Fundamentals of Ecology

Week 7, Ecology Lecture 5

Cara Brook

February 20, 2025

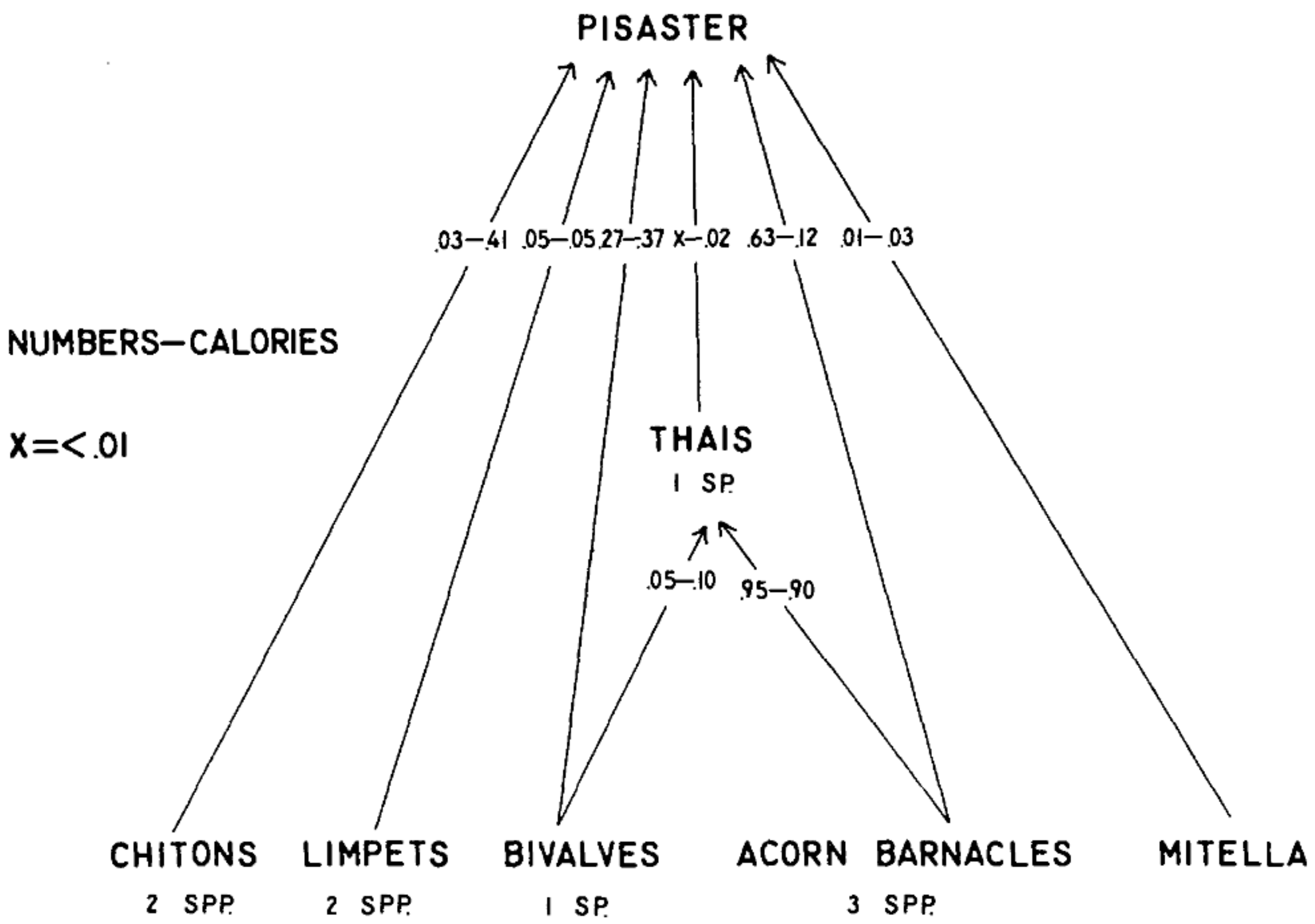
Office hours: On ZOOM
Friday, Feb 21, 2025
4-5pm
I will email out a link!

Learning objectives from Lecture 4

You should be able to:

- Understand and explain source-sink dynamics and an ecological trap
- Describe an Allee effect
- Understand trophic levels and know the direction of energy transfer, including what might happen to one level if there was a perturbation to a different level
- Know the ecosystem-level rules of HSS
- Understand the phase portrait in a Lotka-Volterra predator-prey model, including which direction to move forward in time
- Recognize a trophic cascade.

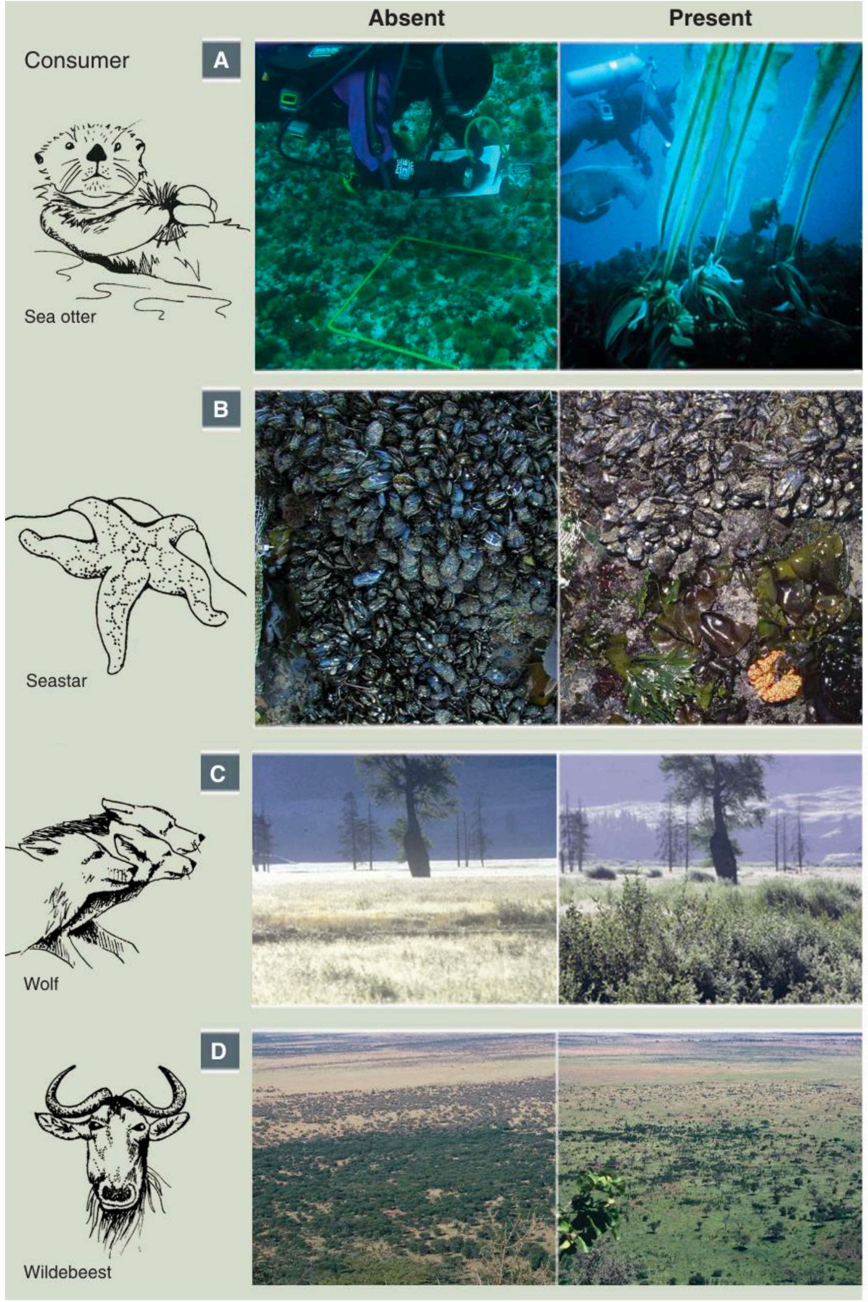
This work inspired empirical studies on **trophic cascades**: *Pisaster* removal on Tatoosh Island



Paine 1966. *The American Naturalist.*

Other famous **trophic cascades:**

Estes et al. 2011. *Science.*

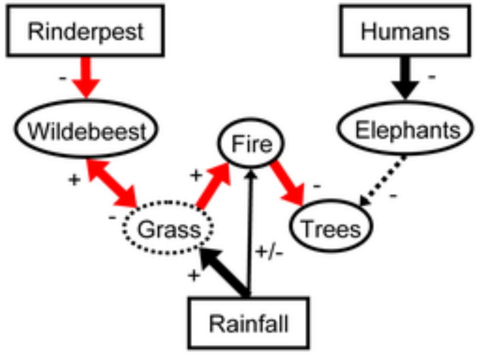


CA sea otters maintain kelp forest diversity by consuming herbivorous sea urchins. (Estes & Duggins 1995. *Ecological Monographs*)

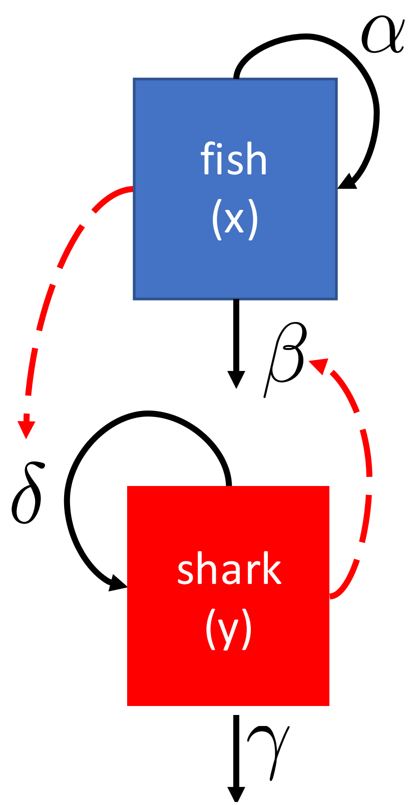
Starfish maintain diversity in Pacific intertidal by consuming space-dominating mussels. (Paine 1966 *The American* Naturalist)

Yellowstone wolves promote willow recovery by consuming overbrowsing elk (Ripple & Beschta 2005. *Forest Ecology & Management*)

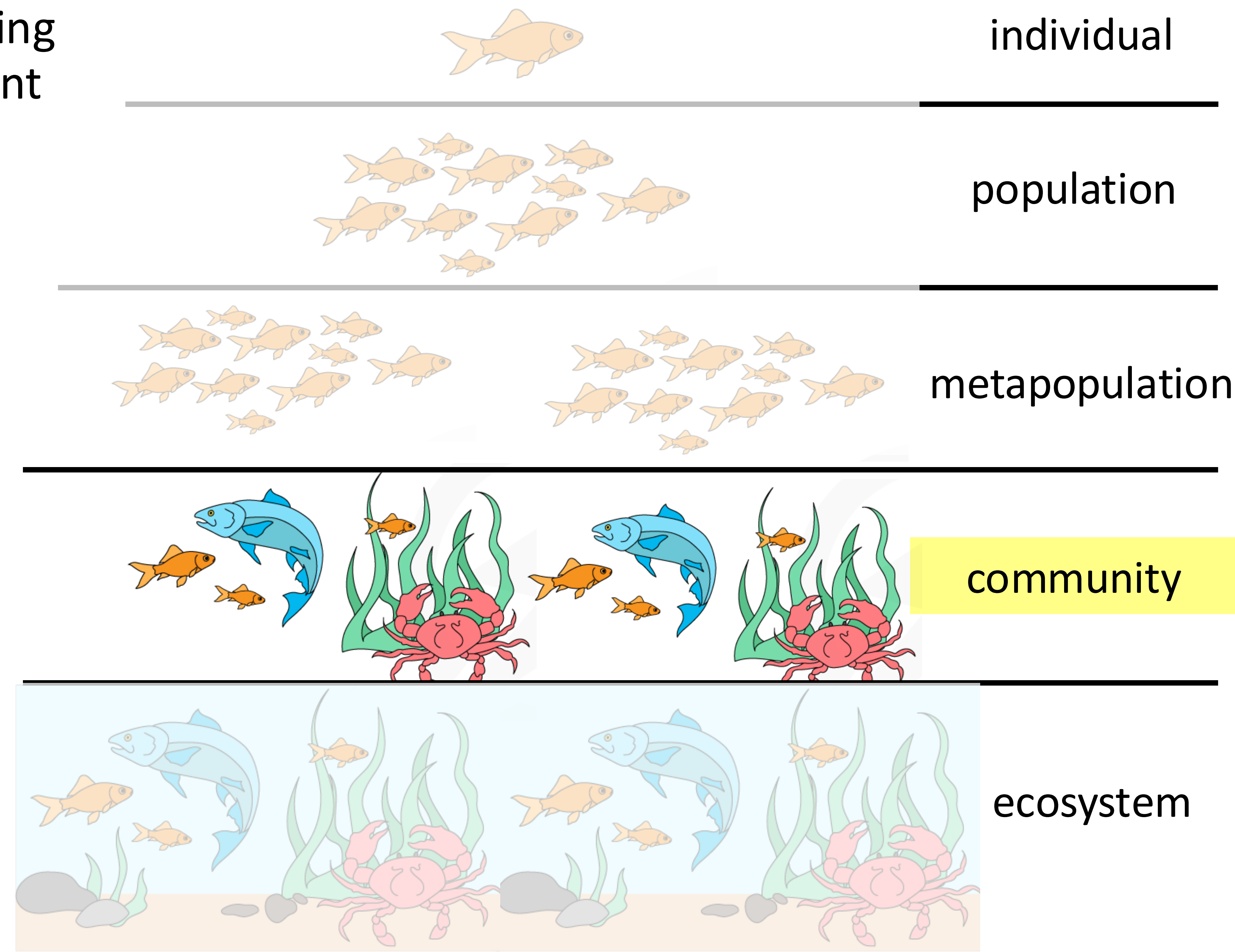
Rinderpest eradication releases wildebeest populations that control savanna, limit fire, and promote tree regrowth (Holdo et al. 2009. *PLoS Biology*)



Community = interacting populations of different species



*How does fish abundance **vary** with **changes** in shark abundance?*



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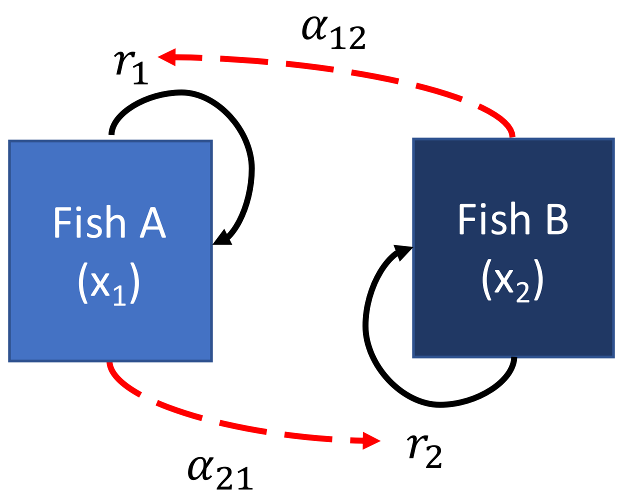

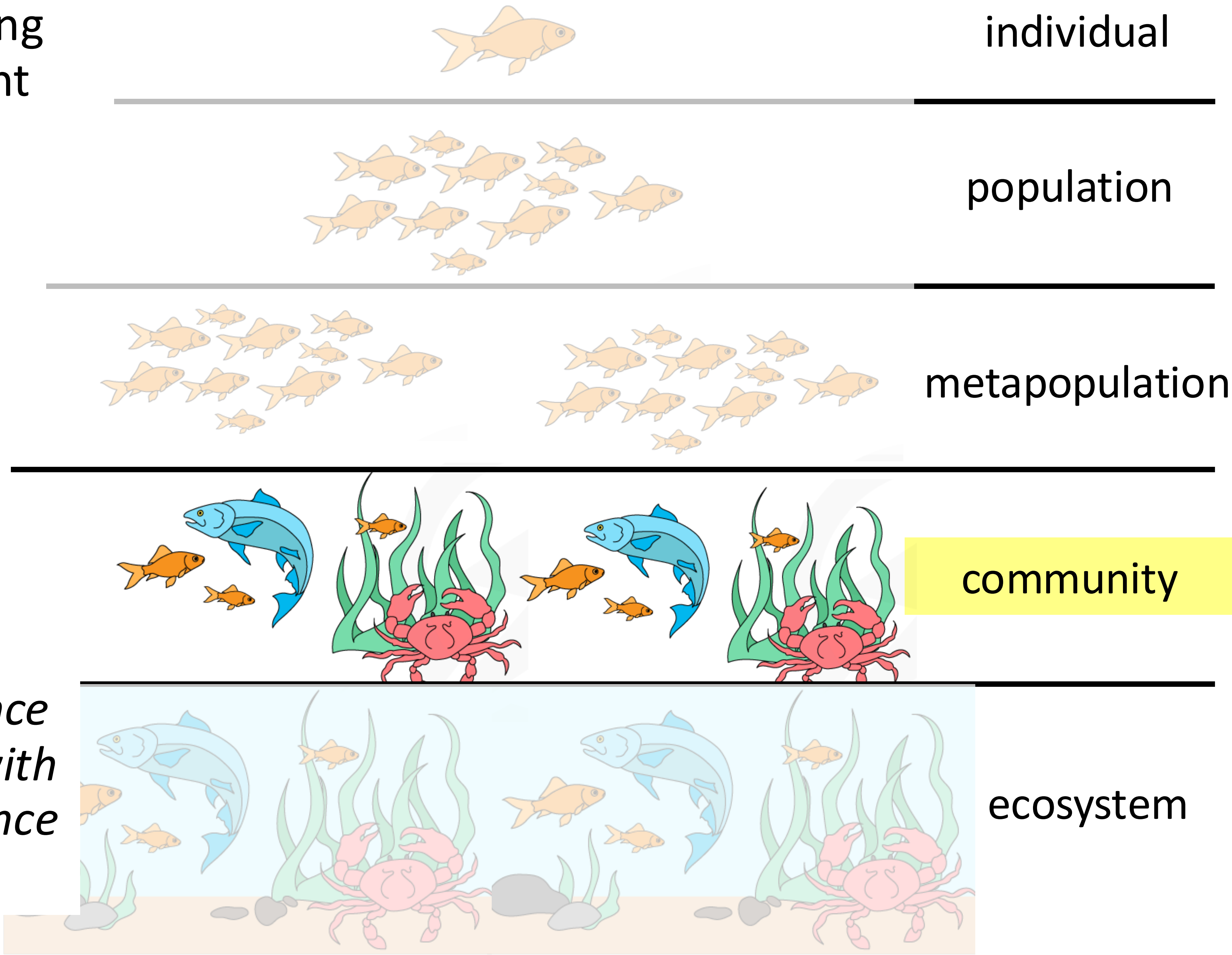

*How does the abundance of **fish species A** vary with changes in the abundance of **fish species B**?*

Lotka-Volterra equation can be modified for **interspecies competition.**

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1 + \alpha_{12} x_2}{K_1}\right)$$

$$\frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2 + \alpha_{21} x_1}{K_2}\right)$$

Lotka-Volterra equation can be modified for **interspecies competition.**

$$\frac{dx_1}{dt} = r_1 x_1 - \frac{r_1 (x_1)^2}{K_1} - \frac{r_1 x_1 x_2 \alpha_{12}}{K_1}$$

$$\frac{dx_2}{dt} = r_2 x_2 - \frac{r_2 (x_2)^2}{K_2} - \frac{r_2 x_2 x_1 \alpha_{21}}{K_2}$$

Lotka-Volterra equation can be modified for **interspecies competition.**

$$\frac{dx_1}{dt} = r_1x_1 - \overbrace{\frac{r_1(x_1)^2}{K_1}}^{\text{intraspecies competition of species 1 (akin to logistic growth)}} - \overbrace{\frac{r_1x_1x_2\alpha_{12}}{K_1}}^{\text{interspecies competition with species 2}}$$

$$\frac{dx_2}{dt} = r_2x_2 - \underbrace{\frac{r_2(x_2)^2}{K_2}}_{\text{intraspecies competition of species 2}} - \underbrace{\frac{r_2x_2x_1\alpha_{21}}{K_2}}_{\text{interspecies competition with species 1}}$$

Each species is self-regulated by logistic growth and its own carrying capacity (K) and growth rate (r).

Each species is also regulated by the density of its competitor (e.g. for a specific resource).

$\boldsymbol{\alpha_{12}}$ = effect of species 2 on the population of species 1

$\boldsymbol{\alpha_{21}}$ = effect of species 1 on the population of species 2

The 2-species **Lotka-Volterra competition model** has **four equilibria**.

Remember: equilibrium occurs when neither population is changing!

$$0 = \frac{dx_1}{dt} = r_1 x_1 - \frac{r_1 (x_1)^2}{K_1} - \frac{r_1 x_1 x_2 \alpha_{12}}{K_1}$$

$$0 = \frac{dx_2}{dt} = r_2 x_2 - \frac{r_2 (x_2)^2}{K_2} - \frac{r_2 x_2 x_1 \alpha_{21}}{K_2}$$

Four equilibria at:

$x_1^* = 0\,; x_2^* = 0$ Trivial.

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Four equilibria at:

$$x_1^* = 0\,; x_2^* = 0$$

$$x_1^* = 0\,; x_2^* = K_2$$

Species 1 extinct. Species 2 at carrying capacity.

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Four equilibria at:

$x_1^* = 0\,; x_2^* = 0$

$x_1^* = 0\,; x_2^* = K_2$

$x_1^* = K_1;\; x_2^* = 0$ Species 2 extinct. Species 1 at carrying capacity.

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Four equilibria at:

$$x_1^* = 0\,;\, x_2^* = 0$$

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$$x_1^* = K_1;\ x_2^* = 0$$

$$x_1^* = \frac{K_1 - K_2 \alpha_{12}}{1 - \alpha_{21}\alpha_{12}}\,;\, x_2^* = \frac{K_2 - K_1 \alpha_{21}}{1 - \alpha_{12}\alpha_{21}}$$

Coexistence.

Nullclines (or **isoclines**) of the **Lotka-Volterra competition model**

These are the lines that correspond to the conditions when the rate of change for **one species** is not changing!

Nullclines (or isoclines) of the Lotka-Volterra competition model

These are the lines that correspond to conditions when the rate of change for one species is 0.

