Lecture 12

Interspecific Interactions

Dr. Ido Filin
ifilin@univ.haifa.ac.il

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Outline

1. Population fluctuations
2. Life tables and R_0 calculations
3. Interspecific interactions – competition and predation

Fluctuations in population size/density

- Self-induced
  - Time lags.
  - Overcompensating density-dependence.
  - High fecundity.

- Interspecific interactions – e.g., predator-prey.

- Stochastic effects.

  - Demographic stochasticity – individuals come in discrete units; random individual variation in demographic performance.

  - Environmental stochasticity – random variability in the environment (e.g., among years) that affect all individuals similarly.

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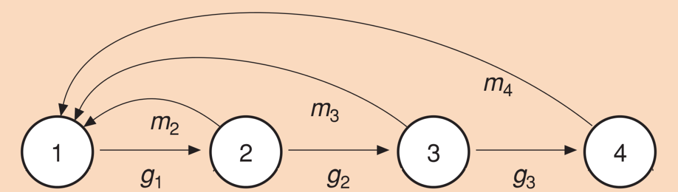
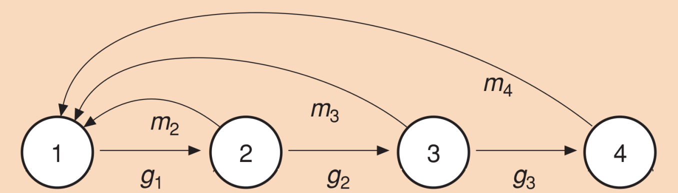
2. Life tables and R_0 calculations
3. Interspecific interactions – competition and predation

Population dynamics with age-structure



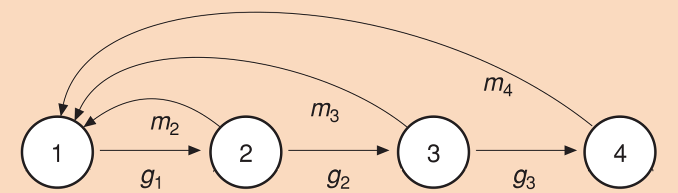
- Fecundity, m_a, summed over all age-classes is translated into the age-class of newborns (age 1 in the above diagram) for any given year.
- Survival from one age to the next is given by g_a.
- Such that $l_2 = g_1$, $l_3 = g_1 g_2$ and $l_4 = g_1 g_2 g_3$.
  If $g_a = 0.5$ for all ages, $l_2 = 0.5$, $l_3 = 0.25$, $l_4 = 0.125$, etc.
- Obviously, the population finite rate of increase or net reproductive rate will depend on the values of age-dependent survival and fecundity.

Population dynamics with age-structure



- For example, assume that reproduction occurs only in the fourth year ($m_2 = m_3 = 0$), and $l_4 = 0.1$, while $m_4 = 5$.
- Starting with 100 newborns (age 1) after 3 years only 10 will remain – i.e., only 10 successfully reached age 4.
- They then reproduce and die. leaving after them 50 newborns.
- Compared to the 100 individuals that started the parent generation, there are now only 50 individuals starting the second generation. $\Rightarrow R_0$ or λ in this case are 0.5.

Population dynamics with age-structure



- The general expression for R_0 given age-dependent survival and fecundity is

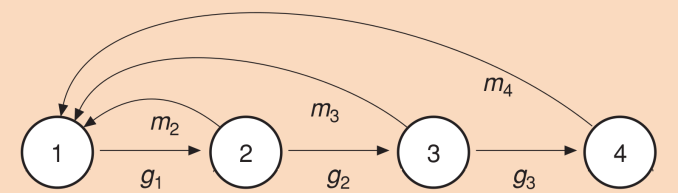
$$R_0 = \sum_a l_a m_a \ .$$

- This is a weighted sum where each age-dependent fecundity value (m_a) is weighted according to the probability (l_a) to reach that age alive.
- In the above diagram, given $l_1 = 1, l_2 = 0.5, l_3 = 0.25, l_4 = 0$ and $m_1 = 0, m_2 = 2, m_3 = 0.5$ and $m_4 = 1000$, we get $R_0 = 0 + 1 + 0.125 + 0 = 1.125$

