpha_{21}}$	Species 2 invades
$\frac{K_1}{K_2} > \frac{1}{\alpha_{21}}$	Species 2 cannot invade

Lotka-Volterra Model for competition

- Competitive exclusion principle:

Inequality	Species 1 invade?	Species 2 invade?	Outcome
$\frac{1}{\alpha_{21}} < \frac{K_1}{K_2} > \alpha_{12}$	Yes	No	Case I: Species 1 wins
$\frac{1}{\alpha_{21}} > \frac{K_1}{K_2} < \alpha_{12}$	No	Yes	Case II: Species 2 wins
$\frac{1}{\alpha_{21}} < \frac{K_1}{K_2} < \alpha_{12}$	No	No	Case III: Unstable equilibrium
$\frac{1}{\alpha_{21}} > \frac{K_1}{K_2} > \alpha_{12}$	Yes	Yes	Case IV: Stable coexistence

Case I: values of $\boldsymbol{\alpha} \approx \mathbf{1}$

$\alpha_{12} = 0.9$ and $\alpha_{21} = 0.9$

Region of stable coexistence will be:

$\frac{1}{0.9} > \frac{K_1}{K_2} > 0.9$ or $1.11 > \frac{K_1}{K_2} > 0.9$

Case II: values of $\boldsymbol{\alpha} \approx \mathbf{0}$

$\alpha_{12} = 0.2$ and $\alpha_{21} = 0.2$

Region of stable coexistence will be:

$\frac{1}{0.2} > \frac{K_1}{K_2} > 0.2$ or $5 > \frac{K_1}{K_2} > 0.2$

Lotka-Volterra Model for competition

- Model assumption:
  - Resources are in limited supply. If, resources are unlimited then an infinite number of species can coexist regardless of their intensity of competition.
  - Competition coefficients and carrying capacities are constants.
  - Linear density dependence

Lotka-Volterra Model for predation

$$\frac{dN}{dt} = rN - cNP$$

$$\frac{dP}{dt} = acNP - mP$$

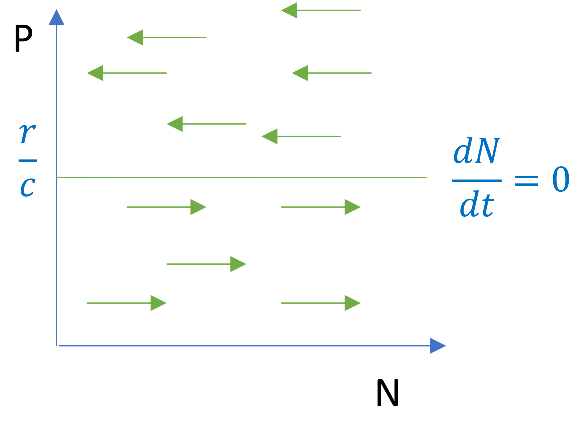
Here, r is growth rate of prey, c is catching efficiency or predation efficiency, cN is the *functional response* of the predator (the rate of prey capture by a predator as a function of prey abundance), a is the efficiency of converting captured prey to the offspring of predator and m is the death rate of the predator. $acNP$ is the *predator's numerical response* to increased consumption of prey.

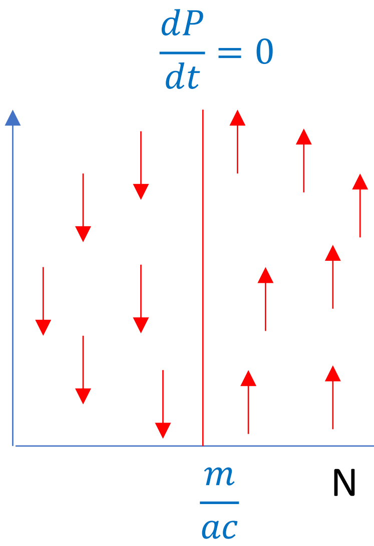
Lotka-Volterra Model for predation

- **Equilibrium condition** $\left(\boldsymbol{\frac{dN}{dt} = \frac{dP}{dt} = 0}\right)$**:**
  - **When** $\boldsymbol{\frac{dN}{dt} = 0}$**:**