- **Nullclines for species 1** occur at all conditions for which $\frac{dx_1}{dt} = 0$

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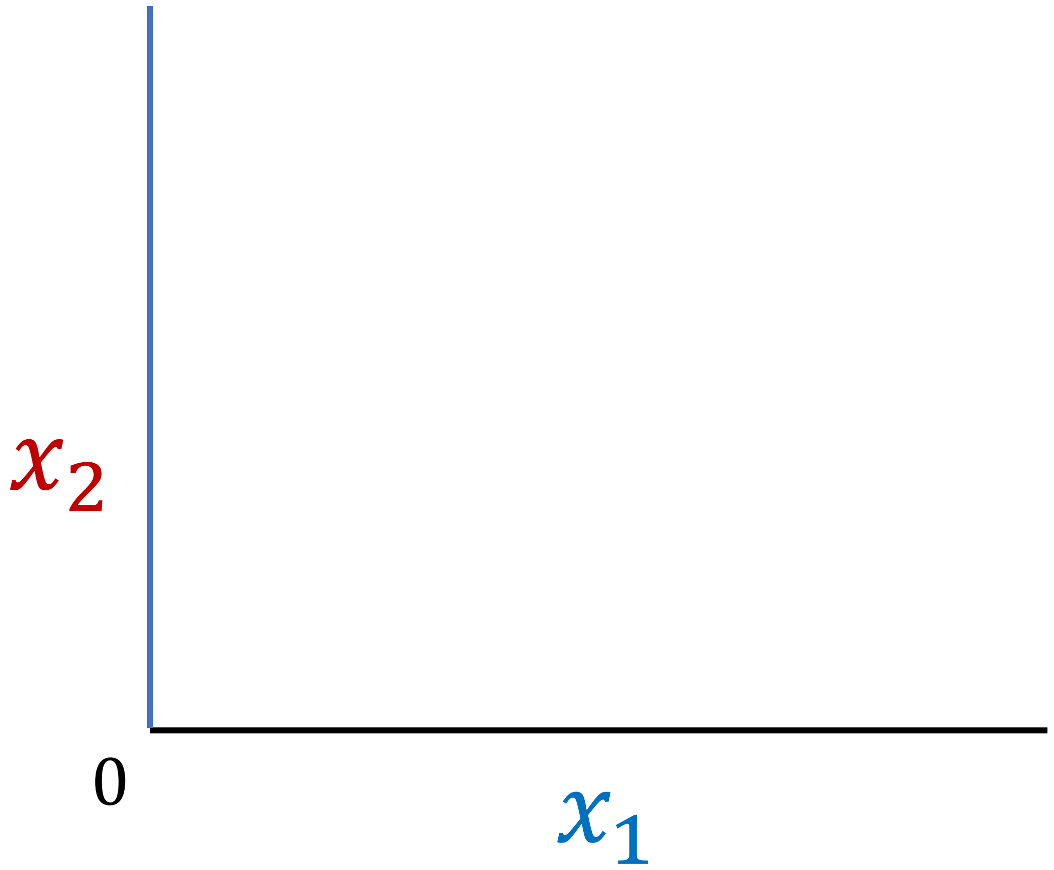
$$0 = r_1 x_1 \left(1 - \frac{x_1}{K_1} - \frac{x_2 \alpha_{12}}{K_1}\right)$$

first nullcline at $x_1 = 0$



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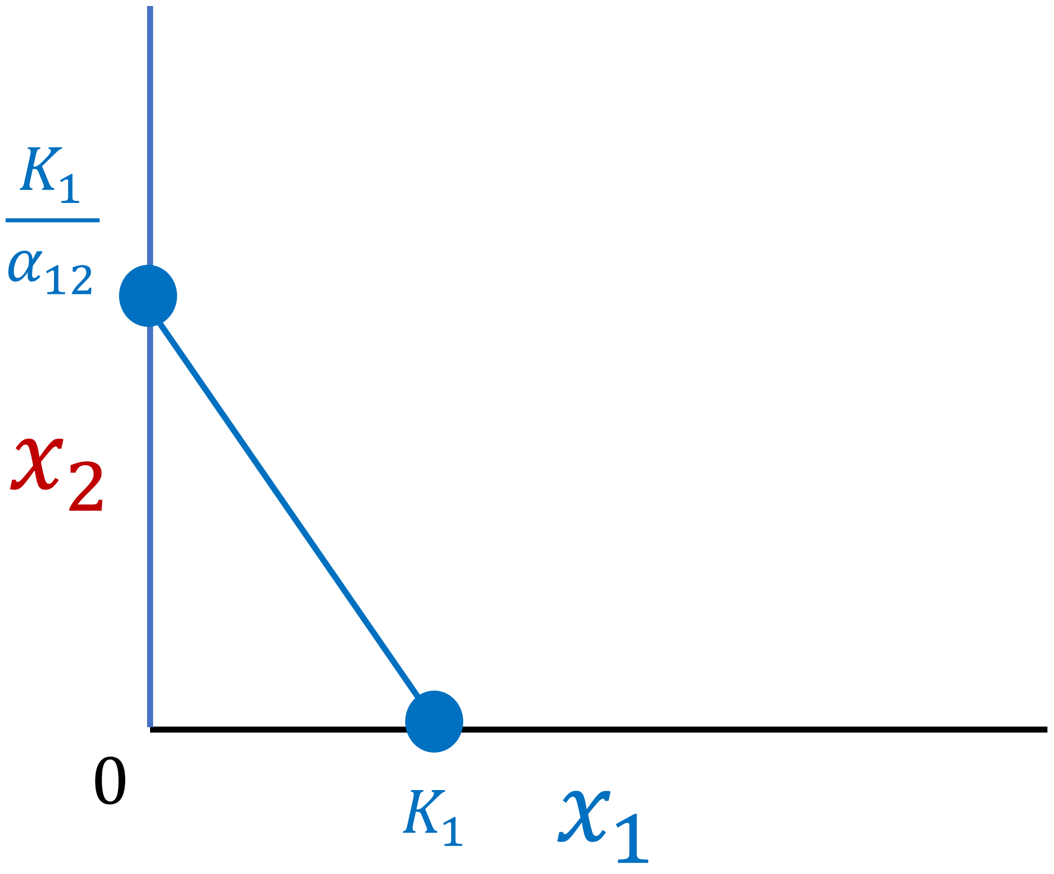
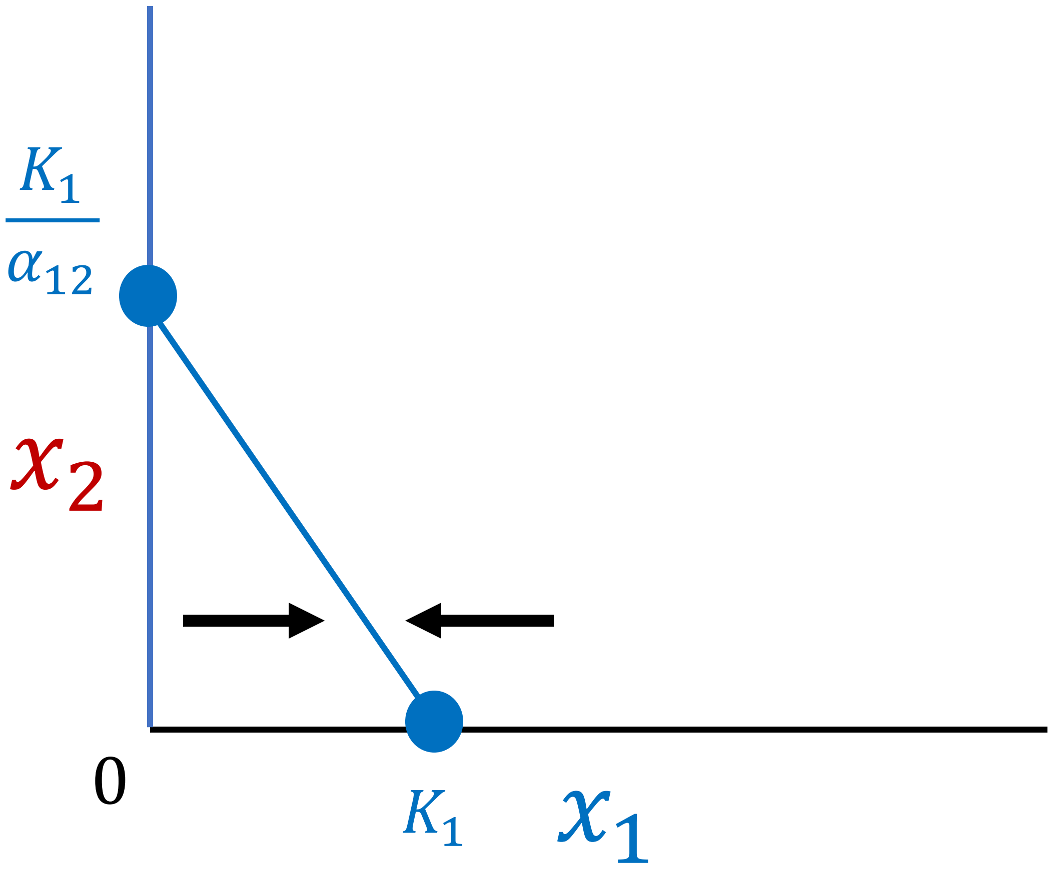
first nullcline at $x_1 = 0$

second nullcline at $x_1 = -\alpha_{12} x_2 + K_1$



Nullclines (or **isoclines**) of the **Lotka-Volterra competition model**

- Following a perturbation, the population should return to equilibrium!
- For x_1, this will always mean moving along the x-axis to the nullcline, then along the nullcline to equilibrium.



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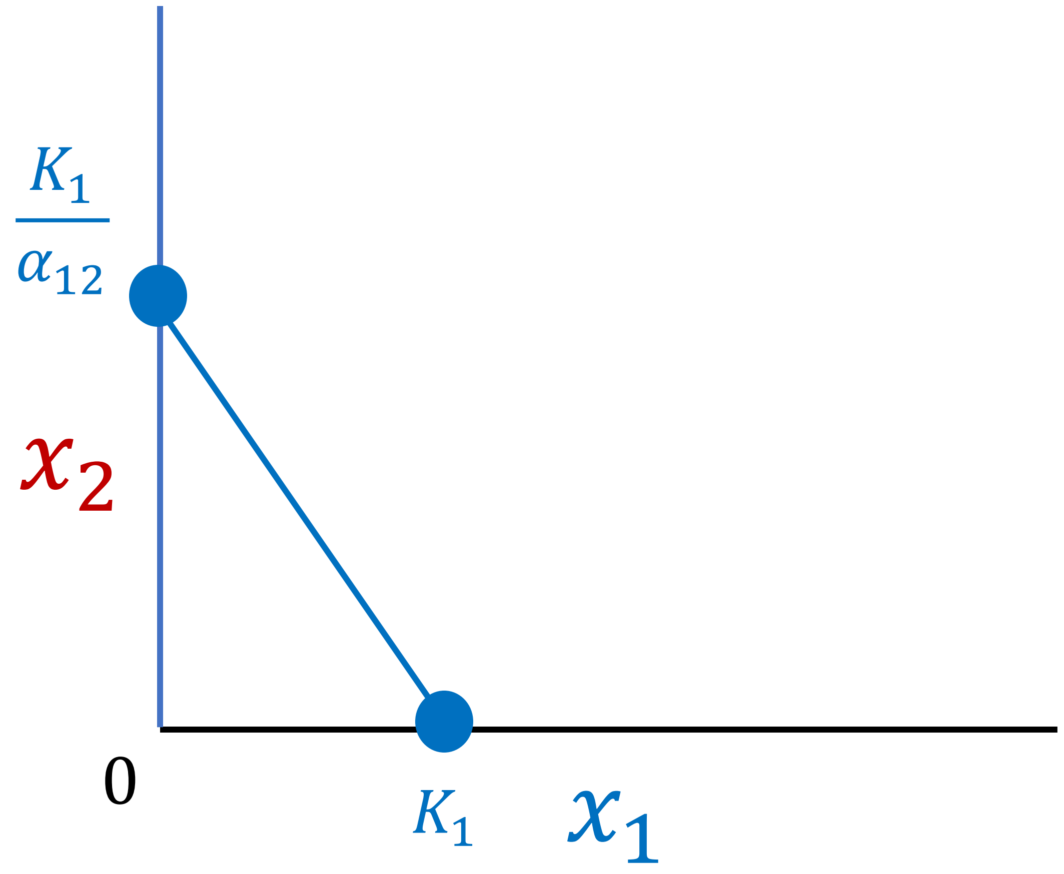

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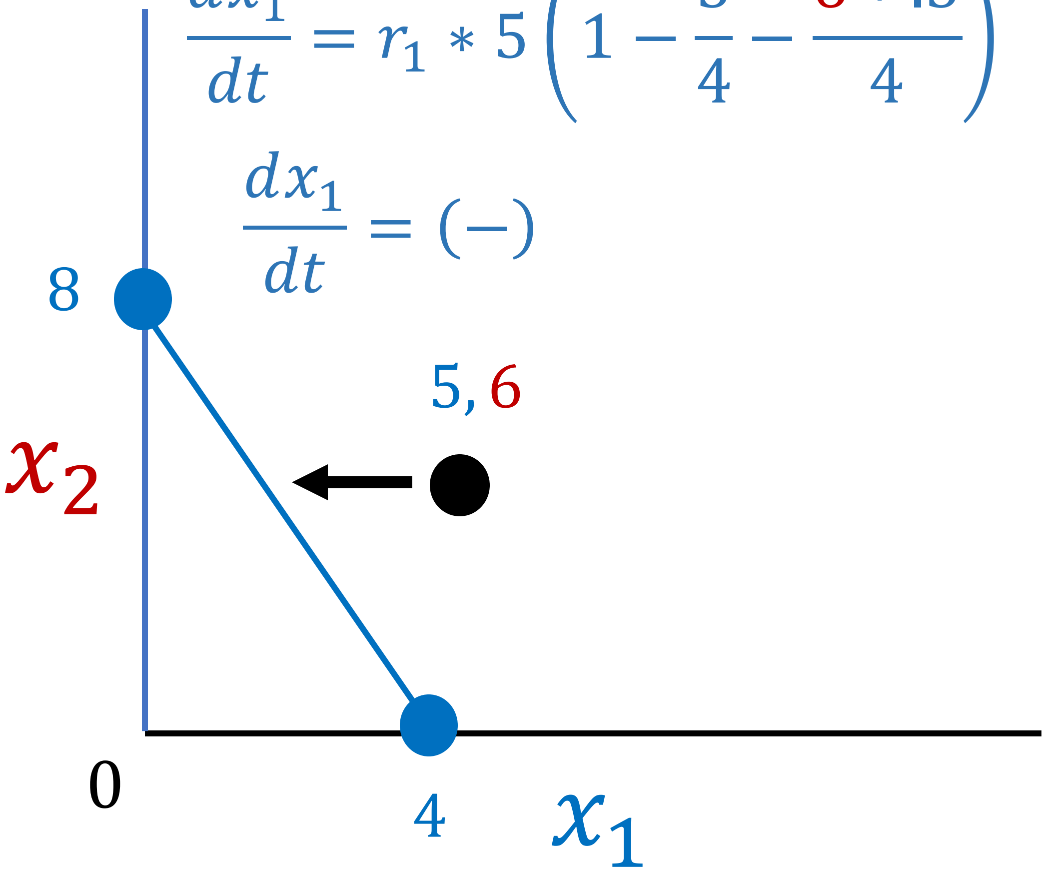
- $K_1 = 4\,; \alpha_{12} = .5$

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1} - \frac{x_2 \alpha_{12}}{K_1}\right)$$

$$\frac{dx_1}{dt} = r_1 * 5 \left(1 - \frac{5}{4} - \frac{6 * .5}{4}\right)$$

$$\frac{dx_1}{dt} = (-)$$



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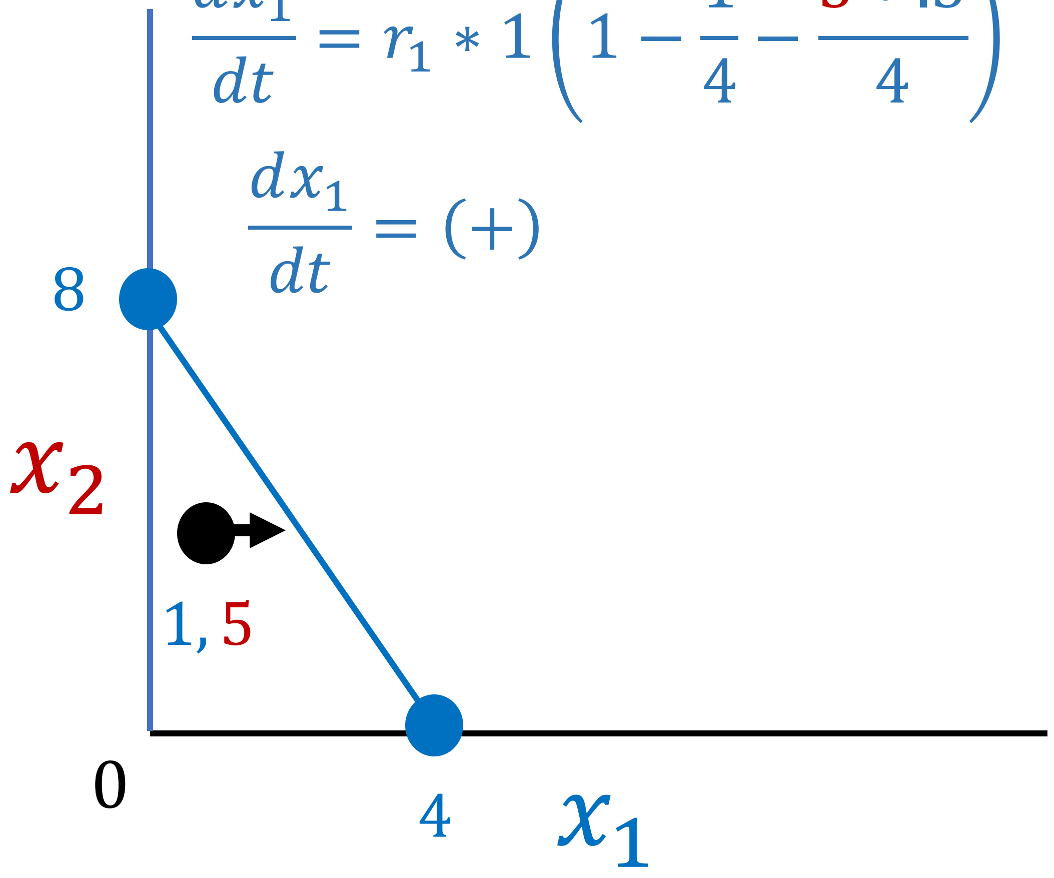

Nullclines (or **isoclines**) of the **Lotka-Volterra competition model**

These are the lines that correspond to conditions when the rate of change for one species is 0.

- **Nullclines for species 2** occur at all conditions for which $\frac{dx_2}{dt} = 0$

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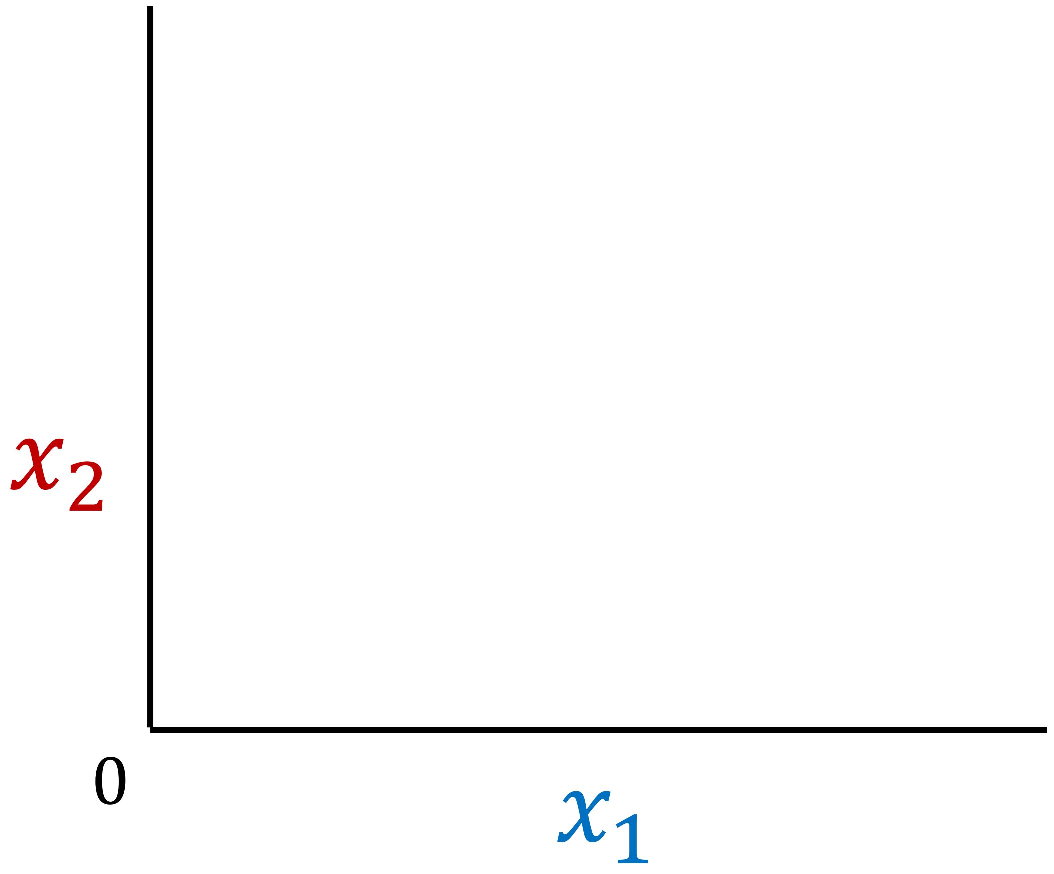

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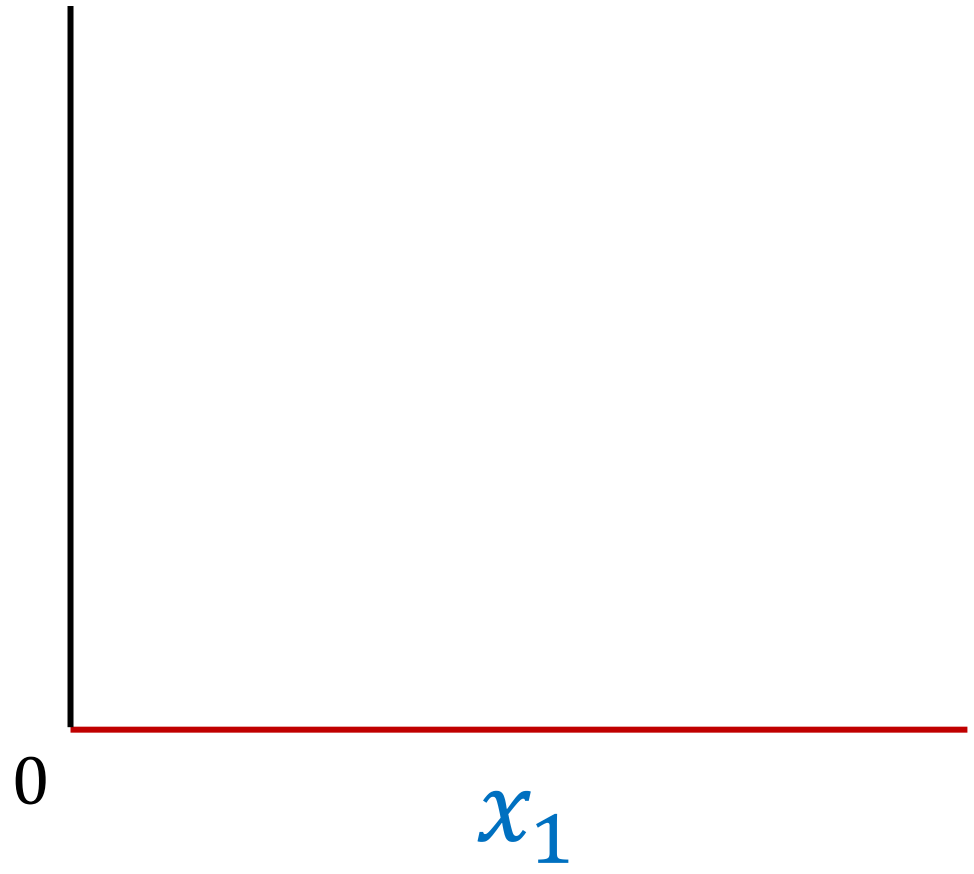
first nullcline at $x_2 = 0$



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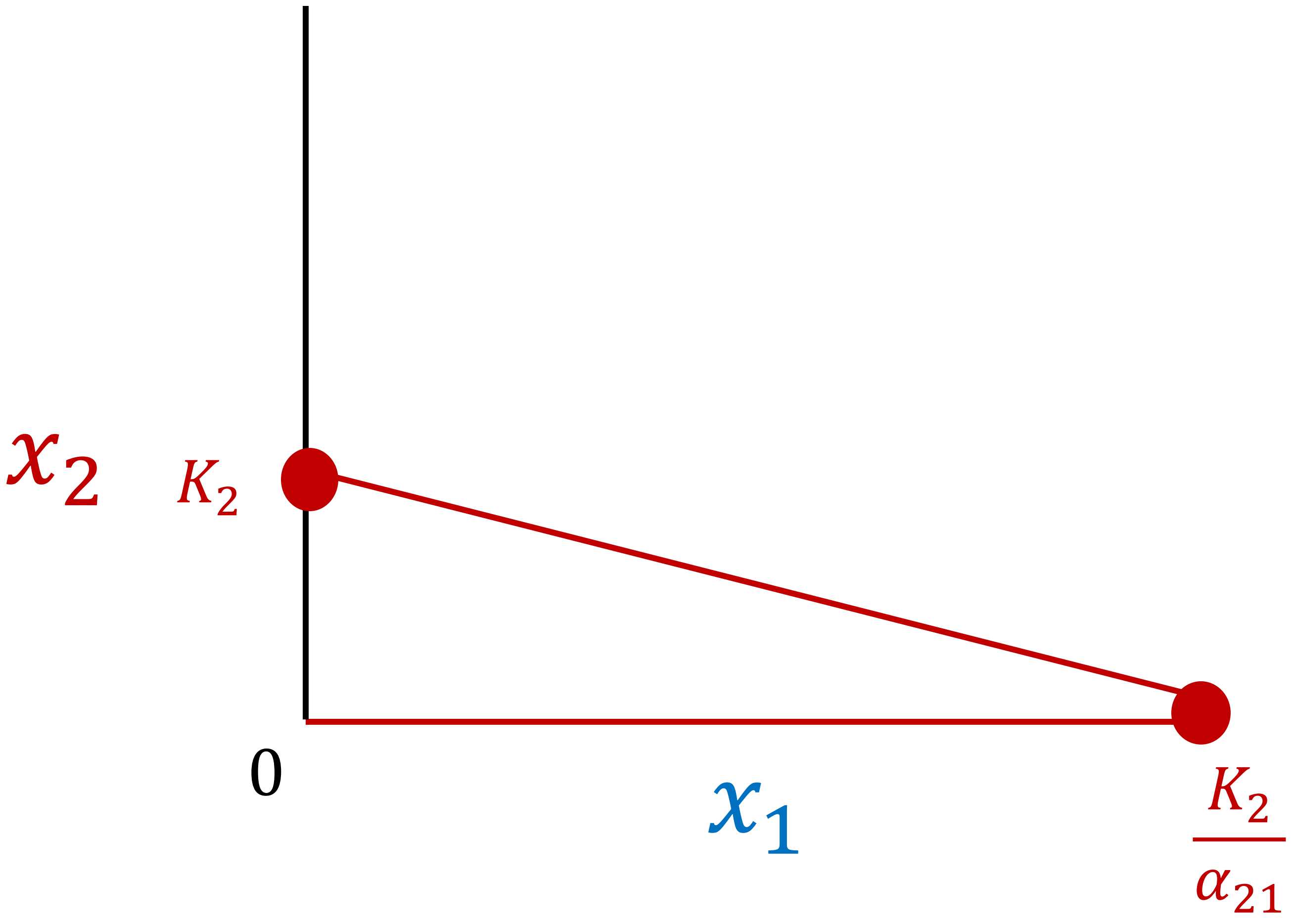