Population dynamics with age-structure

- There is a similar equation for r, which is given by the solution to
$$\sum_a e^{-ra} l_a m_a = 1 \; .$$
- Exponential growth with continuous deaths and births, $r = b$ - d, $R_0 = b/d$; **or** the case of only a single lifetime reproductive event (semelparous lifecycle; e.g., unicellulars), $r = \frac{\log R_0}{T}$; are both special cases of the above general equations for r and R_0 (assuming specific patterns of l_a and m_a).
- Generation time is also found from age schedules of survival and fecundity.
- Generation time is often calculated as a weighted average of reproductive ages:
$$T = \frac{\sum_a a l_a m_a}{\sum_a l_a m_a} = \frac{\sum_a a l_a m_a}{R_0}$$

Population dynamics with age-structure



- In the above diagram, given $l_1 = 1, l_2 = 0.5, l_3 = 0.25, l_4 = 0$ and $m_1 = 0, m_2 = 2, m_3 = 0.5$ and $m_4 = 1000$, we get $R_0 = 0 + 1 + 0.125 + 0 = 1.125$
- The generation time in this example is

$$T = \frac{0 + 2 * 1 + 3 * 0.125 + 0}{1.125} = 2.1111 \text{ years}$$

- An approximate value of r is given by

$$r = \frac{\log R_0}{T} = 0.0558 \text{ year}^{-1}$$

Life Tables

- Calculations of R_0, T and r are often aided by constructing a life table.
- The simplest life table is a **cohort life table**, in which one follows the survival and fecundity schedules of a single age-group (cohort) throughout its existence from birth until (in theory) the last of them dies.
- For example, age-dependent survival and fecundity of a representative group of human females born 1900 in the USA.
- One records events of deaths and births and summarizes them in a table, e.g.,

age, x	no. survivors, a_x	l_x	m_x	$l_x m_x$	$\dots$
0	1000	1	0	0	
1	965	0.965	0	0	
$\dots$					
27	890	0.89	0.7	0.623	
$\dots$					

Life Tables

- After constructing the table, one can sum up the $l_x m_x$ column to get R_0.
- Or an $x l_x m_x$ column to get generation time, T.
- Or draw graphs of l_x or m_x or $l_x m_x$ to study the patterns of age-dependent survival, fecundity, or effective fecundity (respectively) in the population.
- Obviously, for long-lived organisms such as humans today, and given the tremendous technological and social changes occurring during a single lifetime, patterns of survival and fecundity will be different for different cohorts (year groups).
- But in natural populations, such patterns, obtained from a single cohort, may be representative of specific species or populations, and remain more or less the same for several generations.

Life Tables

- An example of a life table for a barnacle population

Age (years)					
x	a_x	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	1,000,000	1.000	0	0	
1	62	0.0000620	4,600	0.285	0.285
2	34	0.0000340	8,700	0.296	0.592
3	20	0.0000200	11,600	0.232	0.696
4	15.5*	0.0000155	12,700	0.197	0.788
5	11	0.000110	12,700	0.140	0.700
6	6.5*	0.0000065	12,700	0.082	0.492
7	2	0.0000020	12,700	0.025	0.175
8	2	0.0000020	12,700	0.025	0.200
				1.282	3.928

$$R_0 = 1.282; \quad T_c = \frac{3.928}{1.282} = 3.1; \quad r \approx \frac{\ln R_0}{T_c} = 0.08014.$$

Life Tables

- A second type of life table is a **static life table**, in which one records deaths and births in all age-classes simultaneously during one year (or a similarly fixed period), and then constructs the relevant columns of l_x, m_x, etc.
- Nowadays, there are more modern statistical techniques to investigate schedules of mortality and reproductive events – this group of statistical methods is collectively known as **survival analysis** or **failure-time analysis** and is widely used in medicine, engineering, and also ecology.
- One can use survival analysis techniques to investigate not only events of mortality or reproduction, but also other vital rates, such as timing of developmental transitions (molts, pupation, emergence, metamorphosis, etc.).