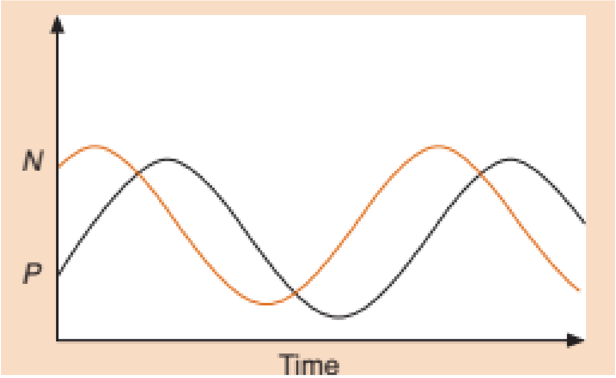
    $rN - cNP = 0$, or $rN = cNP$, or $\boldsymbol{\widehat{P} = \frac{r}{c}}$
  - **When** $\boldsymbol{\frac{dP}{dt} = 0}$**:**

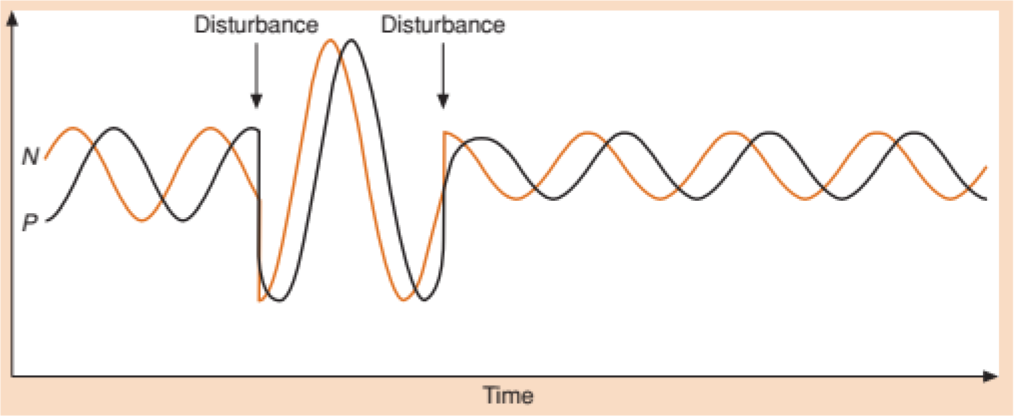
    $acNP - mP = 0$, or $acNP = mP$, or $\boldsymbol{\widehat{N} = \frac{m}{ac}}$

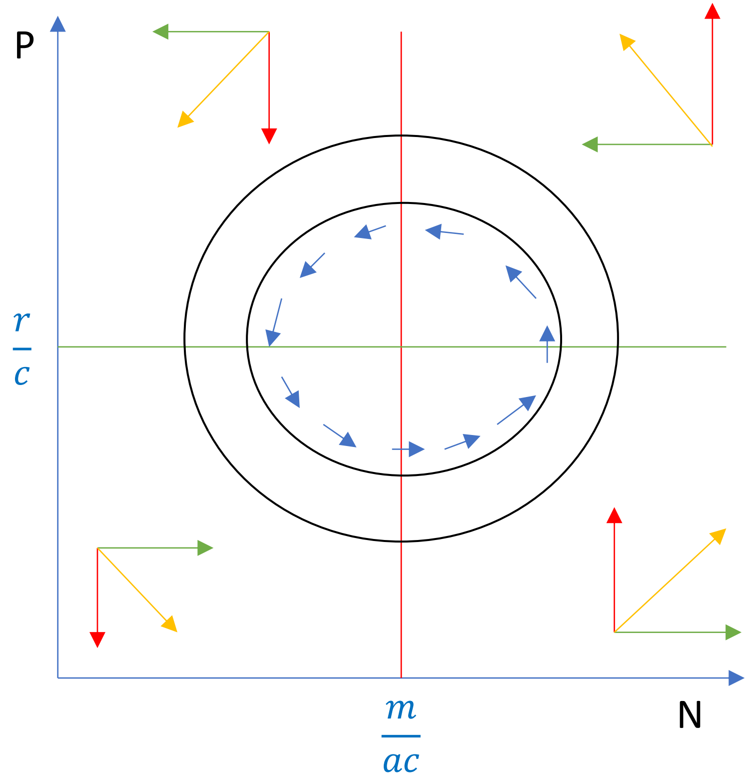




Lotka-Volterra Model for predation







Lotka-Volterra Model for predation

- **Model assumptions:**
  - Growth of the prey population is only limited by predation
  - The predator population is a specialist at it can only survive in the presence of prey population.
  - Predator and prey will encounter randomly in a homogenous environment.

Functional responses

- Type I:

  Rate limiting term=N/k

- Type II:

  Rate limiting term = $N/(a + N)$

  Where, a is half-saturation constant

- Type III:

  Rate limiting term = $N^x/(a^x + N^x)$