Nullclines (or isoclines) of the Lotka-Volterra competition model

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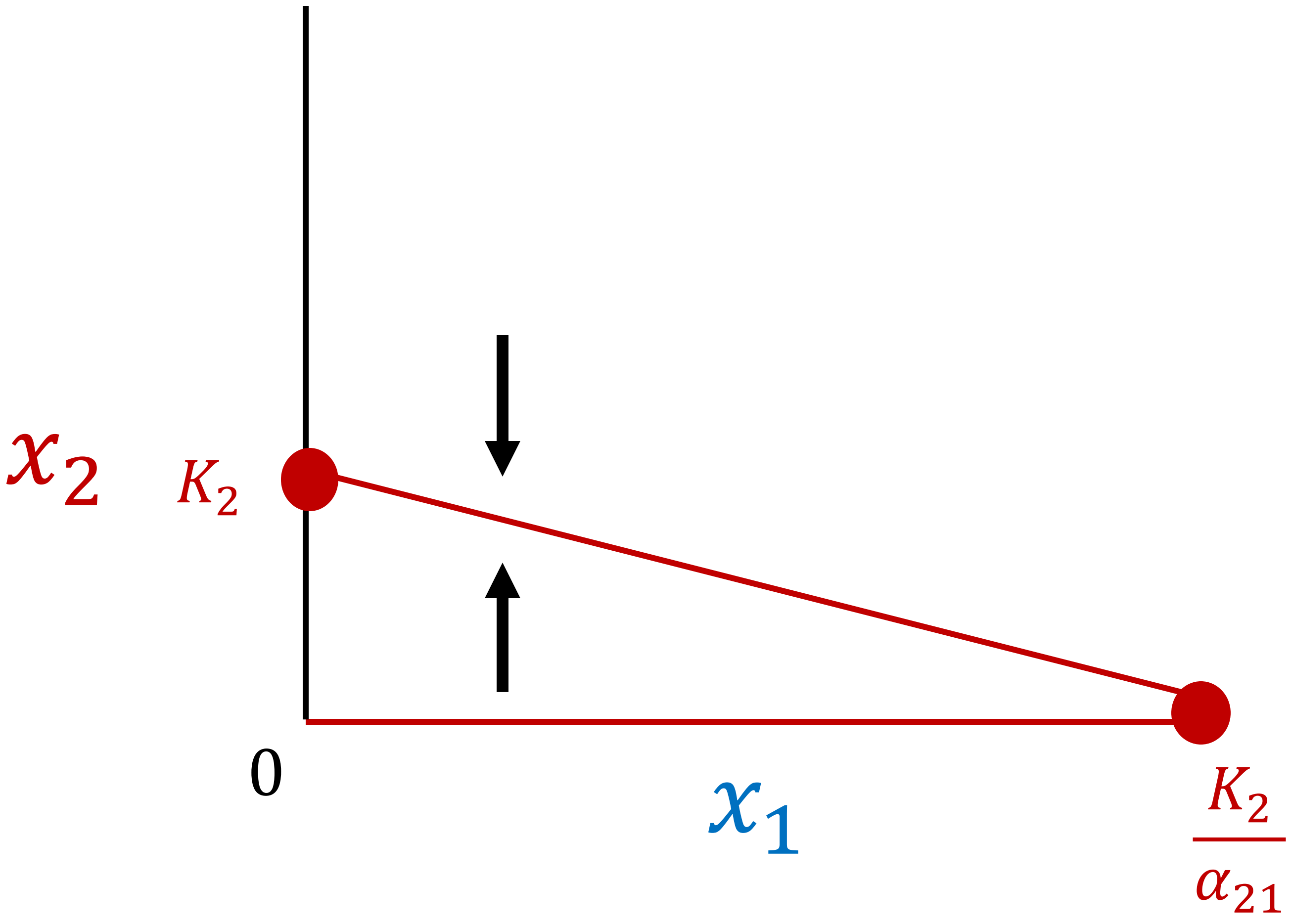


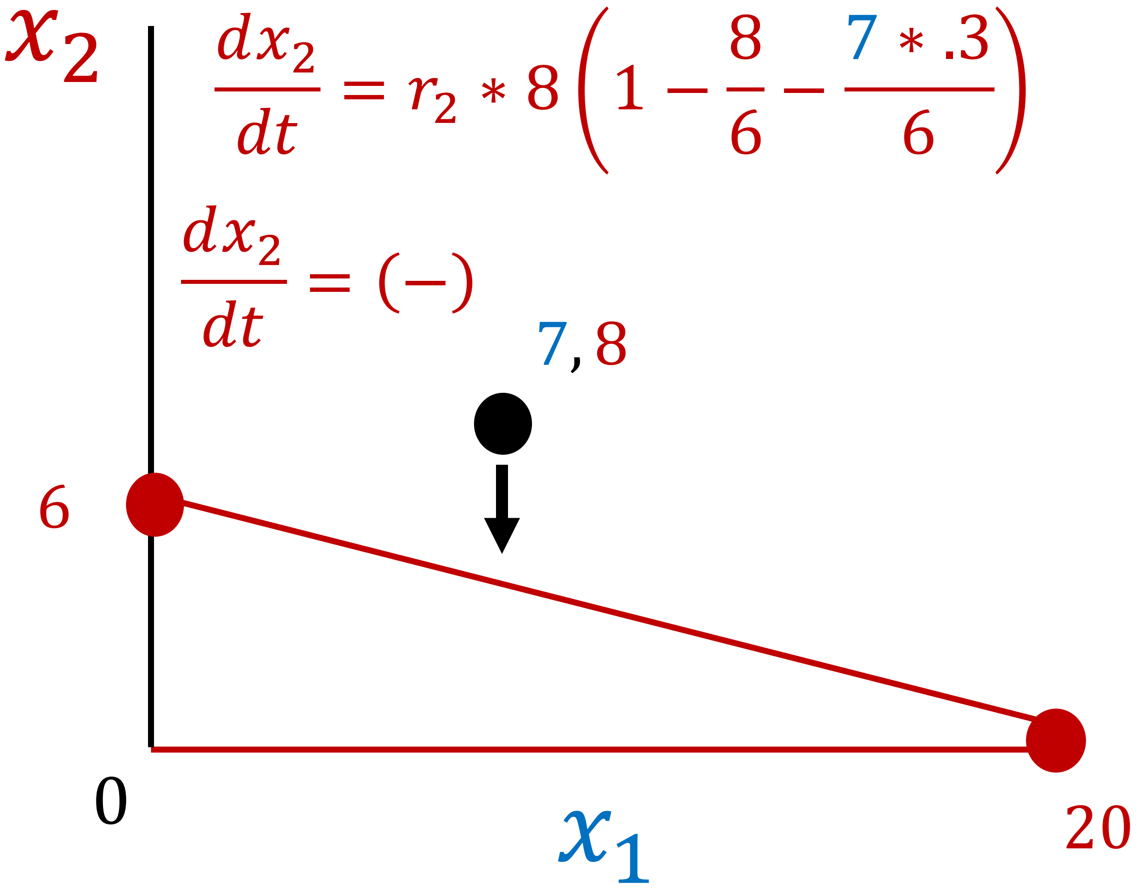
Nullclines (or **isoclines**) of the **Lotka-Volterra competition model**

$$\frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{K_2} - \frac{x_1 \alpha_{21}}{K_2}\right)$$

- Following a perturbation, the population should return to equilibrium!
- For x_2, this will always mean moving along the y-axis to the nullcline, then along the nullcline to equilibrium.
- You can also test it by solving $\frac{dx_2}{dt}$ for different values!
- $K_2 = 6\,; \alpha_{21} = .3$

$$\frac{dx_2}{dt} = r_2 * 8\left(1 - \frac{8}{6} - \frac{7 * .3}{6}\right)$$

$$\frac{dx_2}{dt} = (-)$$



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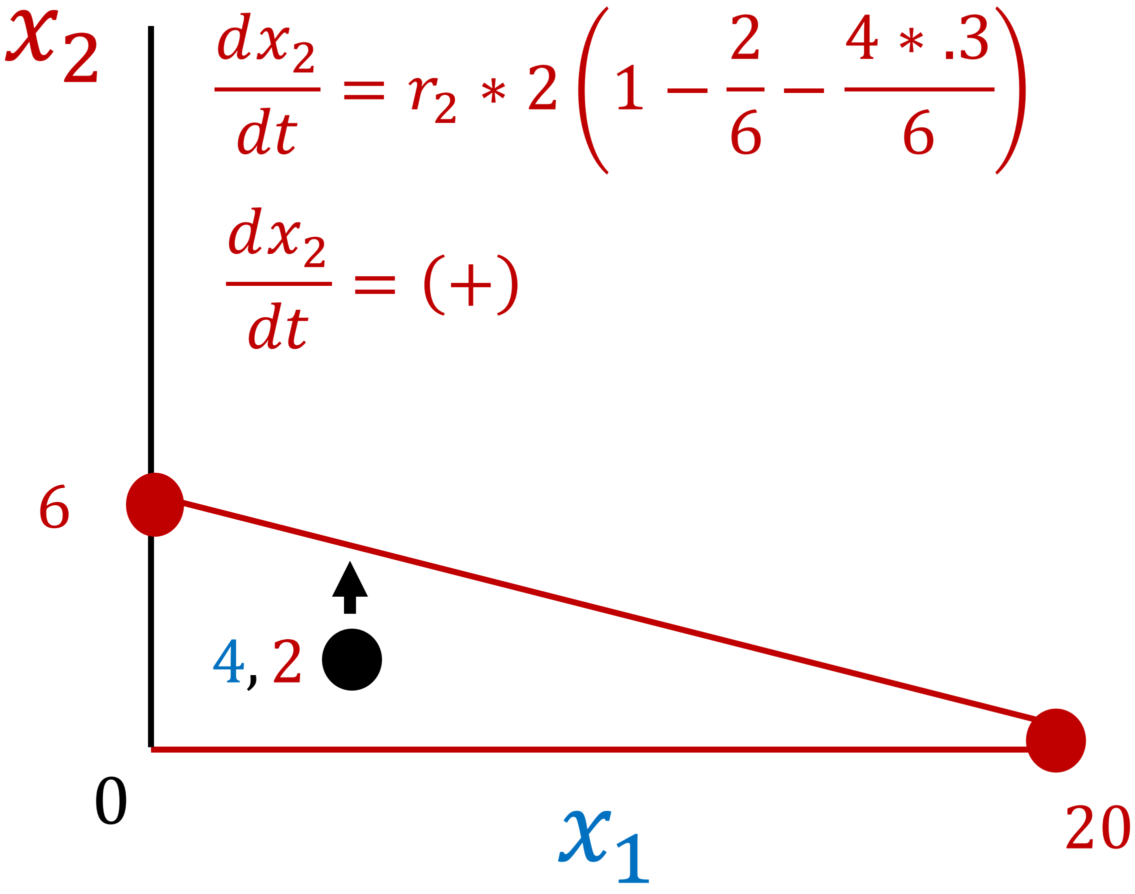
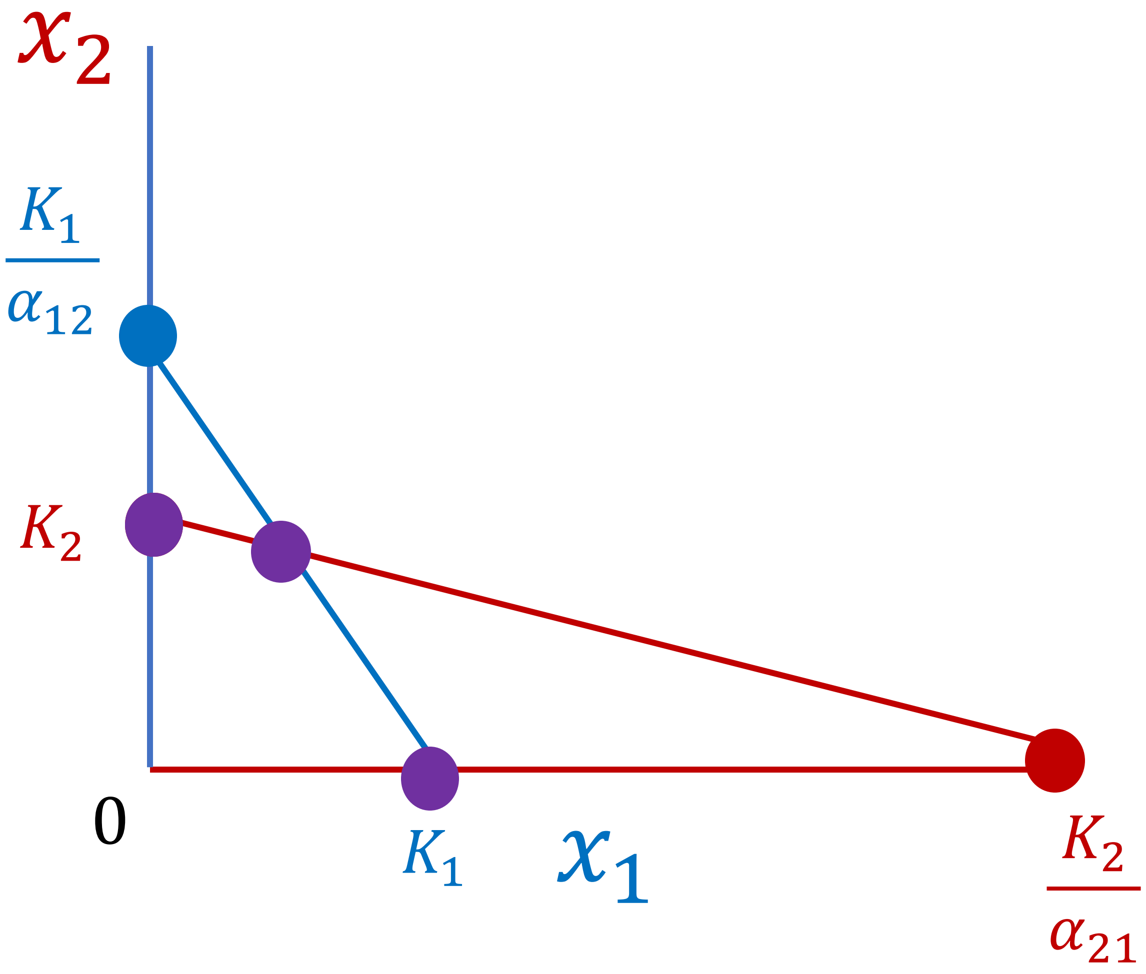
$$\frac{dx_2}{dt} = r_2 * 2 \left(1 - \frac{2}{6} - \frac{4 * .3}{6}\right)$$

$$\frac{dx_2}{dt} = (+)$$



Given different combinations of x_1 and x_2 what is the outcome of competition?

System will converge to one of its equilibria, depending on the values of the competition and carrying capacity parameters.



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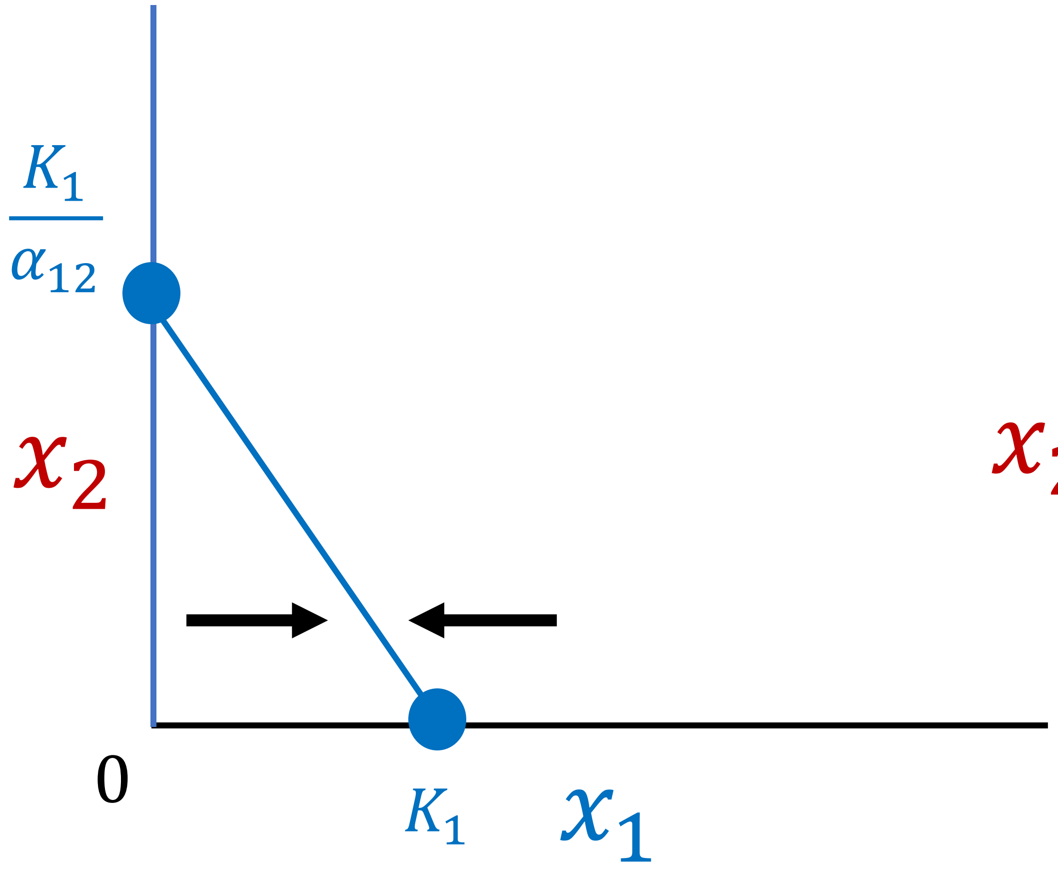
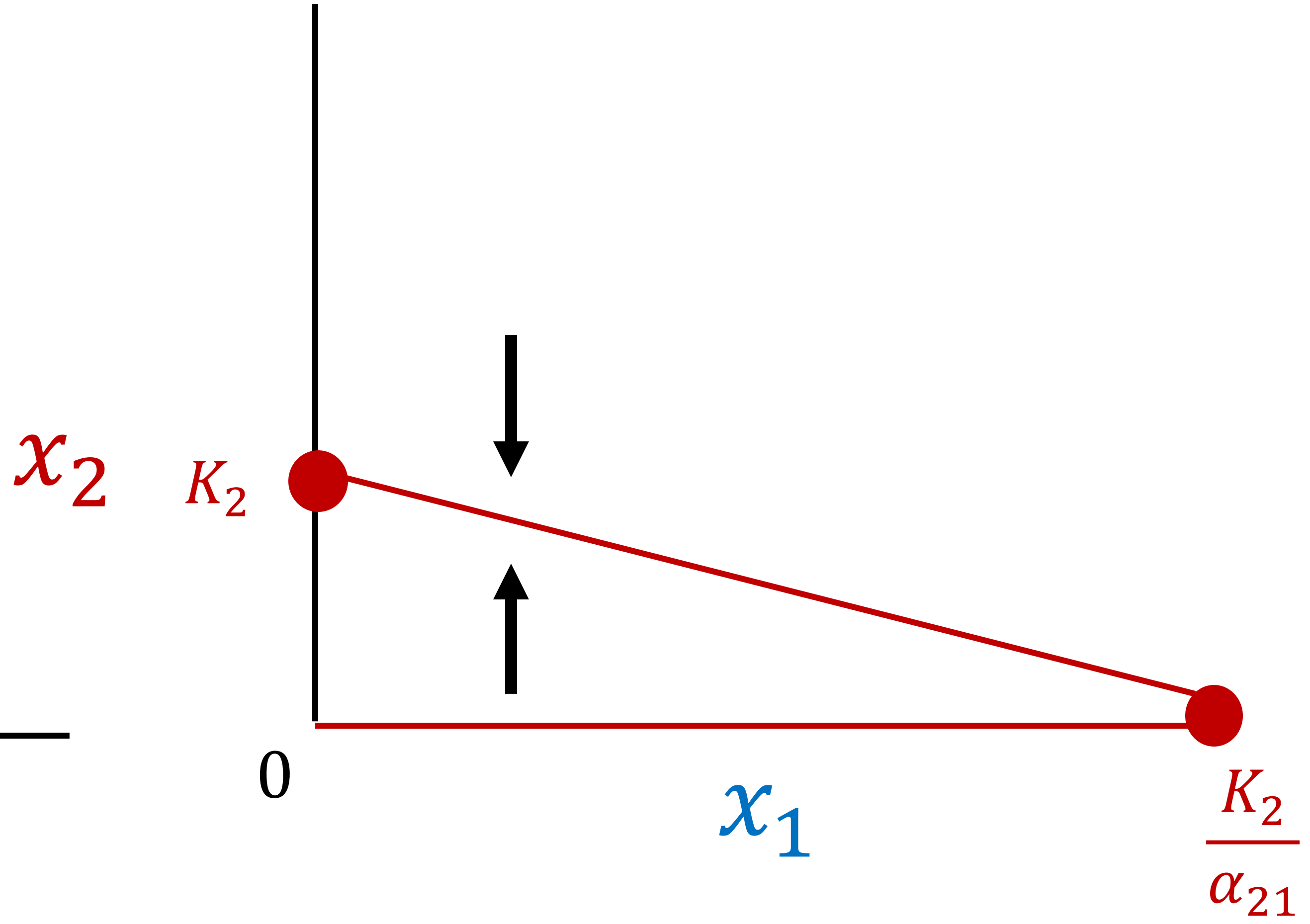




We can use vector addition from the individual nullclines to determine the outcome of competition.

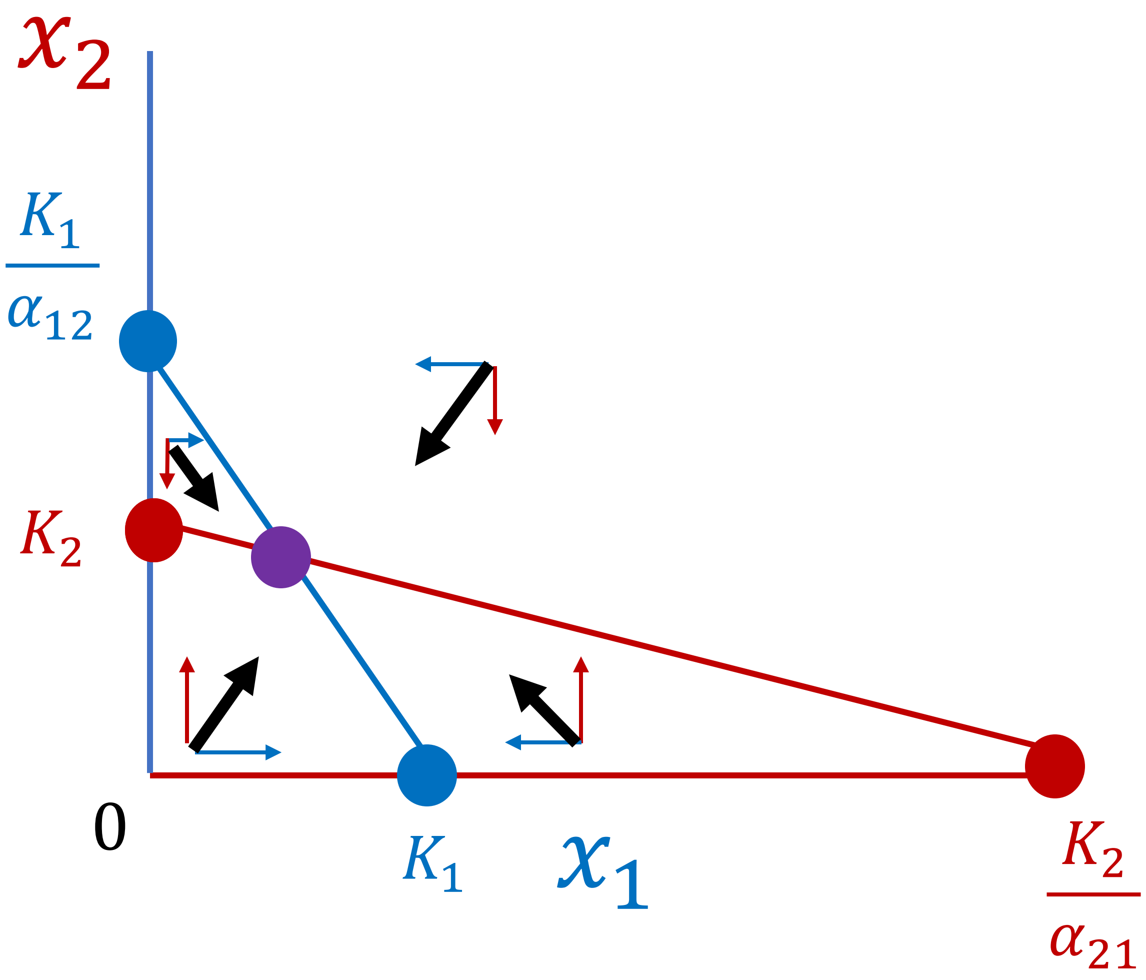
Given different combinations of x_1 and x_2 what is the outcome of competition?