Outline

1. Population fluctuations
2. Life tables and R_0 calculations
3. Interspecific interactions – competition and predation

Interspecific interactions

- Just as per-capita performance of individuals in a population may be affected by presence of conspecifics (intraspecific competition), it can also be affected by presence of individuals of other species:
  - Competitors
  - Predators
  - Prey
  - Parasites
  - etc.

- These interactions are density-dependent.

- For example: the more predators, the higher is per-capita mortality rate of prey.

- We will concentrate on two types of interspecific interactions:
  1. Interspecific competition.
  2. Predation, i.e., Predator-prey interaction.

Interspecific interactions

- By analyzing interspecific interactions, we apply methods from **population ecology** to problems in **community ecology** – e.g., exclusion or coexistence of species.
- On the other hand, studying interspecific interactions may provide insight into population phenomena, such as population cycles (e.g., predator-prey cycles).
- Interspecific interactions relate to the concept of **niche**, a basic concept in ecology.
- The niche is roughly the role of the organism/species in the ecosystem:
  - Range of environmental conditions/microhabitats it occupies,
  - Role in food web – what it eats and what eats it.
- Level of niche overlap / differentiation determines how strongly species will interact.

Interspecific competition

- An example, species of gerbils in sandy habitats in Israel. Two species: *Gerbillus pyramidum* (GP)
  and *G. andersoni allenbyi* (GA).
  Three types of sandy habitat: shifting, semi-stabilized and stabilized sand.
- GP prefers the semi-stabilized and shifting sands.
- GA prefers the semi-stabilized and stabilized sands.
- Overall, there is **niche differentiation** between the two species.
- However, **niche overlap** occurs at the semi-stabilized sand habitat – leading to **interspecific competition**.

Interspecific competition

- Because GP is significantly larger in body size/mass, competition is **asymmetric** (often, interference).
- Leading to **competitive exclusion** of GA from the semi-stabilized sandy habitat, wherever both species occur.
- ⇒ The **realized niche** of GA is narrower than its **fundamental niche**, in the presence of the competing species, GP.
- However, on the larger scale of the entire sand dunes ecosystem, the two species **coexist**, due to niche differentiation.

Interspecific competition

- This example helps to demonstrate general patterns related to interspecific competition:

1. The **realized niche** of a species is often significantly narrower than its **fundamental niche**, because of interactions with other species (competitors, predators, etc.).
2. Interspecific competition (like intraspecific) can be of either the **exploitation** or **interference** type (or a combination of the two), and is often **asymmetric** – i.e., one species suffers stronger effects.

Interspecific competition

- This example helps to demonstrate general patterns related to interspecific competition:

  3. The outcome of interspecific competition between two species can be either **competitive exclusion** of one of them, or **coexistence** of the two species.
  4. Coexistence is facilitated by **niche differentiation** – which tends to decrease the strength of competition between the two species.
  5. We can demonstrate and study interspecific competition by experimentally removing competitors ⇒ allowing the species to expand and occupy its entire fundamental niche.

The Lotka-Volterra competition model

- The Lotka-Volterra model extends the logistic growth model to describe both intraspecific and interspecific competition.
- Consider species #1 (e.g., GP).
- Its population dynamics follows the logistic growth

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) .$$

- In the presence of a competing species (species #2; e.g., GA), the dynamics of species #1 becomes

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \boldsymbol{\alpha_{12} N_2}}{K_1}\right) .$$

- The presence of species #2 also negatively affects the per-capita performance of individuals of species #1.

The Lotka-Volterra competition model

- In the presence of a competing species (species #2; e.g., GA), the dynamics of species #1 becomes

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \boldsymbol{\alpha_{12} N_2}}{K_1}\right) .$$

- The parameter α_{12} is called **competition coefficient** – a conversion factor that allows for different effects of individuals of species #1 and individuals of species #2.
  - $\alpha_{12} > 1$, if the negative effect of an additional #2-individual on #1 per-capita growth is stronger than the effect of an additional #1-individual.
  - $\alpha_{12} < 1$, if the reverse.
  - For example: if #1 = GP and #2 = GA, we expect $\alpha_{12} < 1$, because of the dominance of GP over GA (asymmetric competition).
  - Similarly, we expect $\alpha_{\mathbf{21}} > 1$, for the same reason.