System will converge to one of its equilibria, depending on the values of the competition and carrying capacity parameters.

We can use vector addition **in each quadrat** from the individual nullclines to determine the outcome of competition.

This configuration is a **stable equilibrium**, indicating **stable coexistence** at:

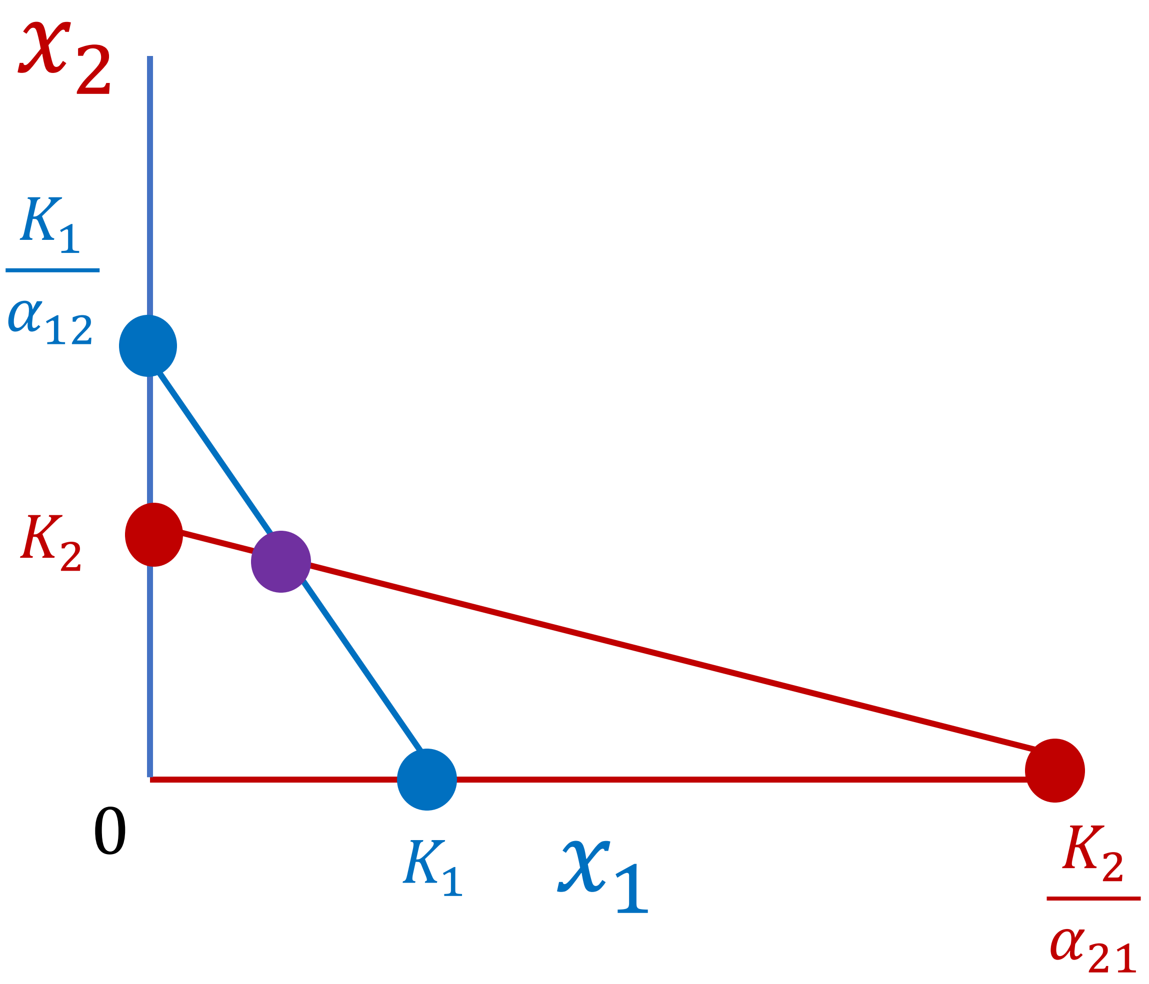
$$x_1^* = \frac{K_1 - K_2\alpha_{12}}{1 - \alpha_{21}\alpha_{12}} \quad x_2^* = \frac{K_2 - K_1\alpha_{21}}{1 - \alpha_{12}\alpha_{21}}$$



Given different combinations of x_1 and x_2 what is the outcome of competition?

Like before, we can also solve $\frac{dx_1}{dt}$ at different combinations of x_1 and x_2 to test the direction the x_1 population will move during competition (always along the x-axis).

We can solve $\frac{dx_2}{dt}$ at different combinations of x_1 and x_2 to test the direction the x_2 population will move during competition (always along the y-axis).



Given different combinations of x_1 and x_2 what is the outcome of competition?

Let's try it!

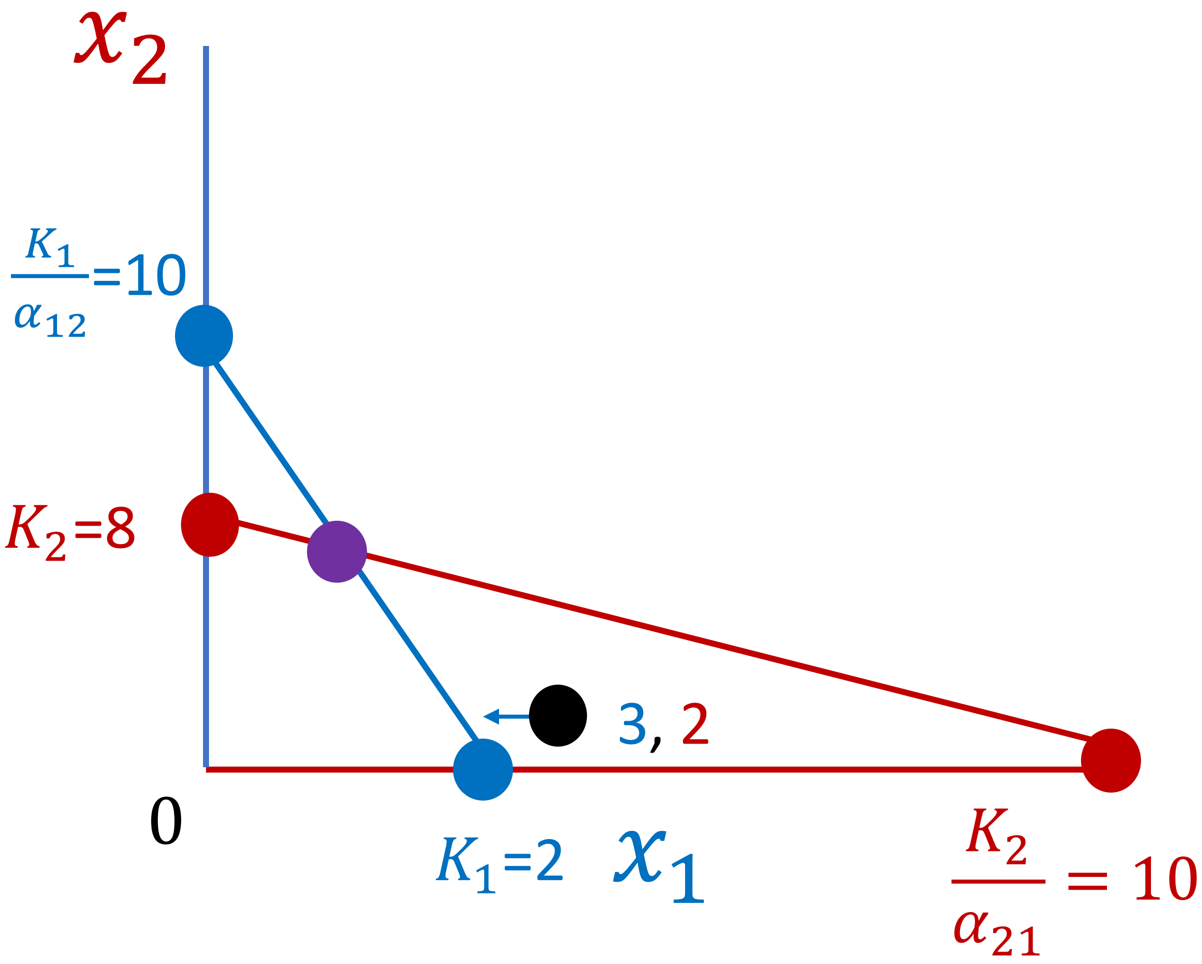
$K_1 = 2\,; \alpha_{12} = .3$
$K_2 = 8\,; \alpha_{21} = .8$

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{K_1} - \frac{x_2 \alpha_{12}}{K_1}\right)$$

$$\frac{dx_1}{dt} = r_1 * 3 \left(1 - \frac{3}{2} - \frac{2 * .3}{2}\right)$$

$$\frac{dx_1}{dt} = r_1 * 3(1 - 1.5 - 0.3)$$

$$\frac{dx_1}{dt} = (-)$$



Given different combinations of x_1 and x_2 what is the outcome of competition?

Let's try it!

$K_1 = 2\,;\alpha_{12} = .3$

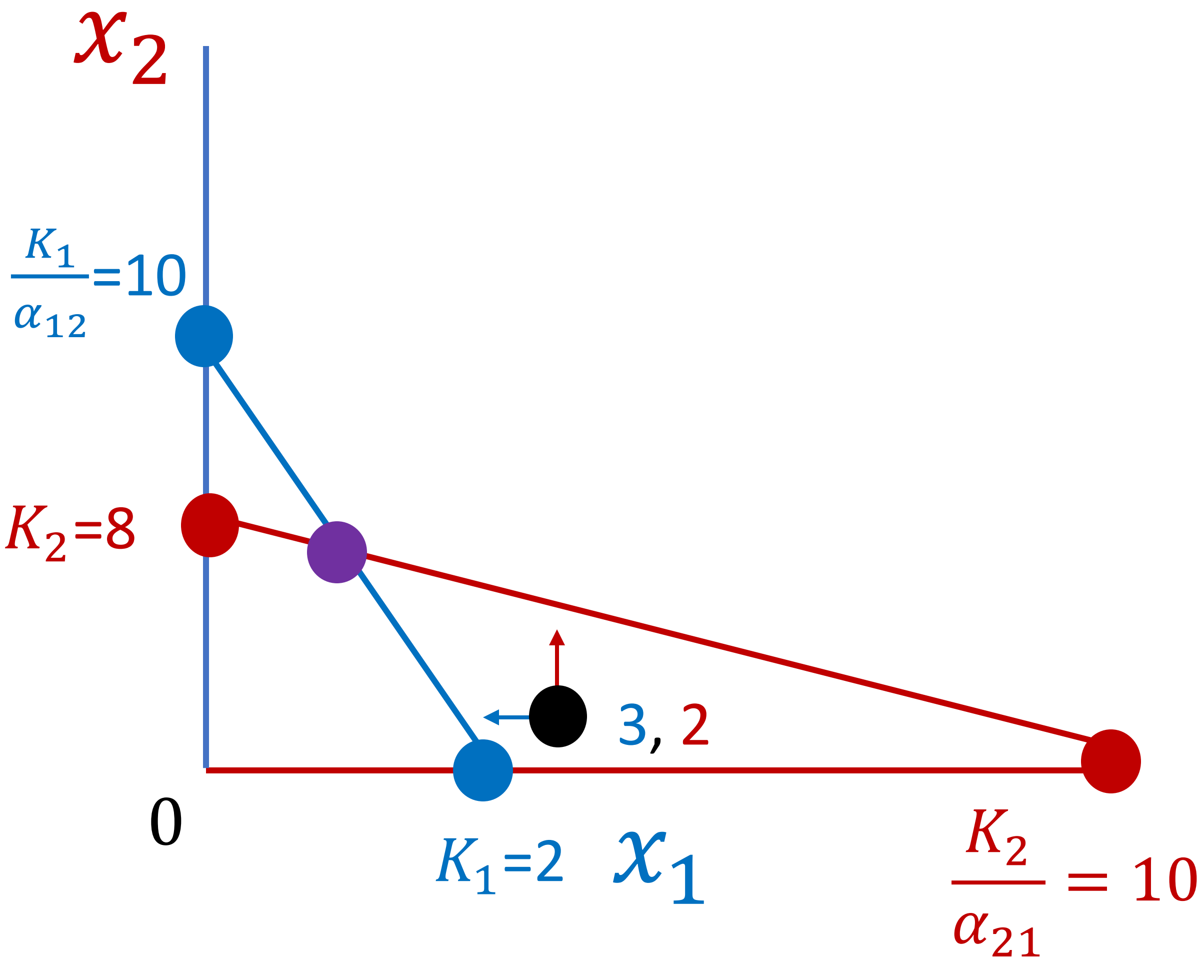
$K_2 = 8\,;\alpha_{21} = .8$

$$\frac{dx_2}{dt} = r_2 x_2\left(1 - \frac{x_2}{K_2} - \frac{x_1\alpha_{21}}{K_2}\right)$$

$$\frac{dx_2}{dt} = r_2 * 2\left(1 - \frac{2}{8} - \frac{3 * .3}{8}\right)$$

$$\frac{dx_2}{dt} = r_2 * 2(1 - .25 - .113)$$

$$\frac{dx_2}{dt} = (+)$$

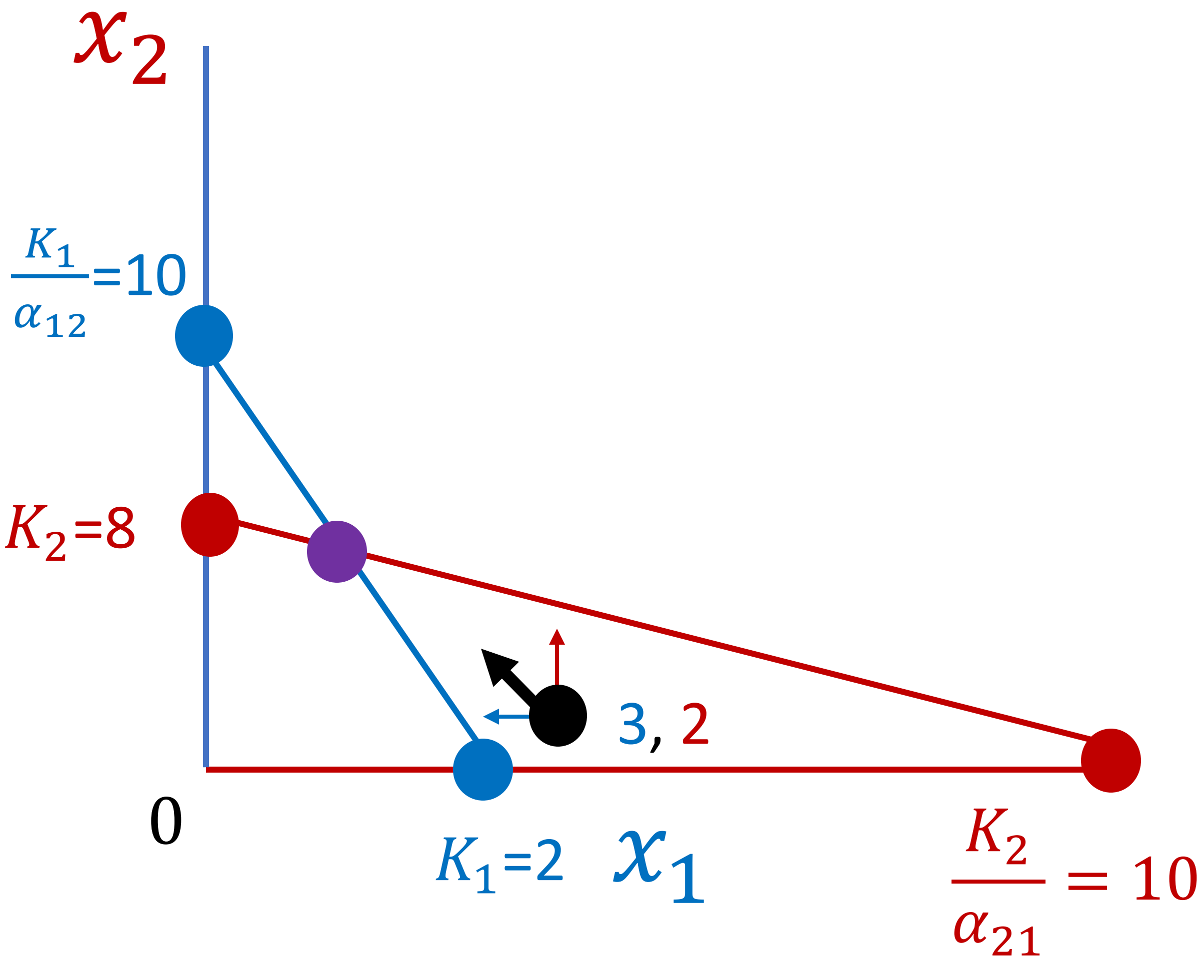


Given different combinations of x_1 and x_2 what is the outcome of competition?

Let's try it!

$K_1 = 2 \, ; \alpha_{12} = .3$
$K_2 = 8 \, ; \alpha_{21} = .8$

Results replicate graphical approach!



Four possible outcomes for competition

Case 1:

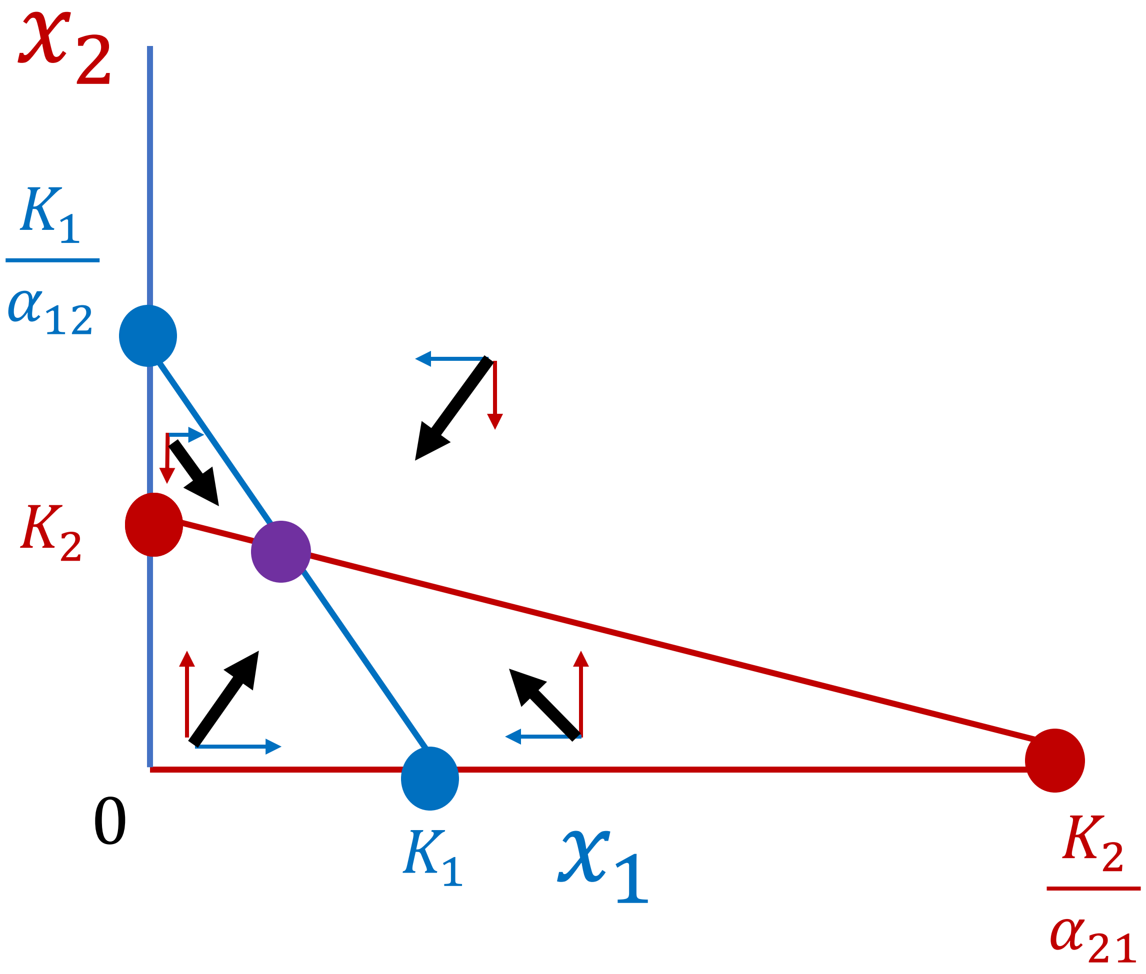
Stable equilibrium, with **coexistence** at:

$$x_1^* = \frac{K_1 - K_2\alpha_{12}}{1 - \alpha_{21}\alpha_{12}} \quad x_2^* = \frac{K_2 - K_1\alpha_{21}}{1 - \alpha_{12}\alpha_{21}}$$

$$\frac{\boldsymbol{K_1}}{\boldsymbol{\alpha_{12}}} > \boldsymbol{K_2} \;\&\; \frac{\boldsymbol{K_2}}{\boldsymbol{\alpha_{21}}} > \boldsymbol{K_1}$$

$$(\alpha_{12} * \alpha_{21} < 1)$$

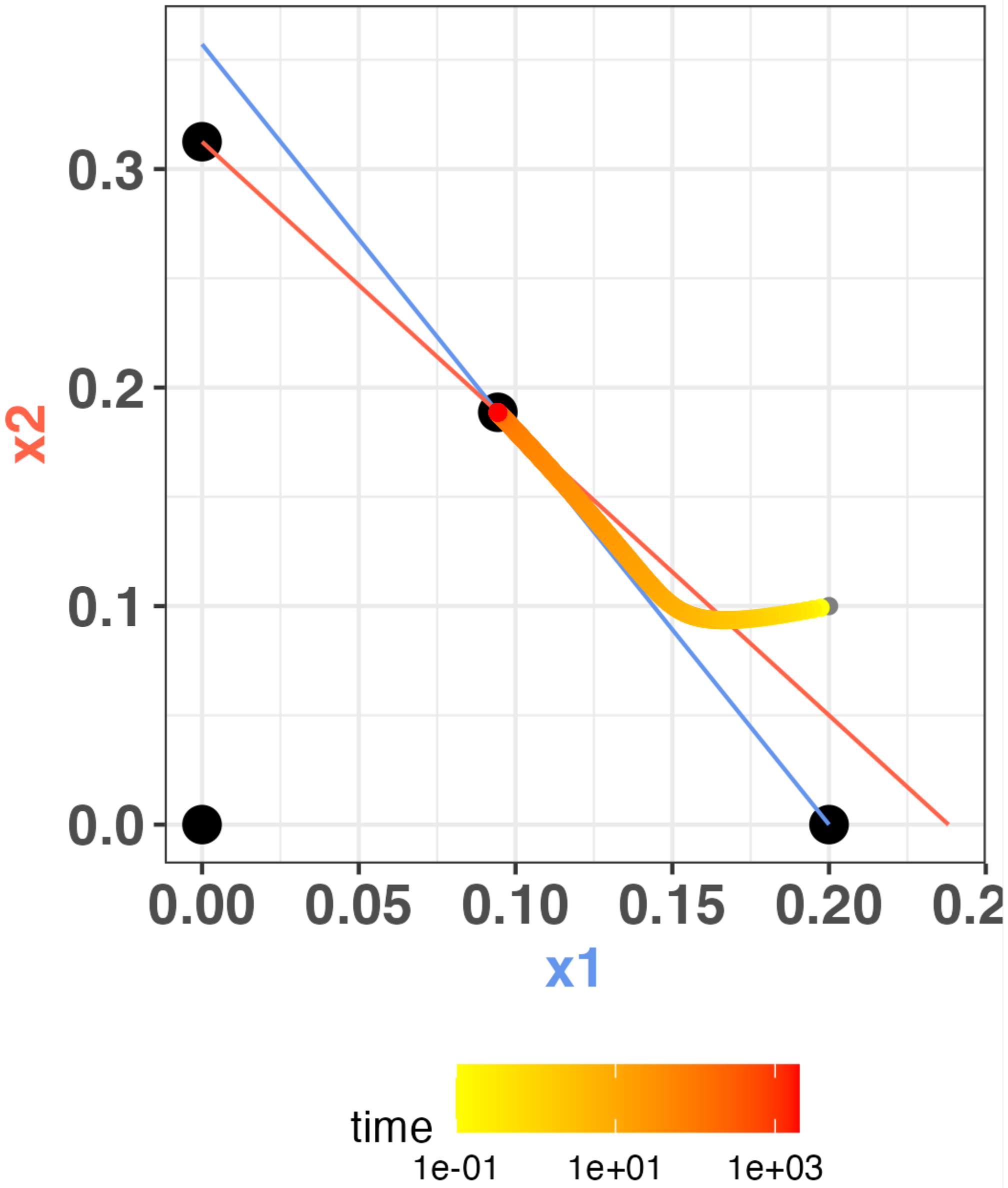
- Species coexist stably but **below carrying capacity** for each individual population.
- **Intraspecific** competition is stronger than **interspecific** competition.

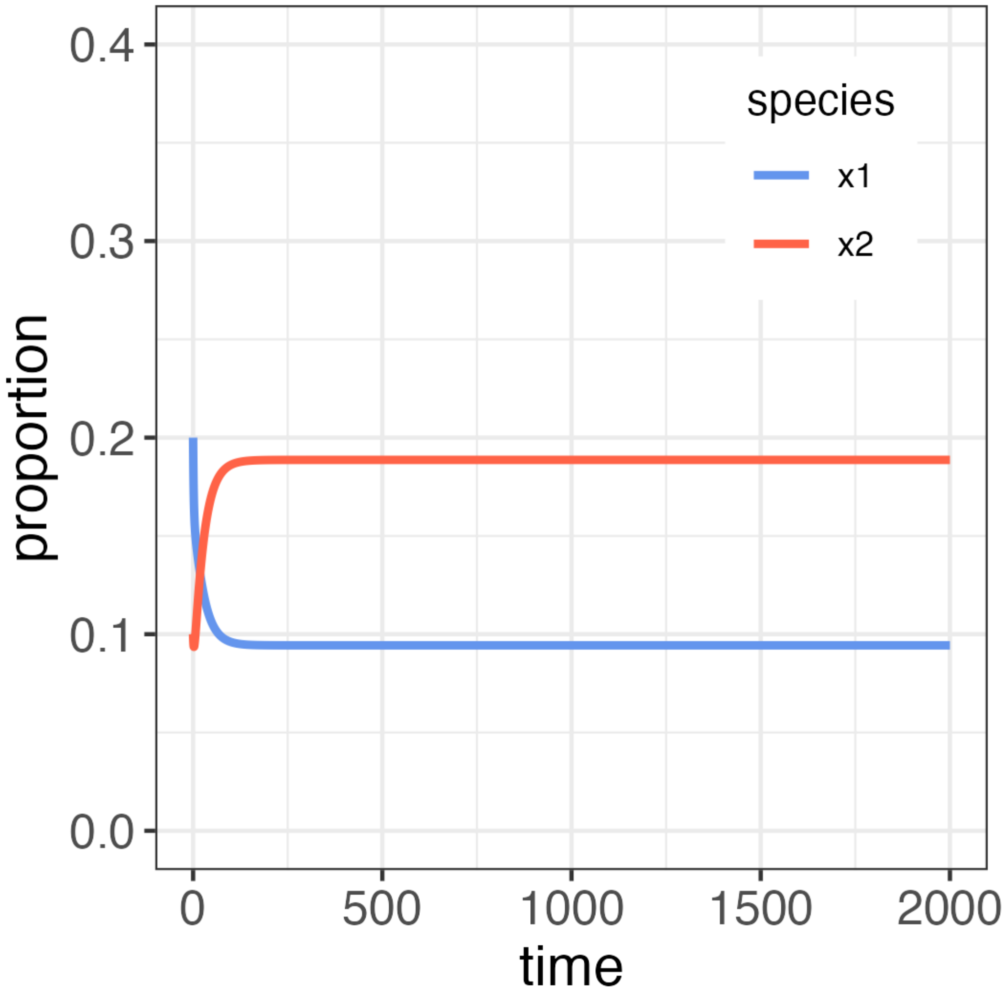


Case 1:

Stable equilibrium, with **coexistence**:

$$\frac{K_1}{\alpha_{12}} > K_2 \;\&\; \frac{K_2}{\alpha_{21}} > K_1 \quad (\alpha_{12} * \alpha_{21} < 1)$$





Four possible outcomes for competition

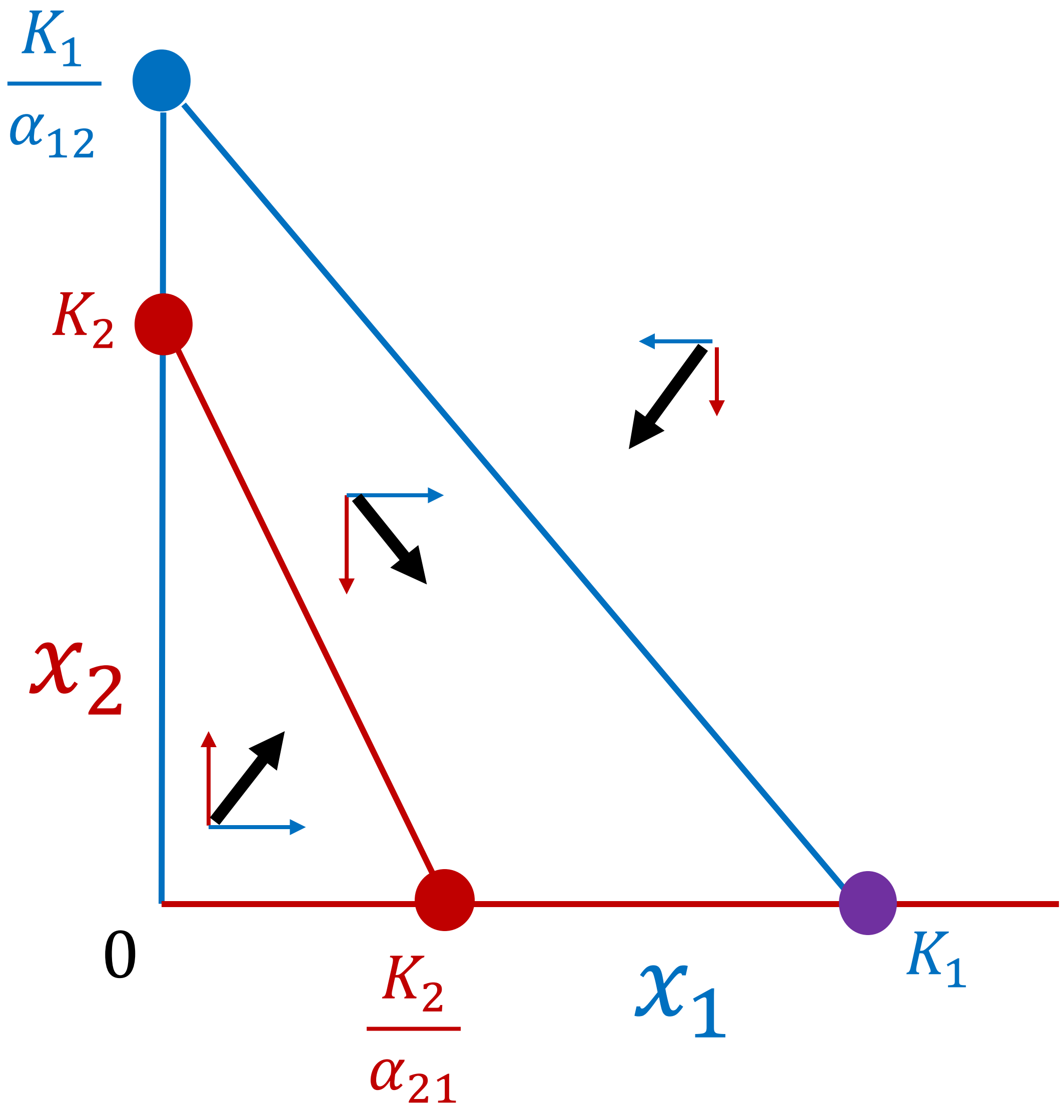
Case 2:

Species 1 outcompetes species 2

$$\frac{K_1}{\alpha_{12}} > K_2 \;\&\; \frac{K_2}{\alpha_{21}} < K_1$$

System collapses to equilibrium:

$$x_1^* = K_1;\ x_2^* = 0$$



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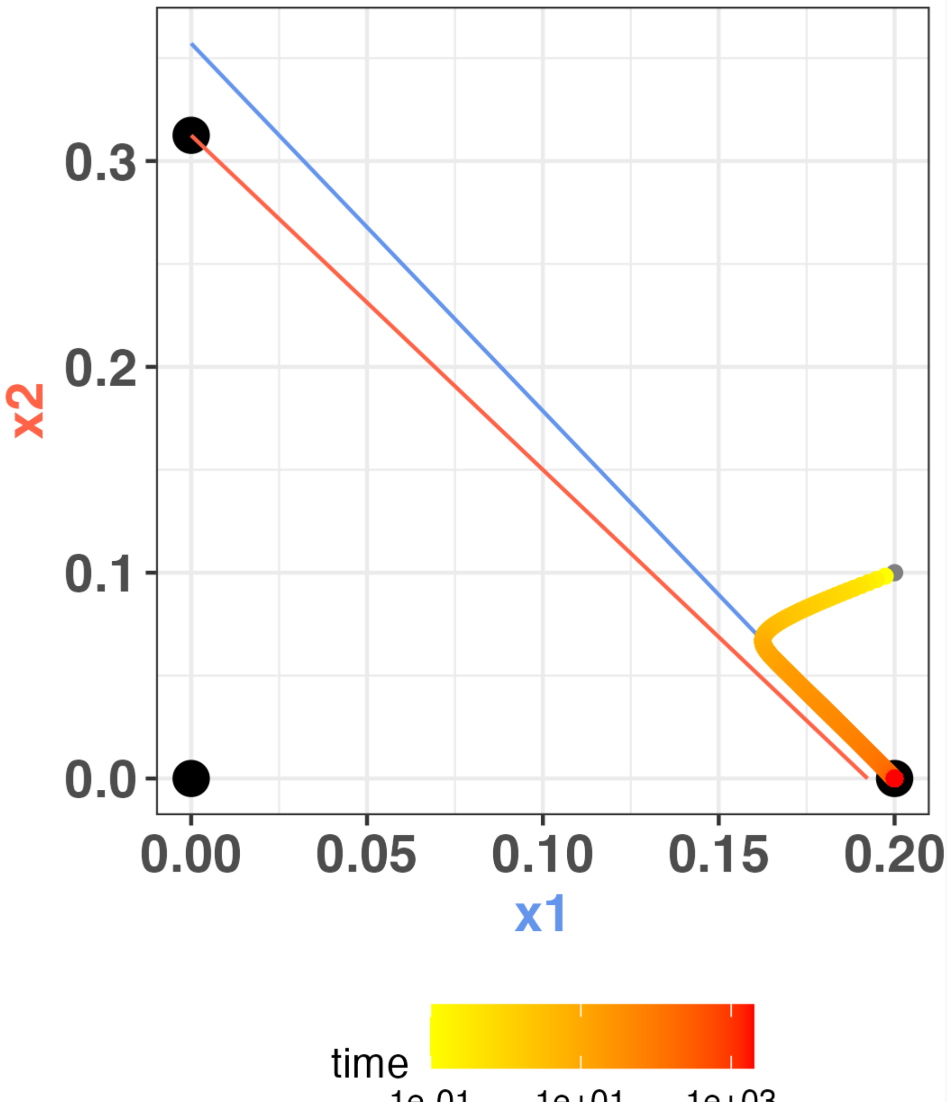
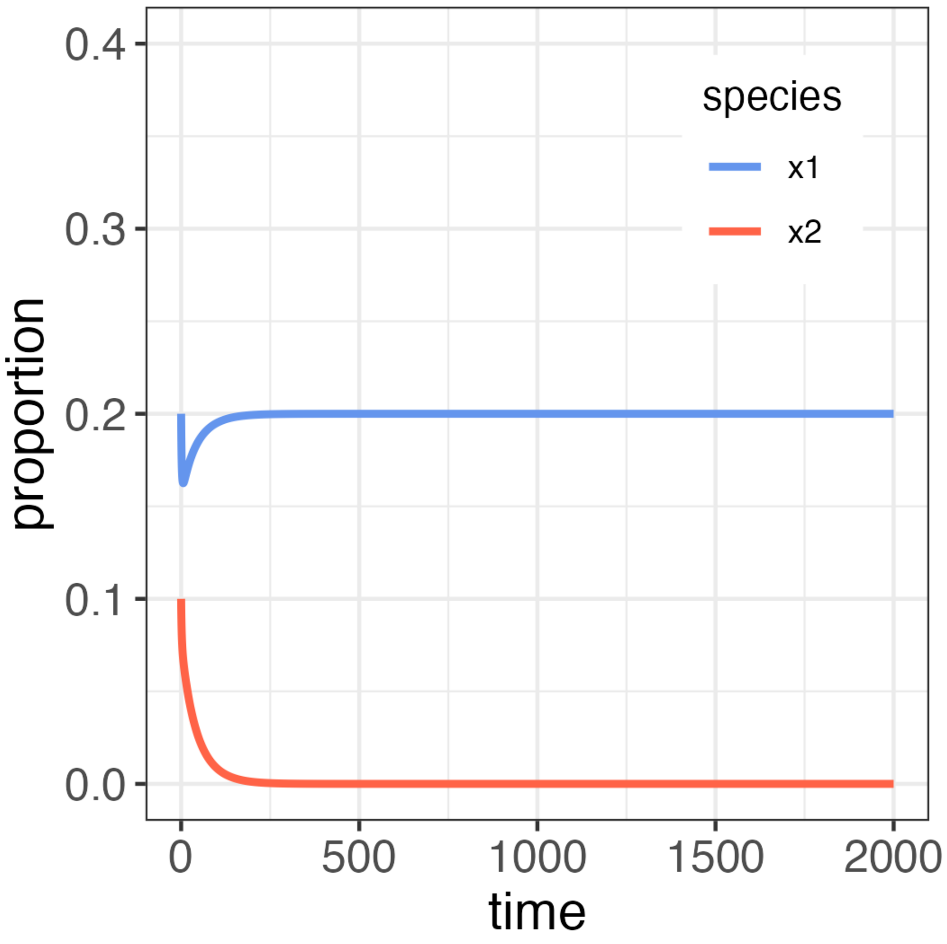




Four possible outcomes for competition

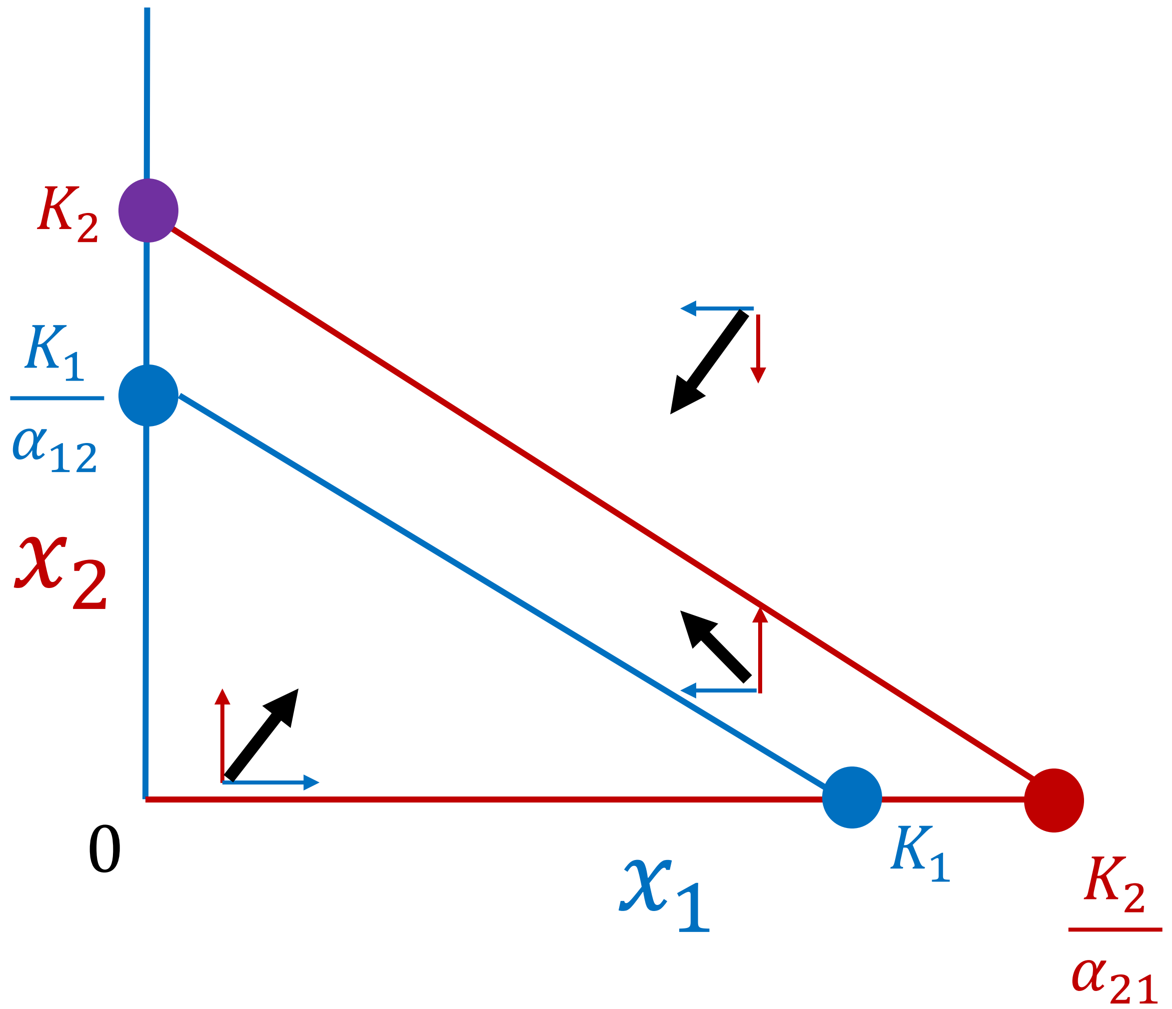
Case 3:

Species 2 outcompetes species 1

$$\frac{K_1}{\alpha_{12}} < K_2 \;\&\; \frac{K_2}{\alpha_{21}} > K_1$$

System collapses to equilibrium:

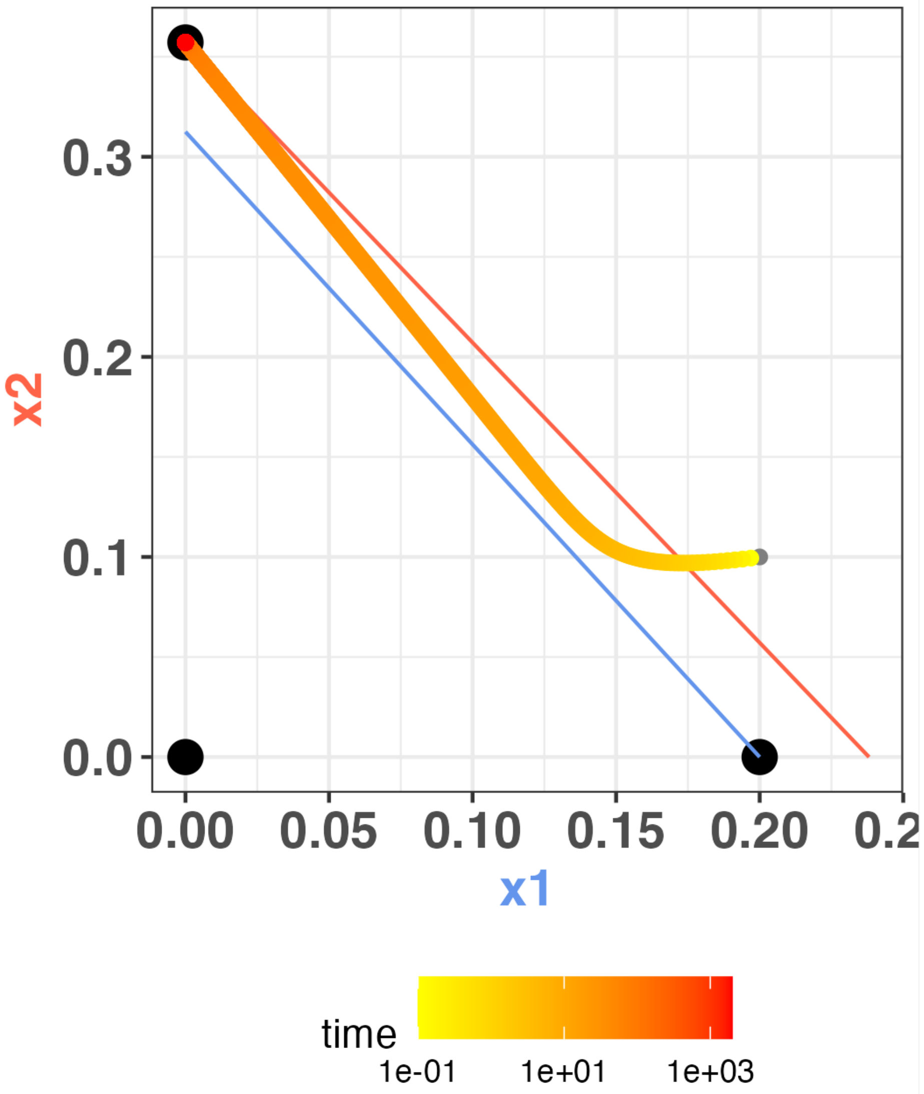
$$x_1^* = 0;\; x_2^* = K_2$$

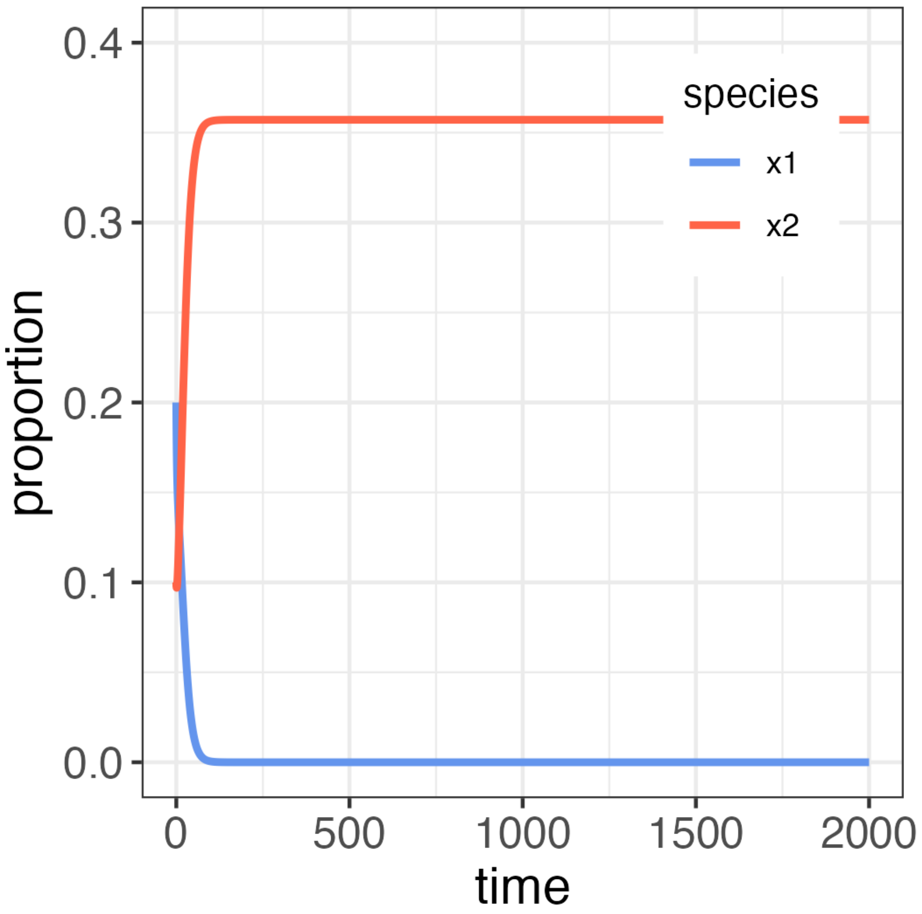


Case 3:

Species 2 outcompetes species 1

$$\frac{K_1}{\alpha_{12}} < K_2 \; \& \; \frac{K_2}{\alpha_{21}} > K_1$$





Four possible outcomes for competition

Case 4: Precedence

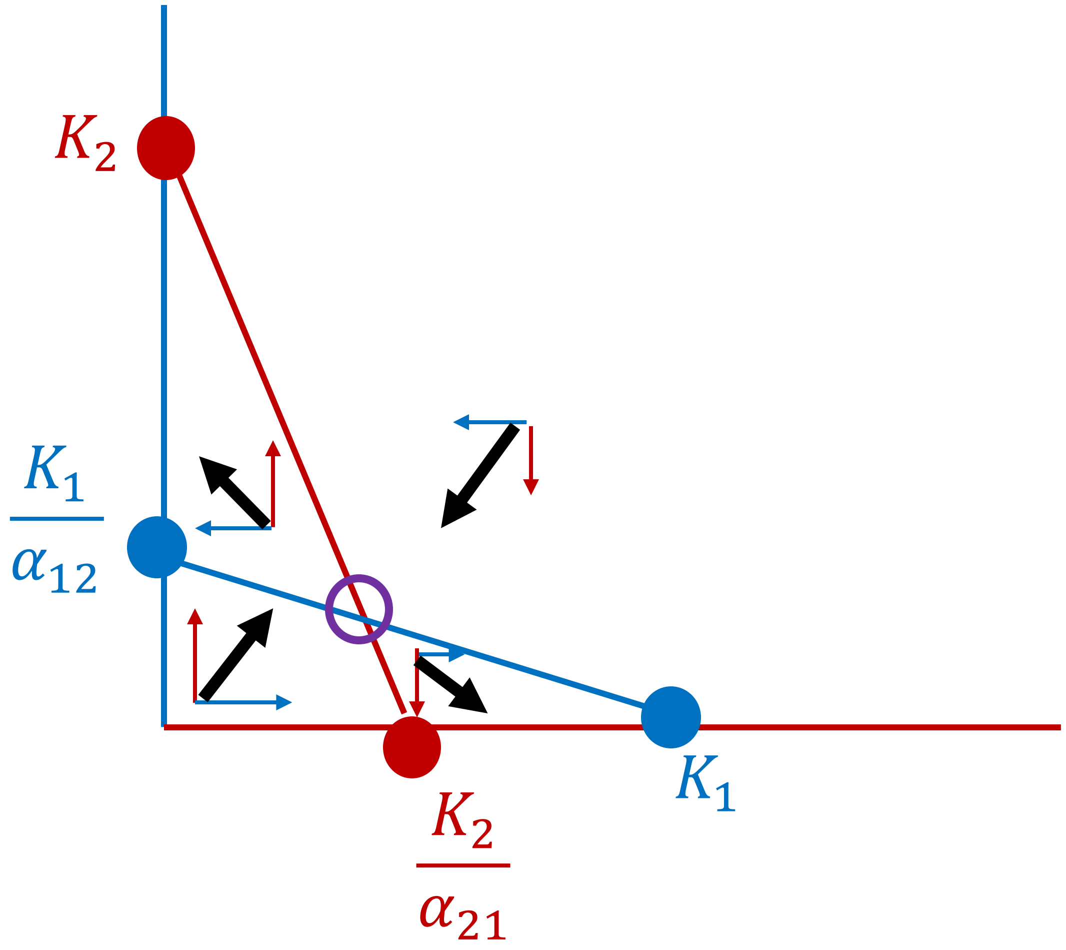
Aggressive interspecific competition.