The Lotka-Volterra competition model

- The full model is given by the two dynamics equations for the two species:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1}\right) , \qquad \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1}{K_2}\right) .$$

- Therefore, this is a two-dimensional system – i.e., the state of the system is described by two state-variables, N_1 and N_2.

- Other multi-dimensional systems in population ecology include
  - Predator-prey – modeling numbers of both prey and predator.
  - Structured populations – e.g., following change in numbers of eggs, juveniles, adults, etc.

The Lotka-Volterra competition model

- The full model is given by the two dynamics equations for the two species:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1}\right), \qquad \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1}{K_2}\right).$$

- In exercise 3 we also had a two-dimensional system: we followed the population dynamics of both the wild-type and the melanic morphs of the peppered moth.

- However, unlike in exercise 3, in the Lotka-Volterra the dynamics of the species is **coupled** – i.e., the dynamics of #1 is affected by #2, and vice versa.

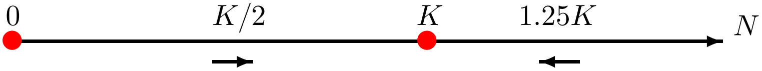
- **Coupling** can lead to complex dynamic patterns, e.g., predator-prey cycles.

Zero isoclines and the outcome of competition

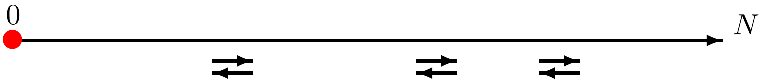
Because the system is two-dimensional, the state is described by a point in two-dimensional space.

Stationarity and stability

- **Stationary points** represent special values of the variable that do not change over time.
- I.e., if we start at a stationary point, we remain on it on subsequent times.
- Therefore, stationary points are defined zero rate of change: $\Delta N = 0$ or $dN/dt = 0$.
- E.g., for the logistic growth model we have two stationary points, $N = 0$ and $N = K$:

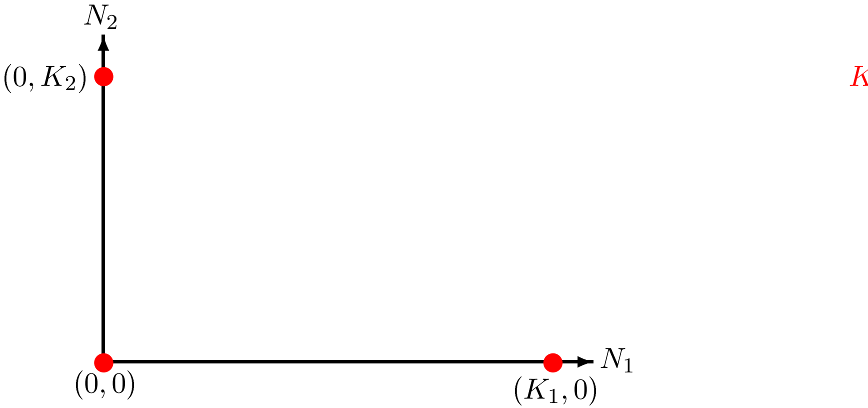


- For exponential growth, only $N = 0$:



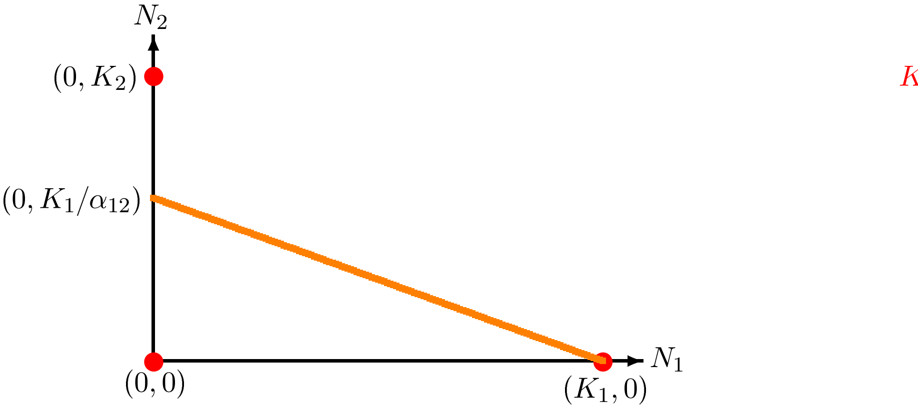
Zero isoclines and the outcome of competition

Three trivial stationary points.
But are they stable? And is there a stationary point in which the two species coexist?
To be able to answer, we need to find the **zero-isoclines** of the two species before we can answer that.



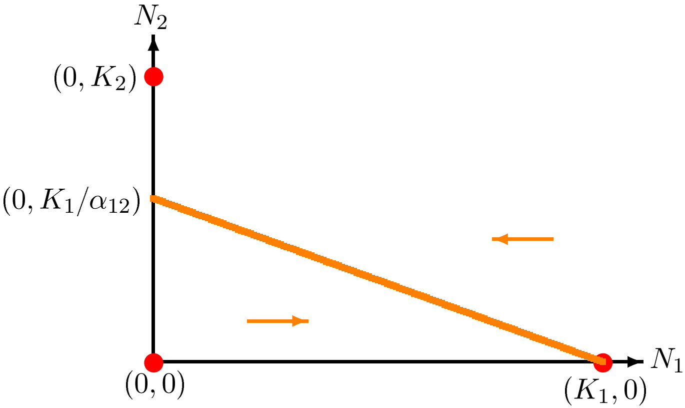
Zero isoclines and the outcome of competition

The **zero-isocline** of species #1 is a curve made of all the points for which $dN_1/dt = 0$.
In the Lotka-Volterra model it is a straight line connecting K_1 on the N_1-axis with K_1/α_{12} on the N_2 -axis.



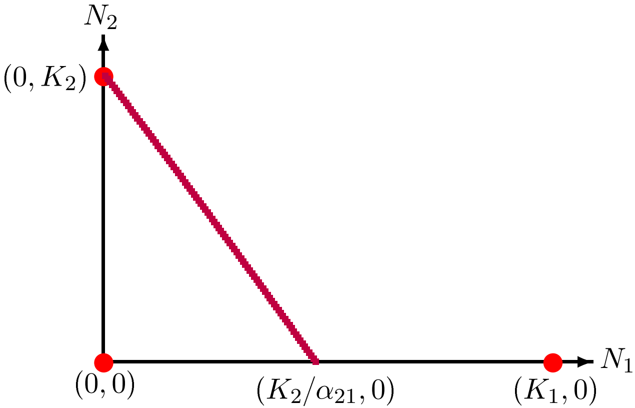
Zero isoclines and the outcome of competition

Above the zero-isocline, $dN_1/dt < 0$.
Below the zero-isocline, $dN_1/dt > 0$.



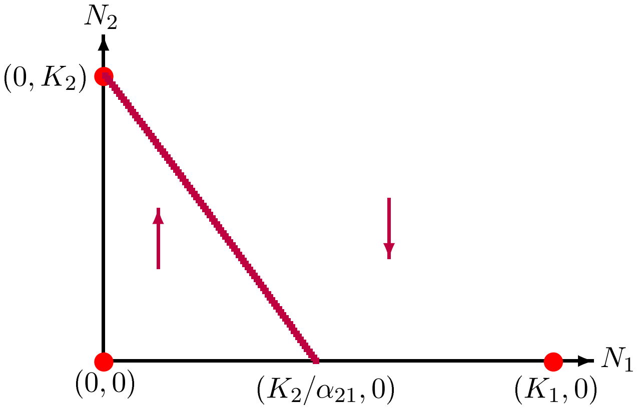
Zero isoclines and the outcome of competition

Similarly, on the zero-isocline of species #1 $dN_2/dt = 0$.
In the Lotka-Volterra model it is a straight line connecting K_2 on the N_2-axis with K_2/α_{21} on the N_1 -axis.



Zero isoclines and the outcome of competition

Above the zero-isocline, $dN_2/dt < 0$.
Below the zero-isocline, $dN_2/dt > 0$.