Outcome depends on starting conditions.

$$\frac{K_1}{\alpha_{12}} < K_2 \;\&\; \frac{K_2}{\alpha_{21}} < K_1$$

$$(\alpha_{12} * \alpha_{21} > 1)$$

- **System will move towards either single species equilibria** ($x_1^* = 0\,; x_2^* = K_2$ OR $x_1^* = K_1; x_2^* = 0$), depending on starting conditions.
- Under extremely unrealistic starting conditions, system will sit at an **unstable equilibrium** that will collapse in either direction following slight perturbation.

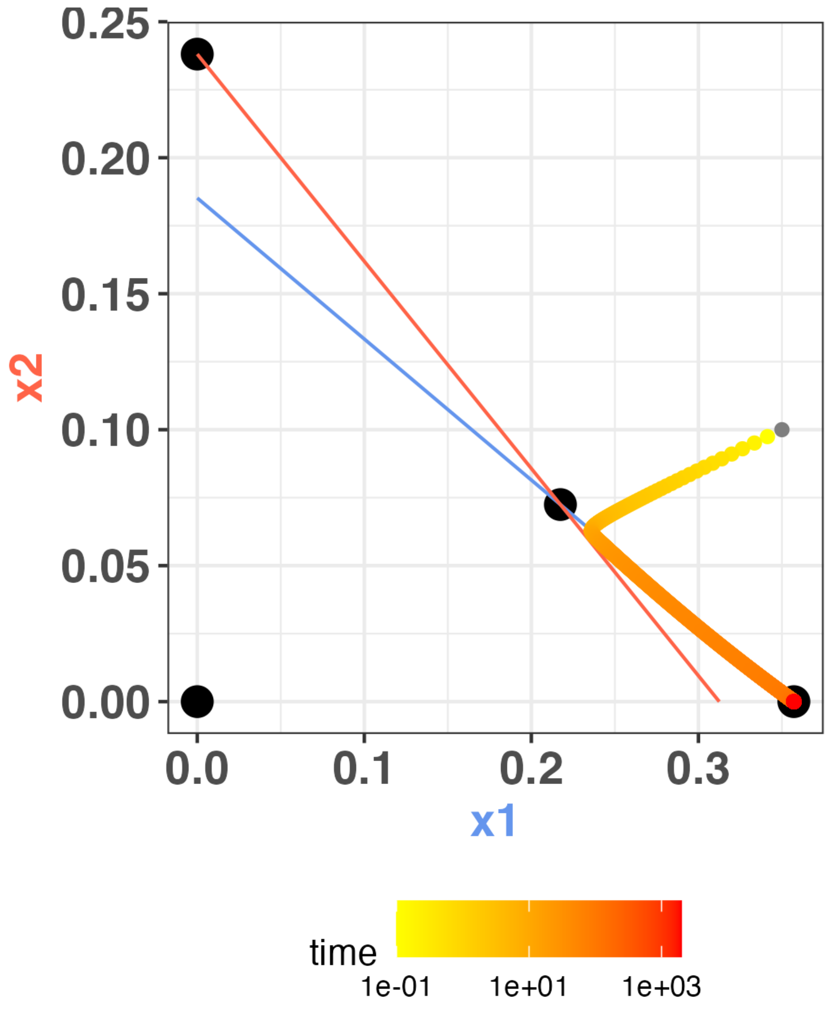


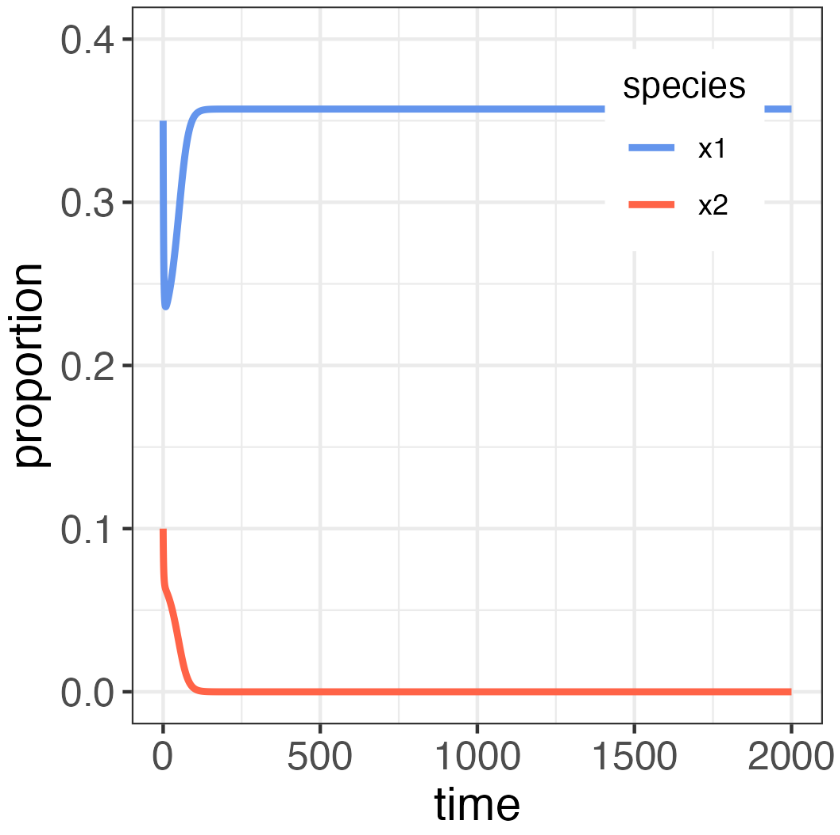
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

Here, x1 outcompetes x2



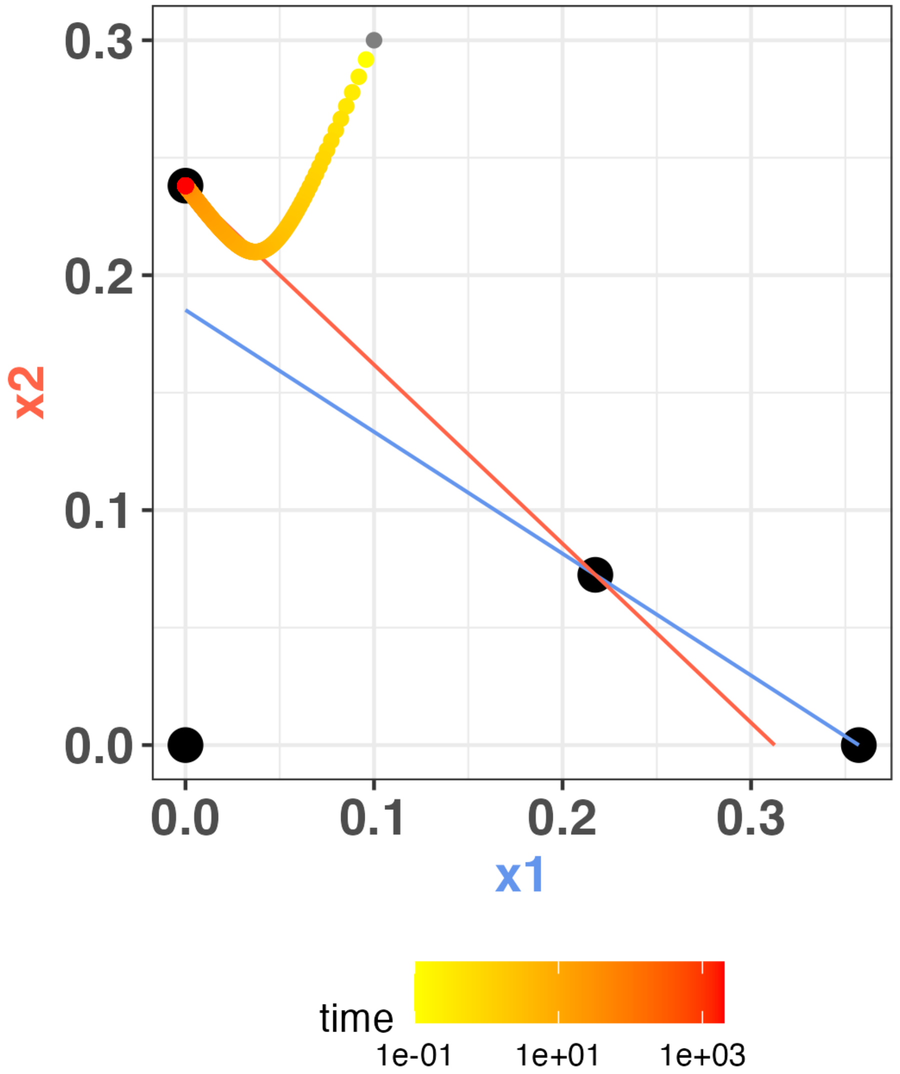


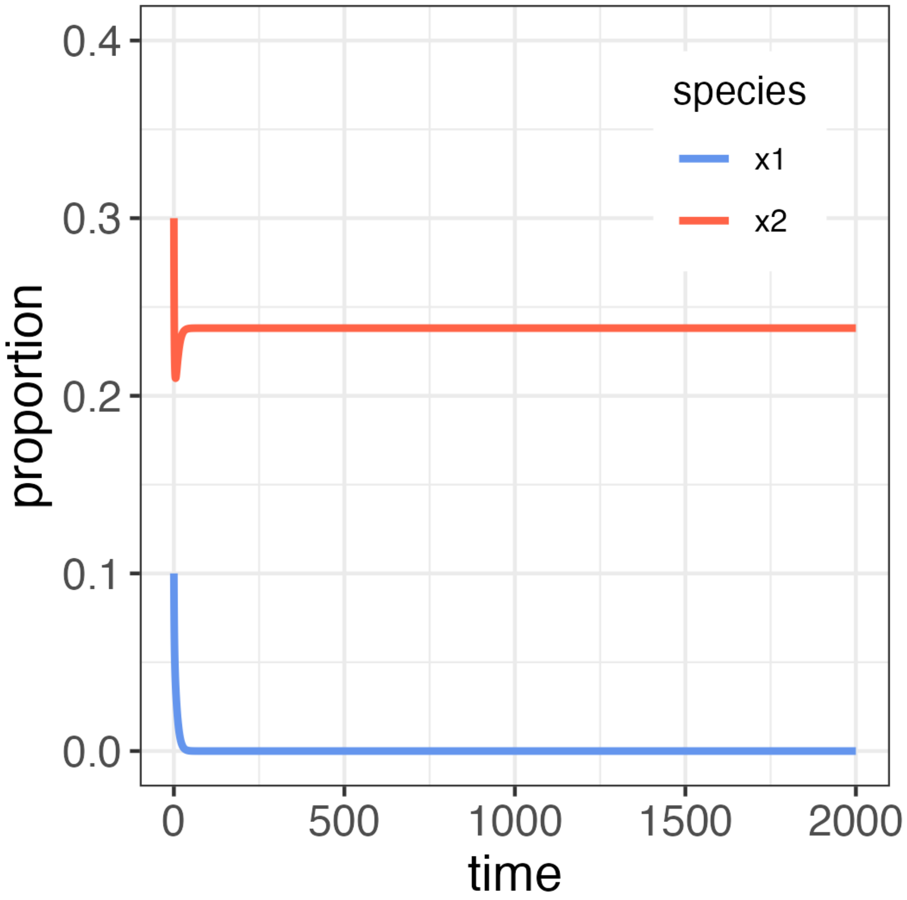
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

Here, x2 outcompetes x1



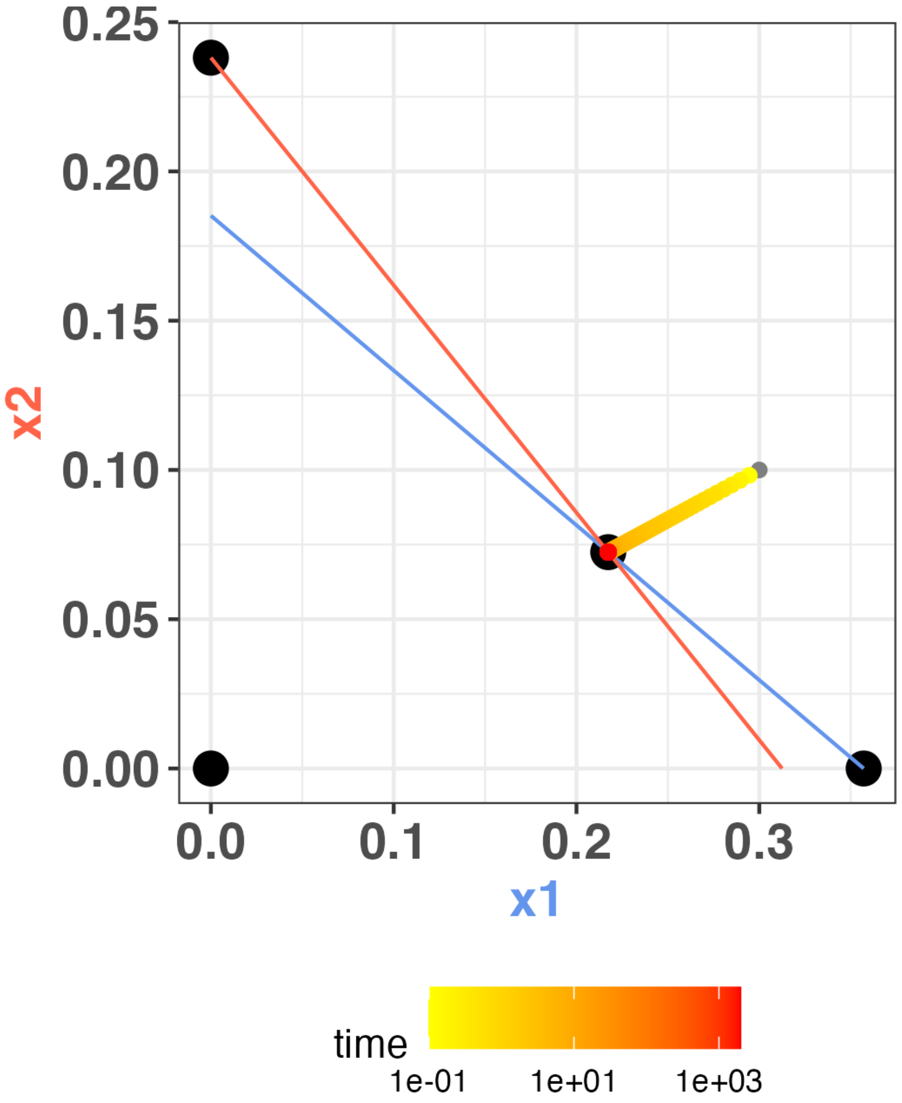


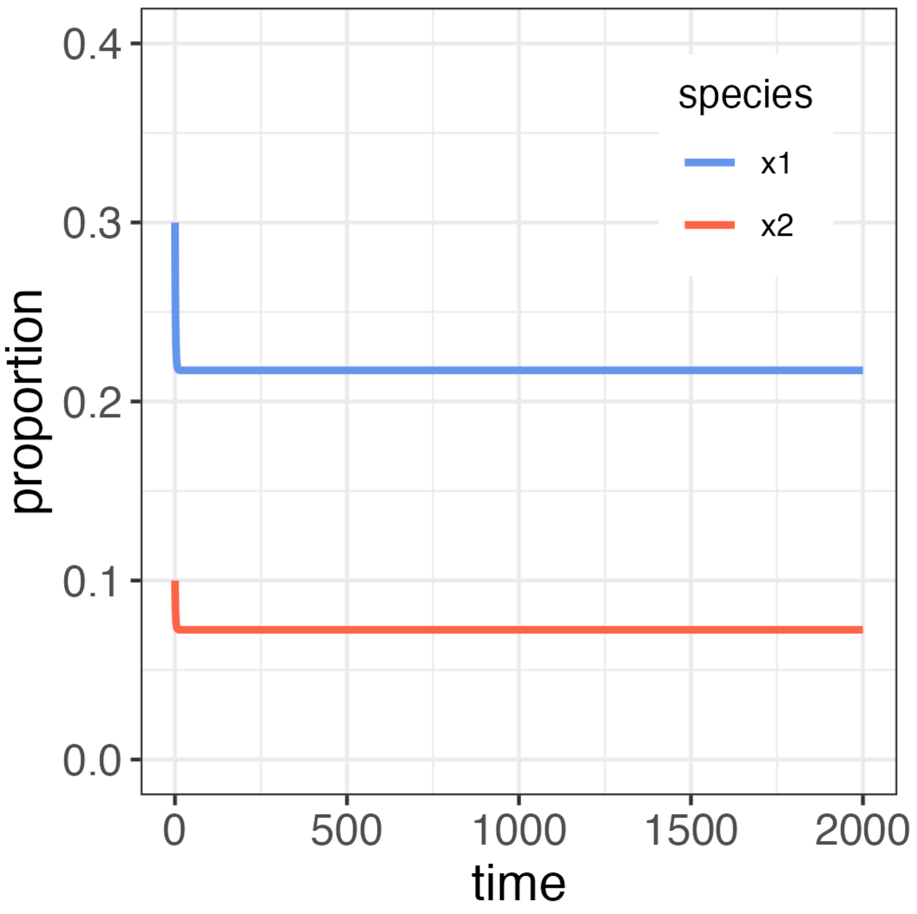
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

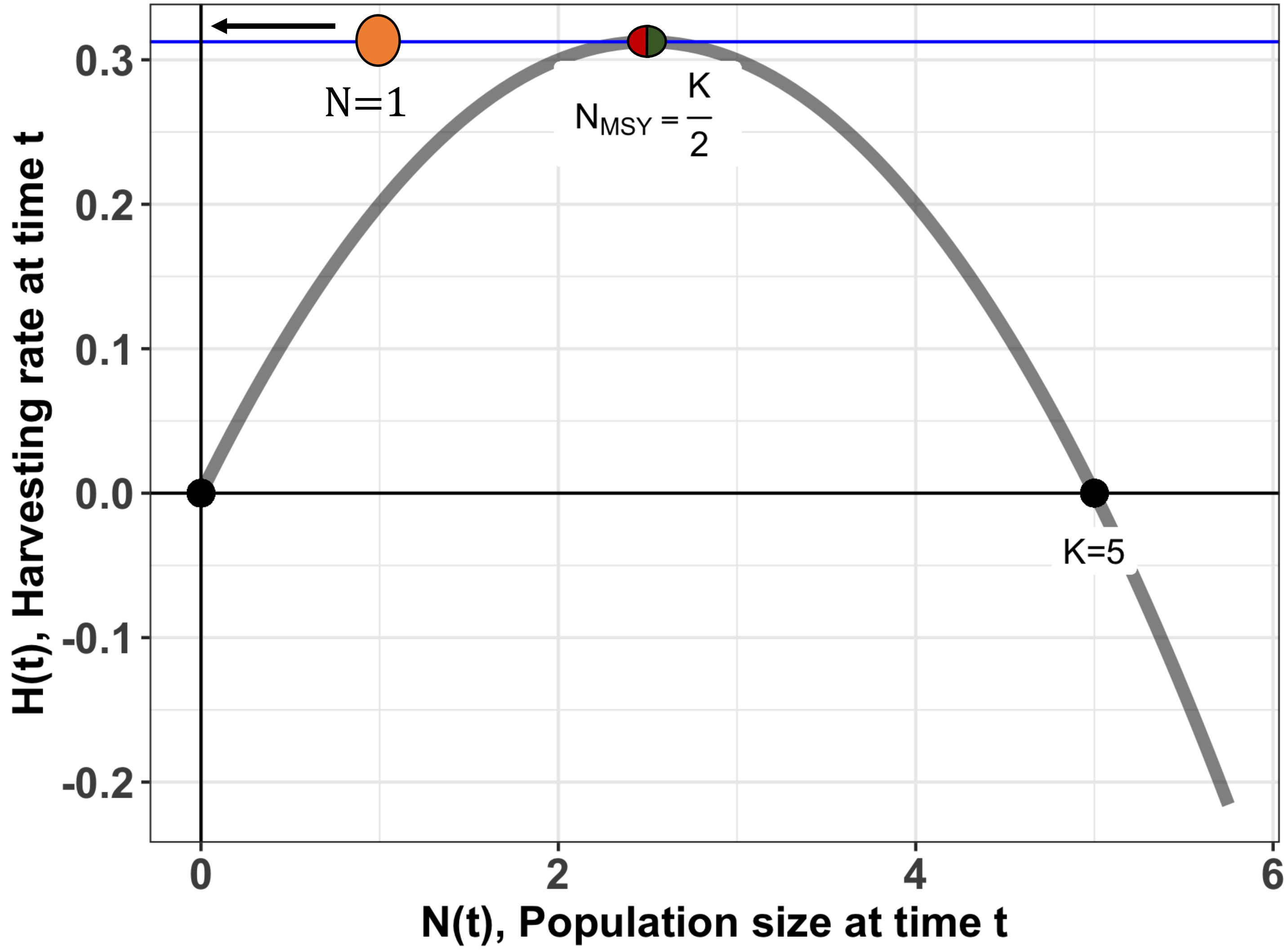
Here, coexistence





Remember MSY, the semi-stable equilibrium:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - H$$



K=5
r=0.25
H=.3125

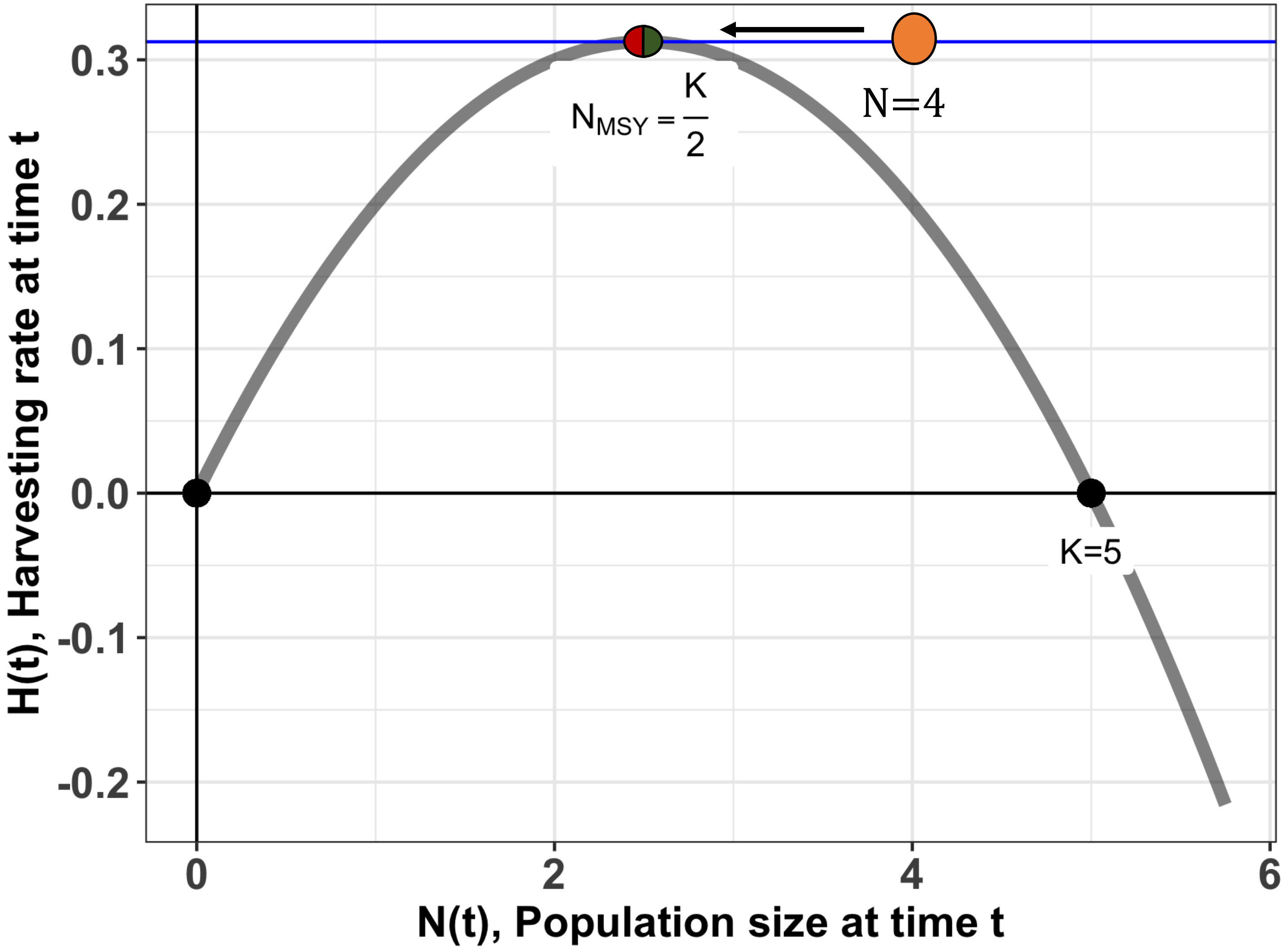
$$\frac{dN}{dt} = 0.25 * 1\left(1 - \frac{1}{5}\right) - .3125$$

$$\frac{dN}{dt} = (-)$$

In a **semi-stable equilibrium**, perturbations ***sometimes*** drive the system away from equilibrium.

Remember MSY, the semi-stable equilibrium:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - H$$



K=5

r=0.25

H=.3125

$$\frac{dN}{dt} = 0.25 * 4\left(1 - \frac{4}{5}\right) -.3125$$

$$\frac{dN}{dt} = (-)$$

Four possible outcomes for competition

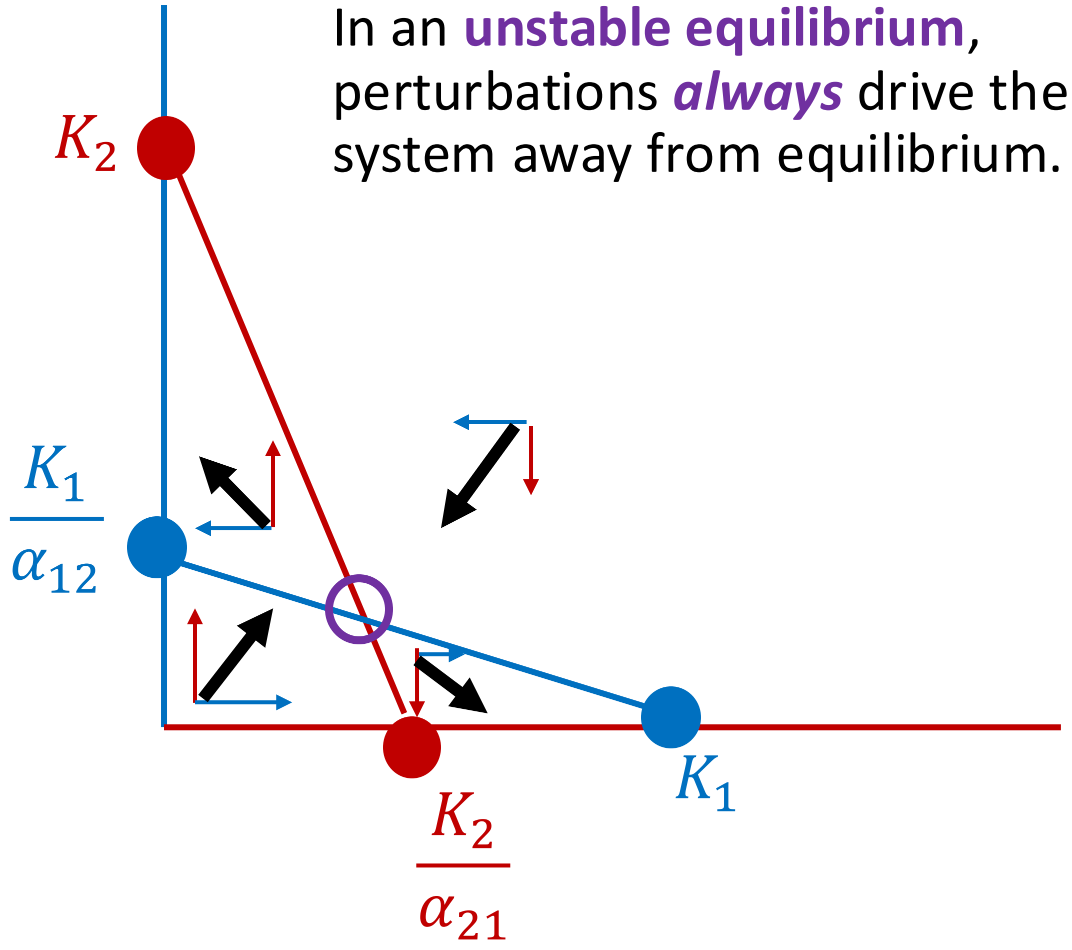
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

$$\frac{K_1}{\alpha_{12}} < K_2 \;\&\; \frac{K_2}{\alpha_{21}} < K_1$$

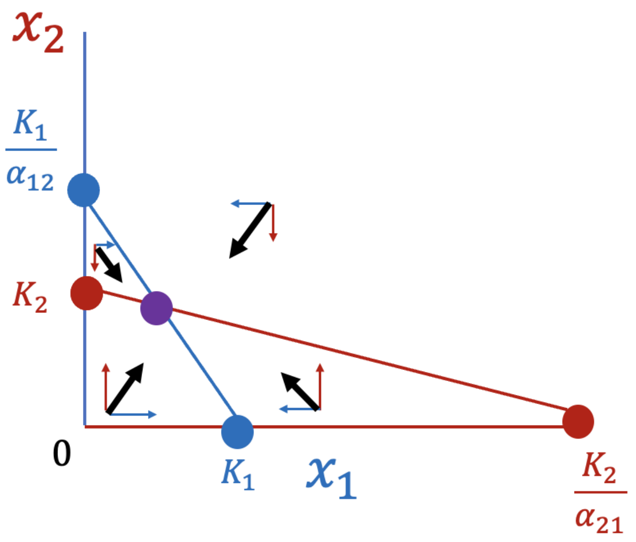
$$(\alpha_{12} * \alpha_{21} > 1)$$



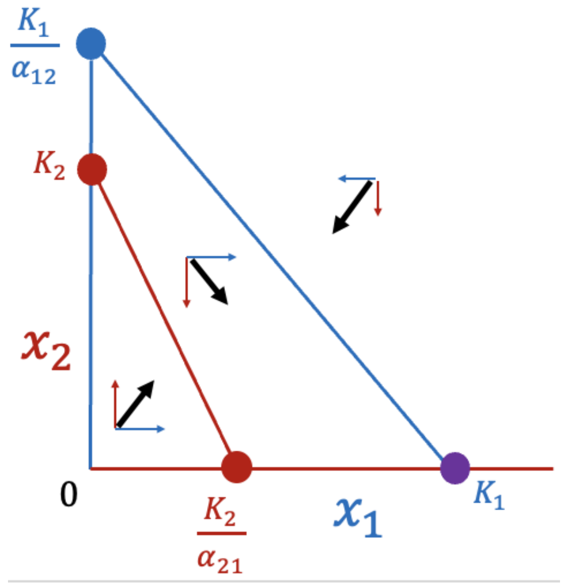
In an **unstable equilibrium**, perturbations ***always*** drive the system away from equilibrium.

Phase plane analysis: graphical determination of the behavior of the state variables in a dynamical system (here, populations of animals)

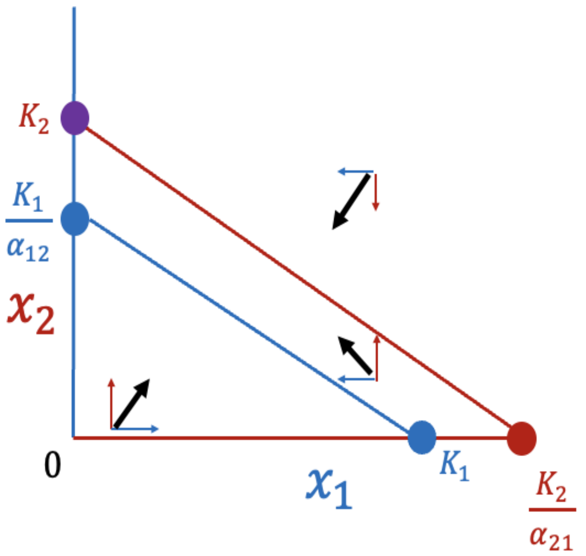
Case 1: Stable coexistence



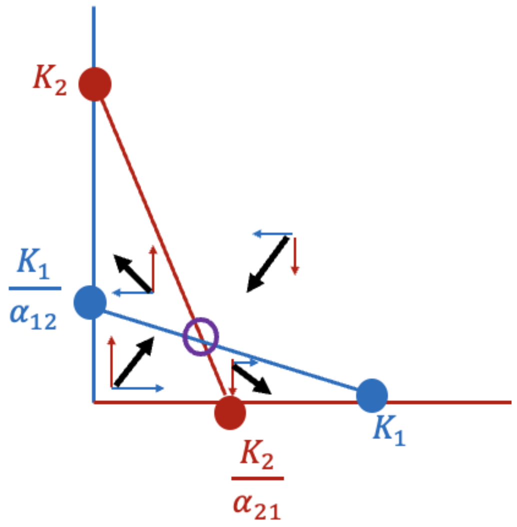
Case 2: Spp. 1 wins



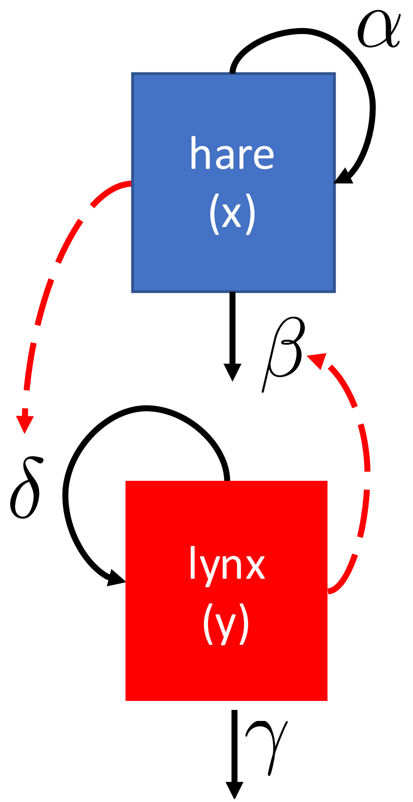
Case 3: Spp. 2 wins



Case 4: Precedence



Note the difference with a predator-prey model!

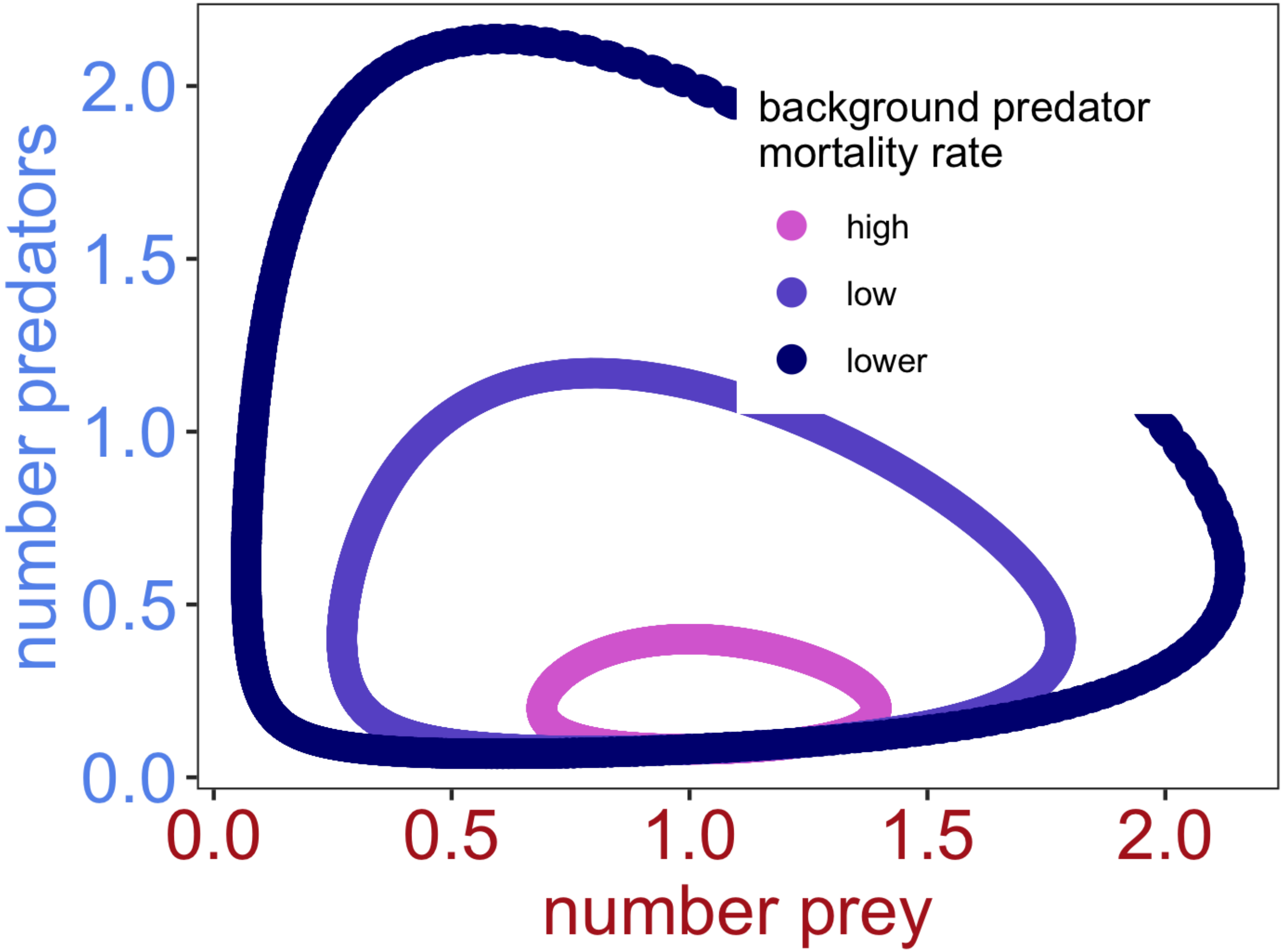


$$\frac{dx}{dt} = \alpha x \; - \beta xy$$

$$\frac{dy}{dt} = \delta xy \; - \gamma y$$

*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*

Predator-prey cycles can be visualized as oscillations.



Phase plane analysis: Why do we care?

We can use these tools to make predictions about the coexistence of species!

Principle of **competitive exclusion**

“Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. ***One will crowd out the other.****”*

- Joseph Grinnell, 1904:

Museum of Vertebrate Zoology

University of California at Berkeley

“Neither can live while the other survives.”

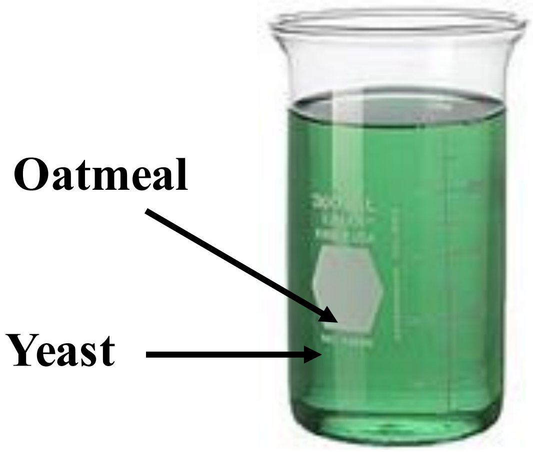
- J.K. Rowling, 2003

Principle of **competitive exclusion**

Paramecium aurelia

Paramecium caudatum

Paramecium bursaria



Gause 1934. *J Experimental Biology.*
Gause 1935. *Science.*

Gause first grew each species in isolation

Paramecium aurelia

Paramecium caudatum

Paramecium bursaria

Gause 1934. *J Experimental Biology.*

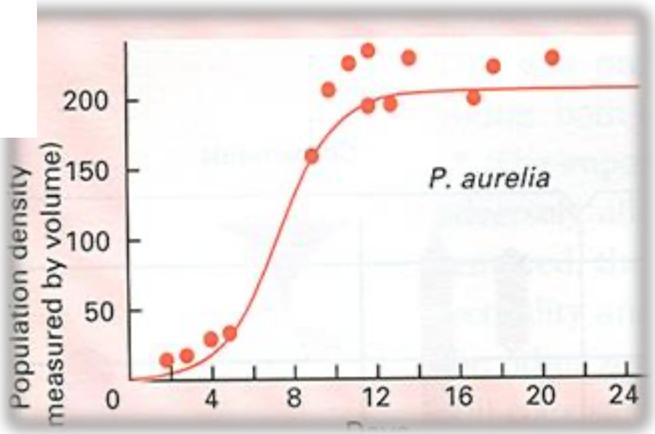
Gause 1935. *Science.*

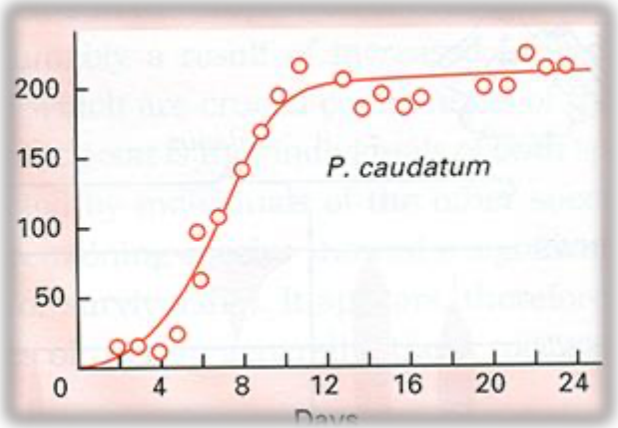
In isolation, each species grew logistically.

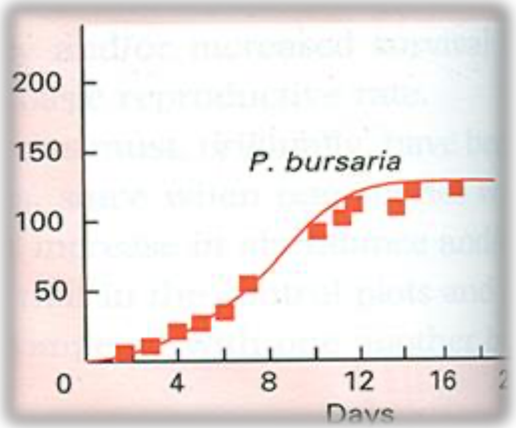
Paramecium aurelia

Paramecium caudatum

Paramecium bursaria







Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

Then, pairs of species were placed in the same beaker.

Paramecium aurelia

Paramecium caudatum

Paramecium caudatum

Paramecium bursaria

Gause 1934. *J Experimental Biology.*

Gause 1935. *Science*.

Competitive exclusion was observed:

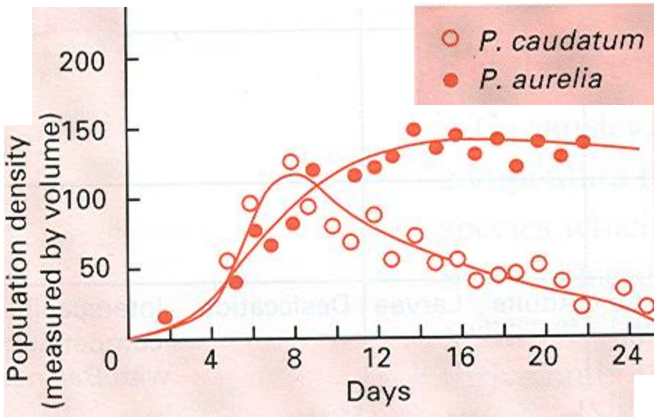
Coexistence was observed:

Paramecium aurelia

Paramecium caudatum

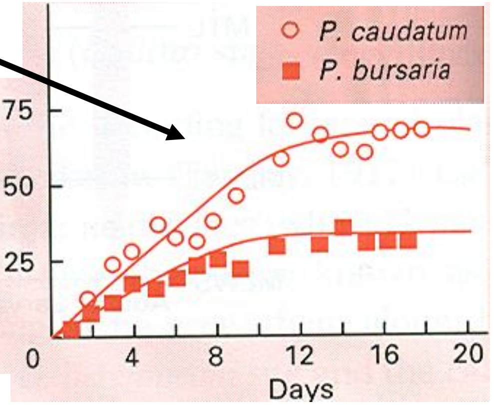
Paramecium caudatum

Paramecium bursaria



Species coexisted below each species' respective individual carrying capacity.

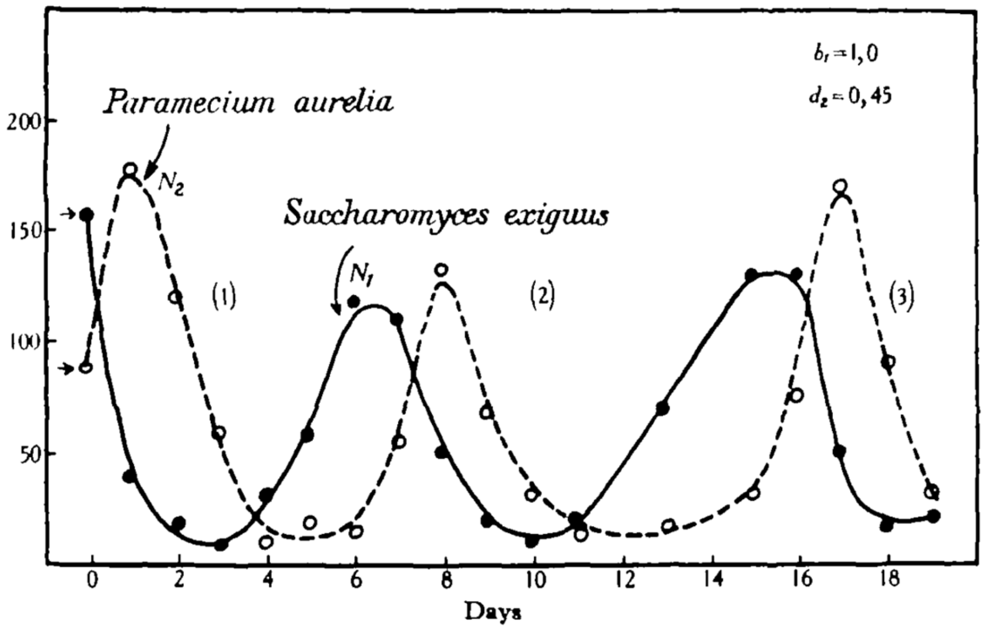
The two coexisting species were largely partitioned in space. *P. bursaria* ate yeast at the bottom and *P. caudatum* consumed bacteria suspended in the medium.