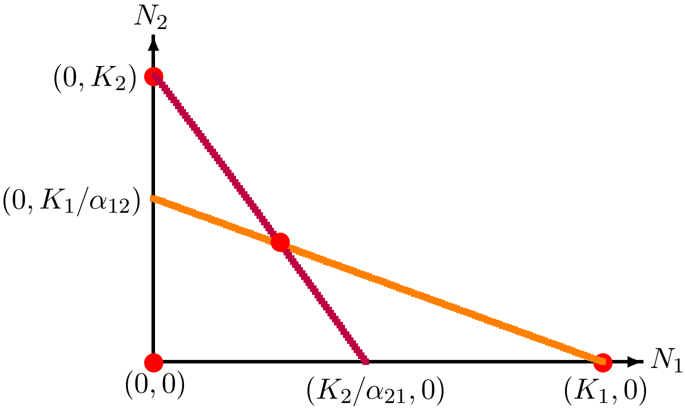


Zero isoclines and the outcome of competition

Combining the two zero-isoclines, if an intersection exists, it constitutes a fourth stationary point

This stationary point describes coexistence.

Unlike the other three, which describe exclusion of at least one species.



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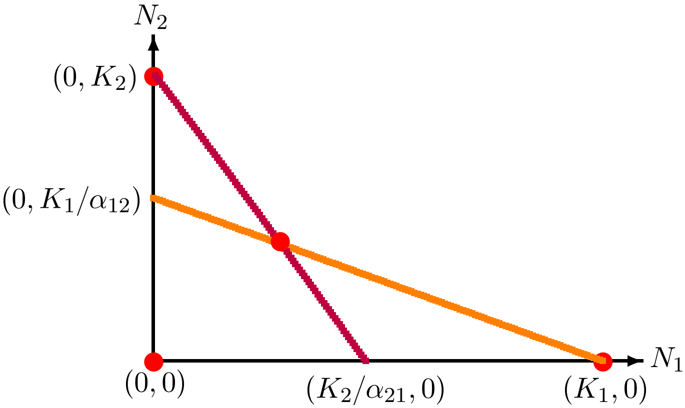
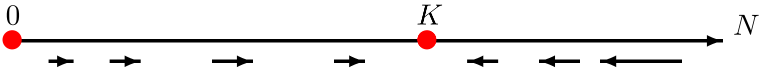
Zero isoclines and the outcome of competition

But is the coexistence stable? i.e., following a perturbation, would the system tend to return towards the coexistence point? Or would it run away towards one of the other stationary points, which describe competitive exclusion?



Stationarity and stability

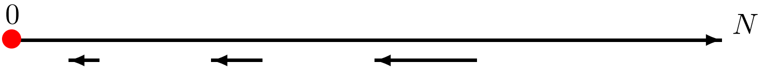
- A stationary point can be either **stable** or **unstable**.
- Any deviation from a stable stationary point would tend to decrease over time – i.e., a restoring "force" operating towards the point.
- Any deviation from an unstable stationary point would tend to increase over time – i.e., a repelling "force" away from the point.
- We can determine stability graphically.
- E.g., for the logistic model $N = 0$ is unstable, and $N = K$ is stable:



Stationarity and stability

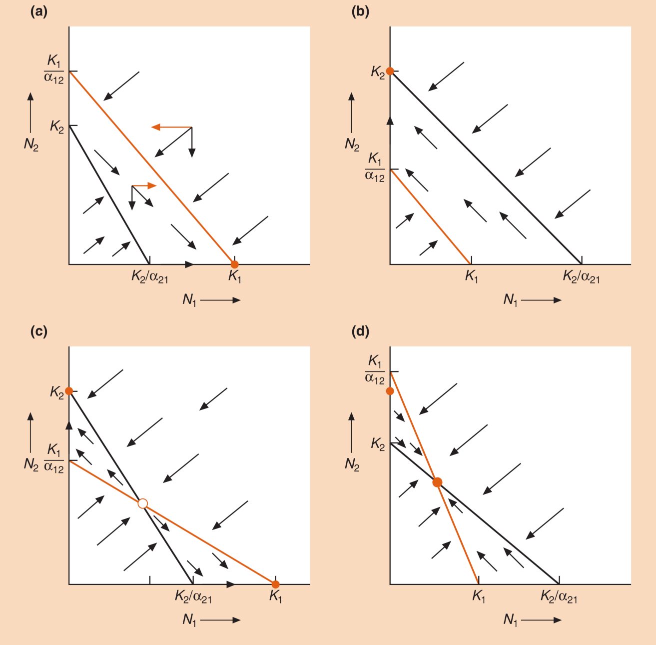
- For the exponential model, $N = 0$ is unstable, if $r > 0$:

- And stable, if $r < 0$:



- Ultimately, checking for stability requires mathematical analysis using methods from calculus, linear algebra and nonlinear dynamics.
- But the graphical method is sufficient for our purposes.
- We will return to this subject when we talk about interspecific competition.

Zero isoclines and the outcome of competition



Zero isoclines and the outcome of competition

- Four different set-ups of the two zero-isoclines.
- Only one leads to stable coexistence: $K_1 < K_2/\alpha_{21}$ and $K_2 < K_1/\alpha_{12}$.
- Assuming similar carrying capacities of the two species ($K_1 \approx K_2$), this leads to the conclusion that **Stable coexistence requires that interspecific competition be weaker than intraspecific competition.**
- Which is a different way to state the **competitive exculsion principle** – species exclude one the other, if their niches overlap.
- Or in other words, coexistence requires sufficient niche differentiation (such that the competition coefficients will be lower than 1).

Zero isoclines and the outcome of competition

- Example: GP (species #1) is dominant over GA (species #2) in the semi-stabilized habitat, therefore, competition is asymmetric and we expect $\alpha_{12} \ll 1$ and $\alpha_{21} \gg 1$.
- Assuming that the carrying capacity of GA is slightly higher than GP, i.e., $K_2 \geqslant K_1$ (because of the larger body mass of GP), we finally obtain

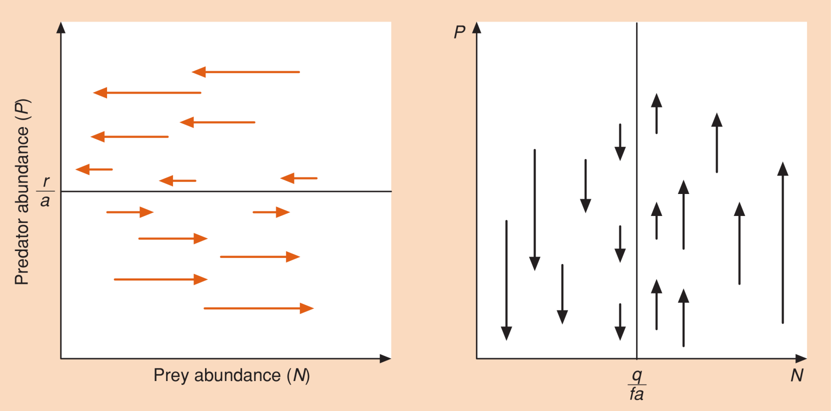
  $$K_1/\alpha_{12} > K_2 \geqslant K_1 > K_2/\alpha_{21} \ ,$$

  which leads to competitive exclusion, as indeed observed in the semi-stabilized sands.
- Note that in the Lotka-Volterra model the outcome of competition depends only on carrying capacities and competition coefficients, not on the maximum per-capita rates, r_1 and r_2.
- These two parameters will nonetheless determine how fast the dynamics would be; e.g., would competitive exclusion occur quickly or slowly.

The Lotka-Volterra predator-prey model:

vertical and horizontal zero-isoclines lead to population cycles

Prey species (N) and predator species (P).
Prey zero-isocline is a horizontal line.
Predator zero-isocline is a vertical line.



The Lotka-Volterra predator-prey model:

vertical and horizontal zero-isoclines lead to population cycles

There is a stationary point. However, it is unstable.
Any deviation from the stationary point result in periodic oscillations – predator-prey oscillations – that persist indefinitely.