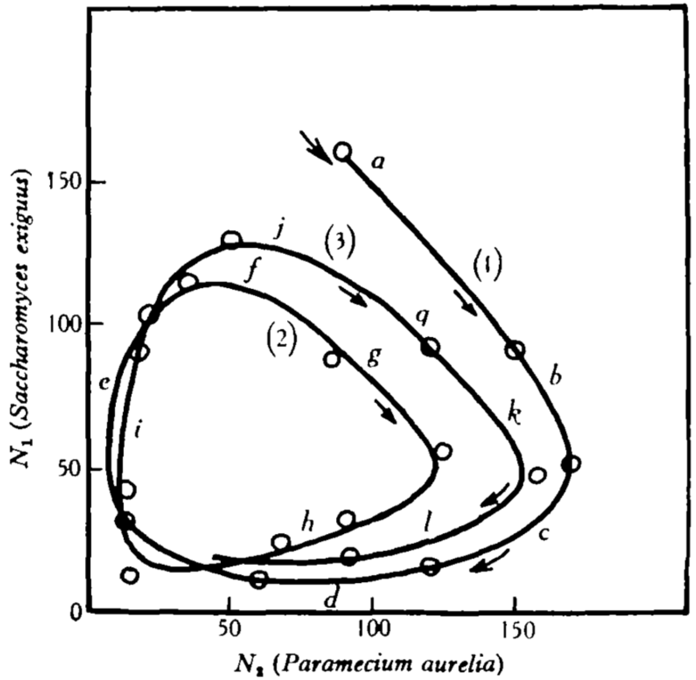


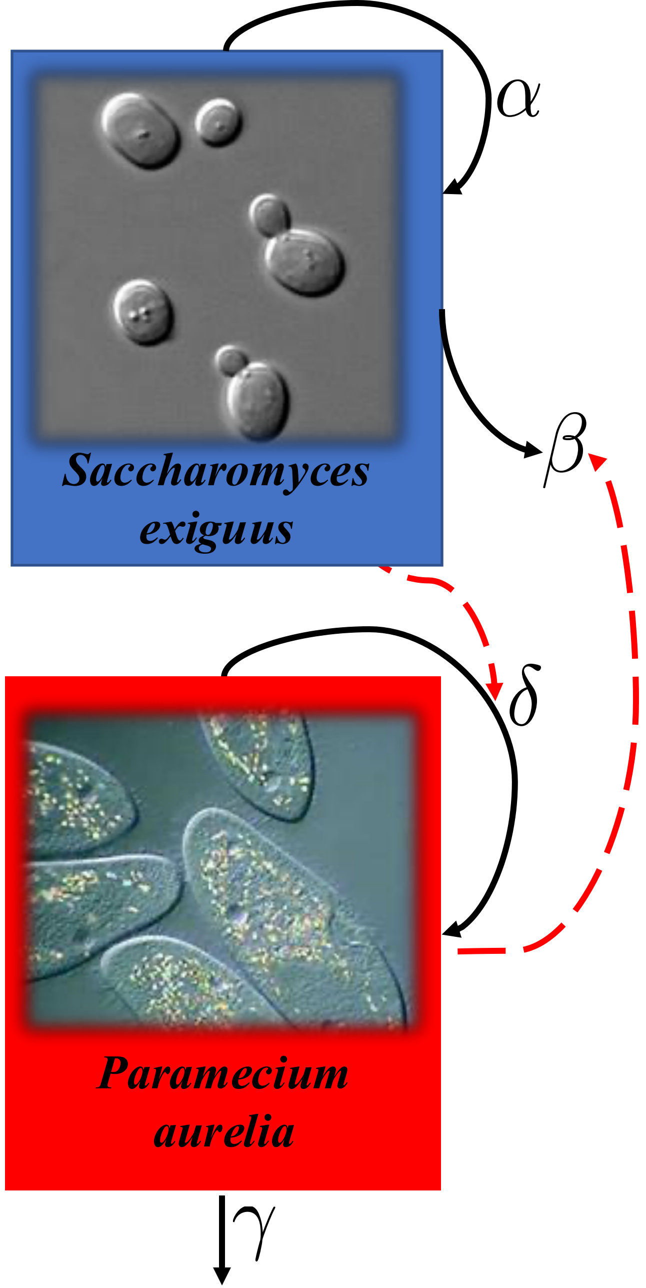
Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

Gause also demonstrated real-life predator-prey cycles with his experiments:







Gause 1935. *Science*.

Gause's experiments:

Competitive exclusion was observed:

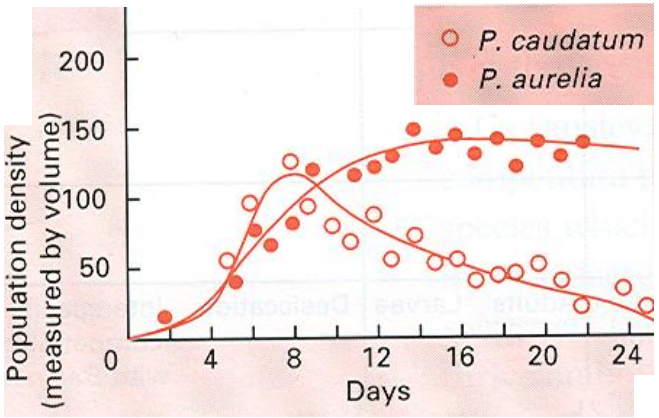
Paramecium aurelia

Paramecium caudatum

Coexistence was observed:

Paramecium caudatum

Paramecium bursaria



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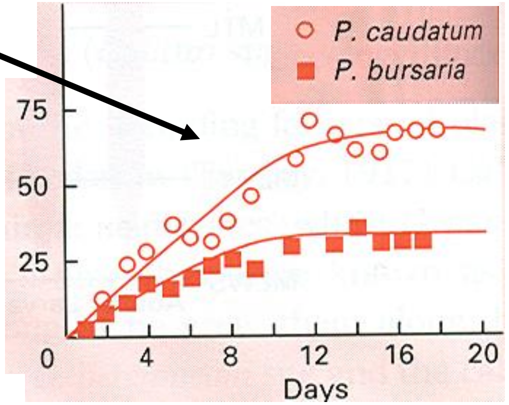
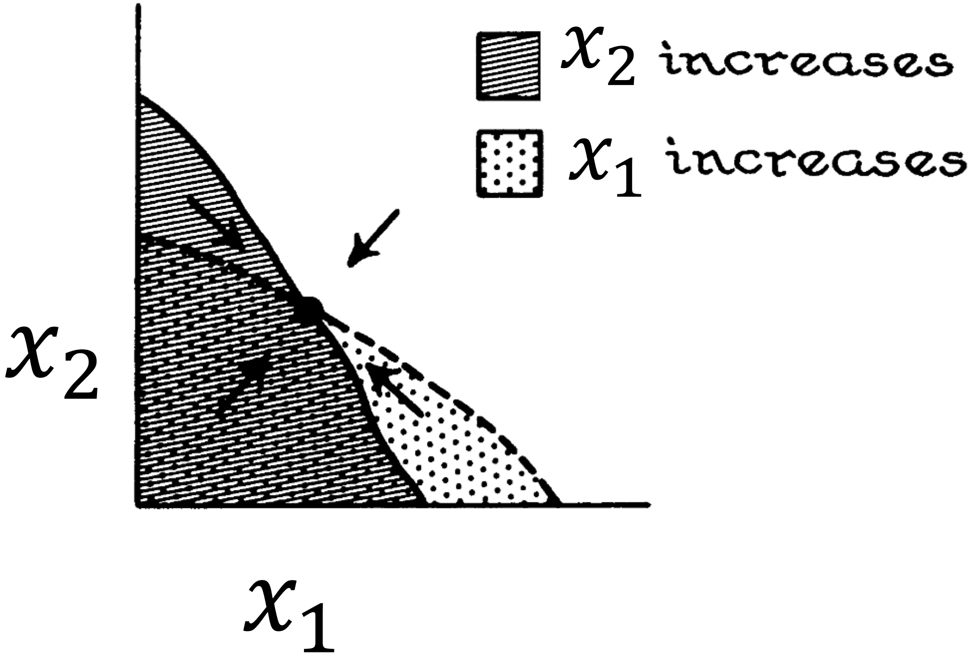


Gause 1934. *J Experimental Biology.*

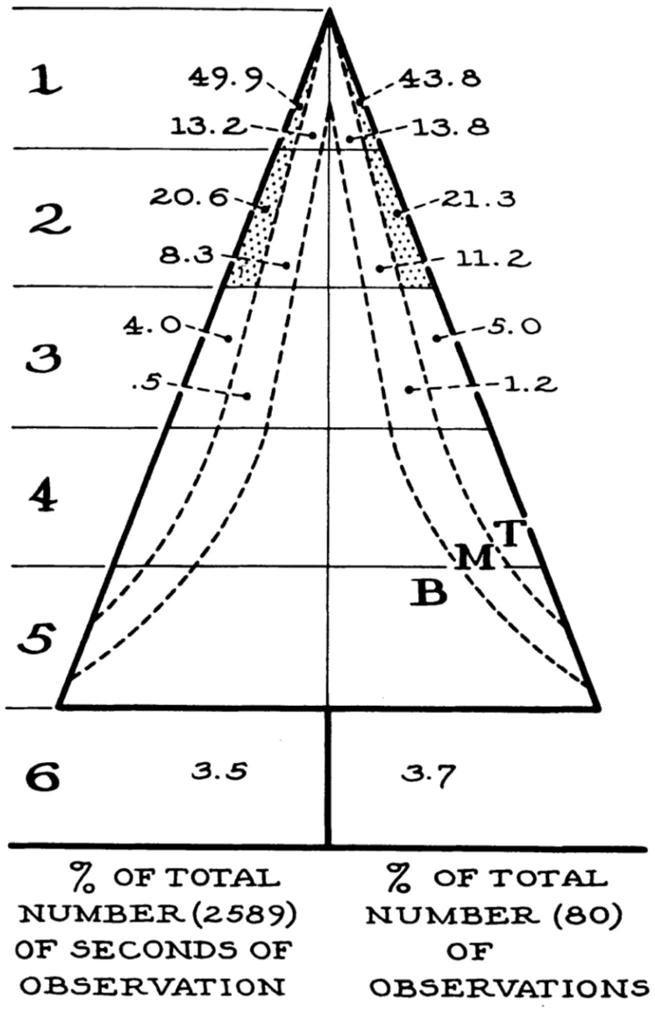
Gause 1935. *Science.*

Niche partitioning enables organisms to avoid competitive exclusion

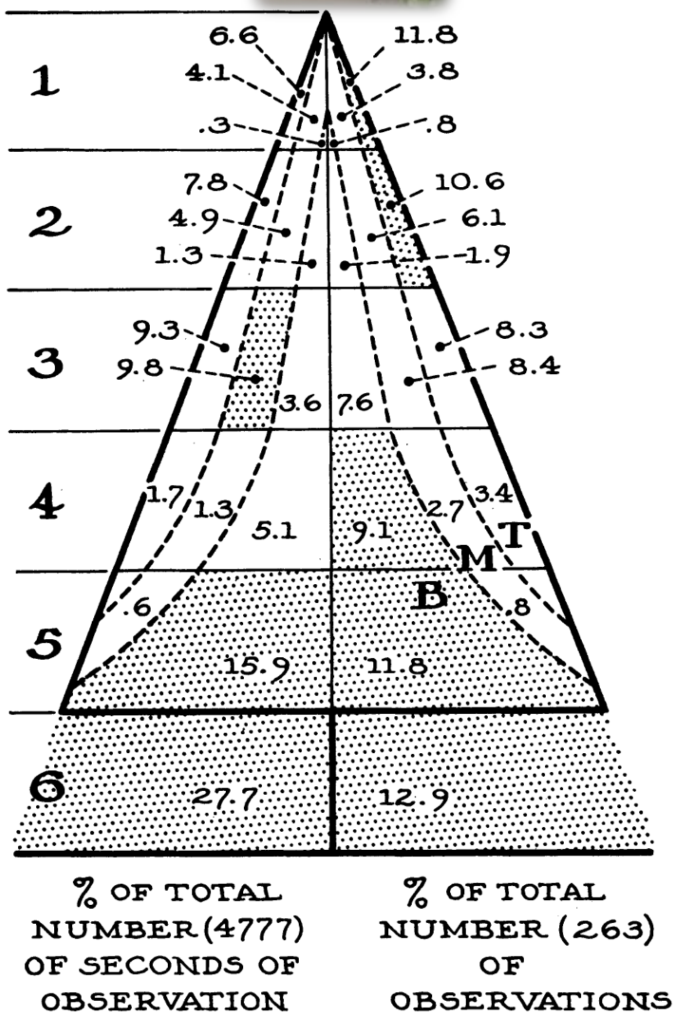
Niche: a match of a species to a specific environmental condition



Cape May Warbler



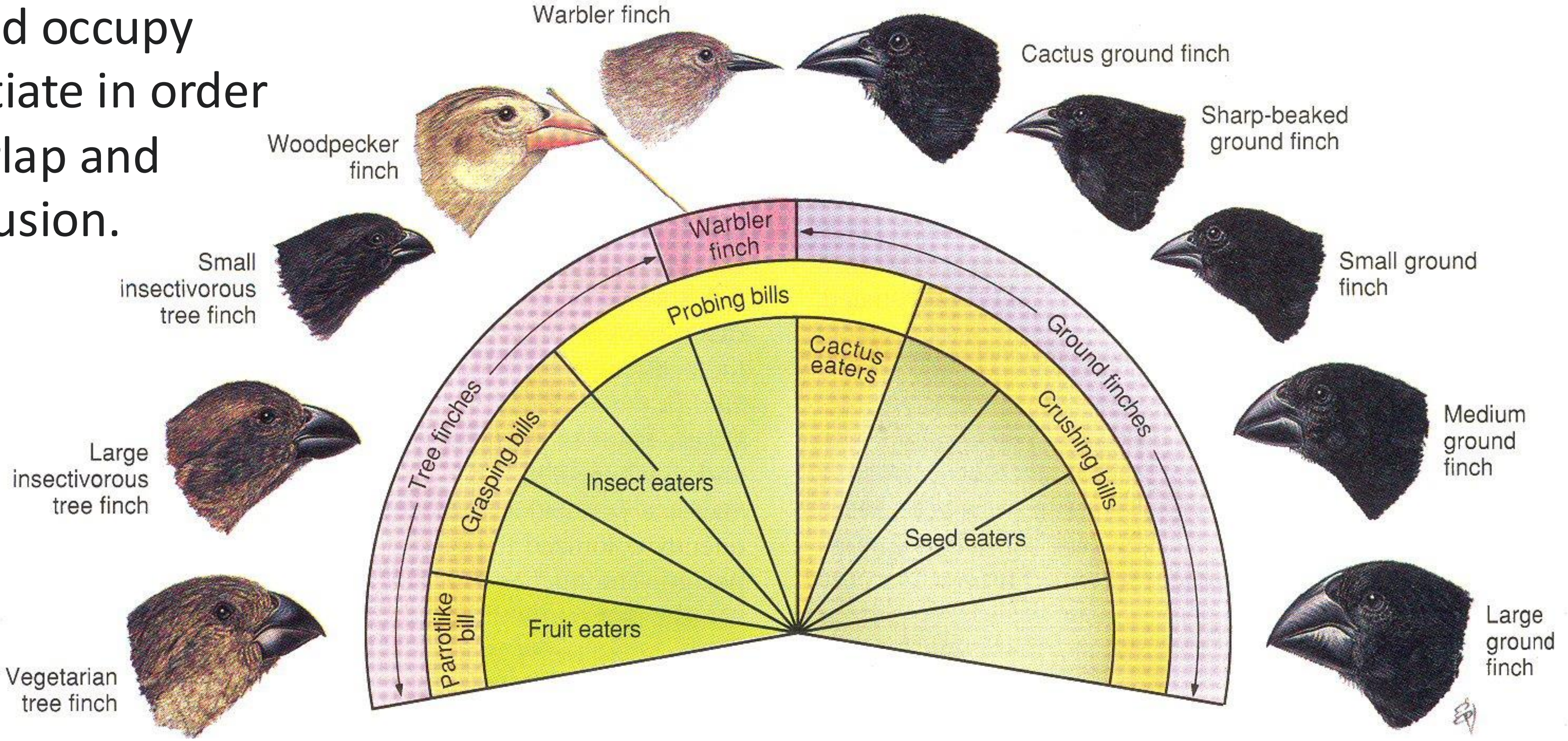
Myrtle Warbler



MacArthur 1968. *Ecology.*

Niche partitioning enables organisms to avoid competitive exclusion

Character displacement: similar species that live in the same geographical region and occupy similar niches differentiate in order to minimize niche overlap and avoid competitive exclusion.



Grant & Grant 2006. *Science.*

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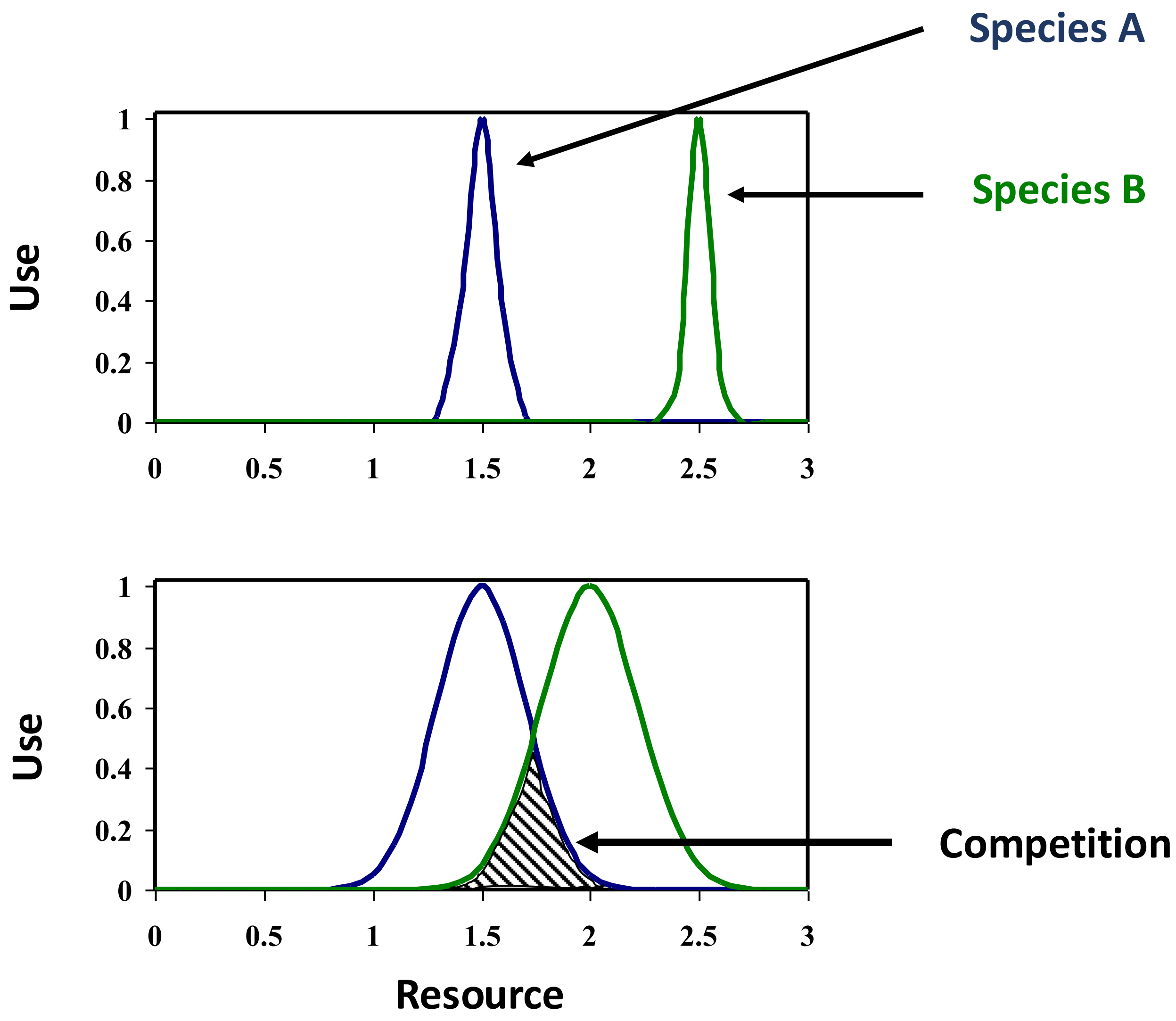
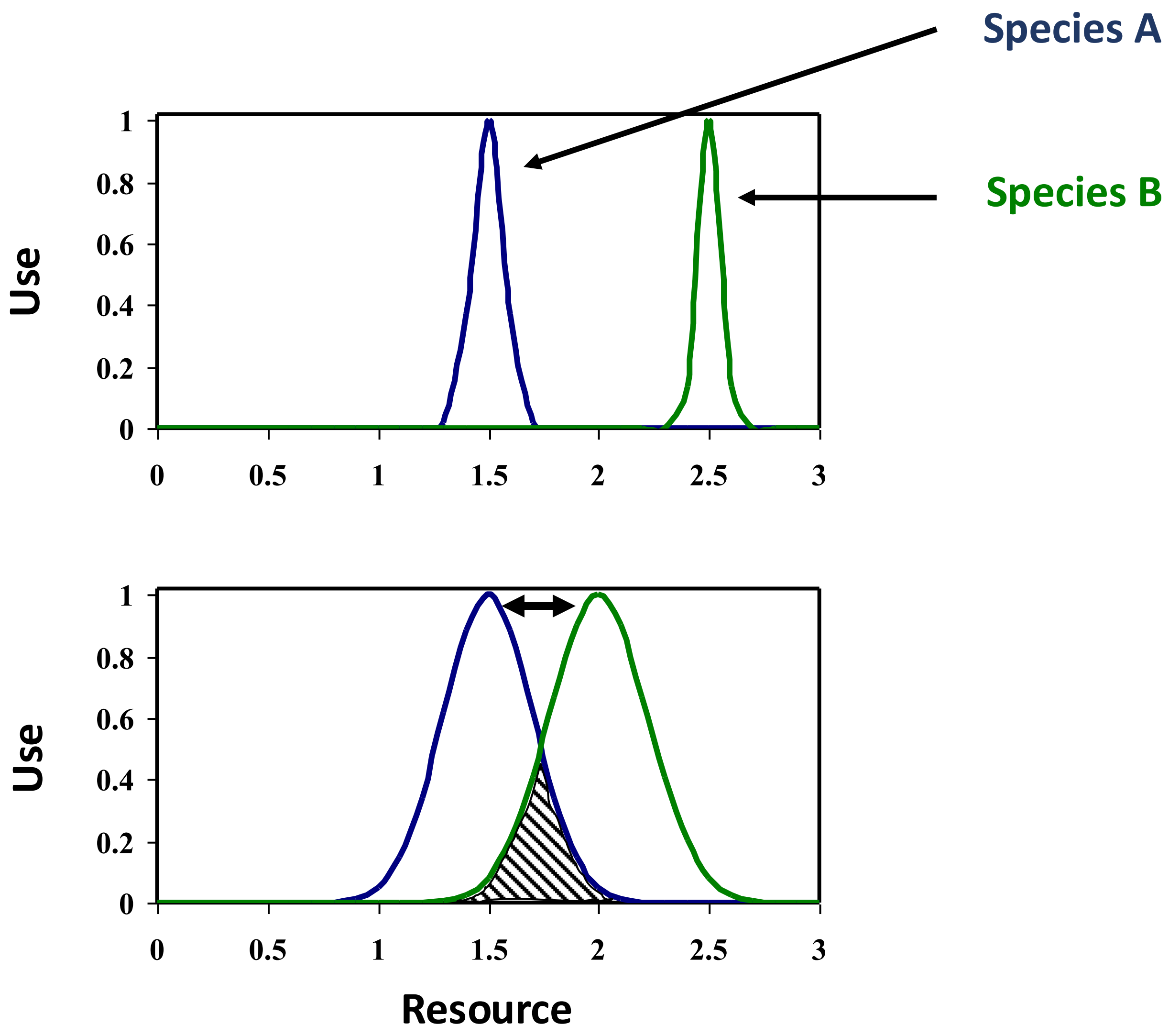
Grant & Grant 2006. *Science.*



When niches overlap, competition results

Niche partitioning enables organisms to avoid competitive exclusion

Character displacement: similar species that live in the same geographical region and occupy similar niches differentiate in order to minimize niche overlap and avoid competitive exclusion.

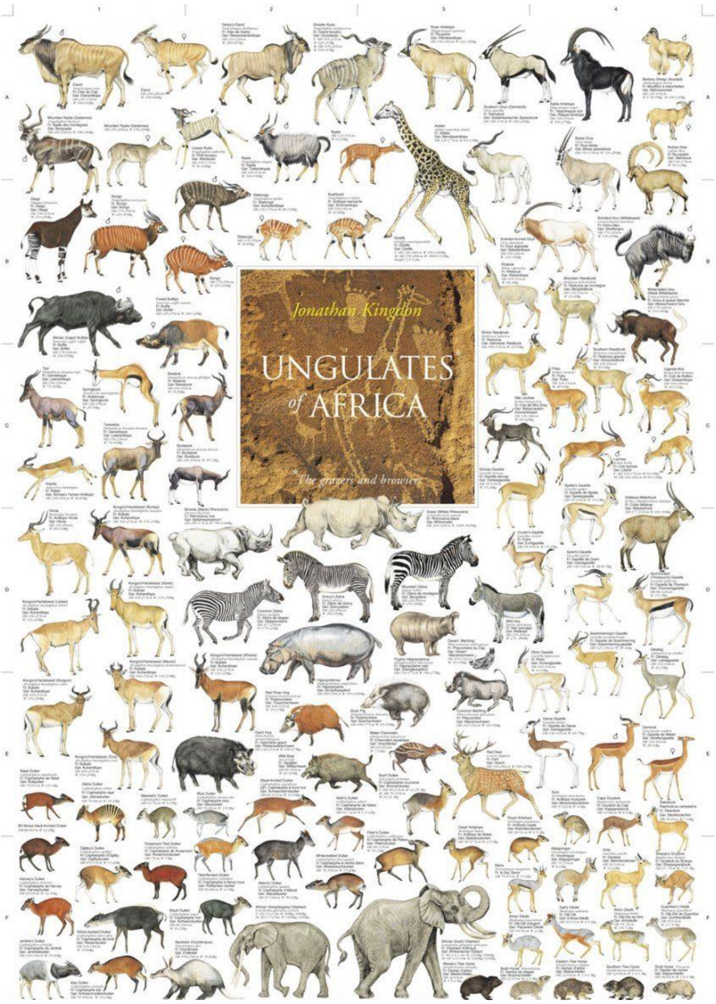


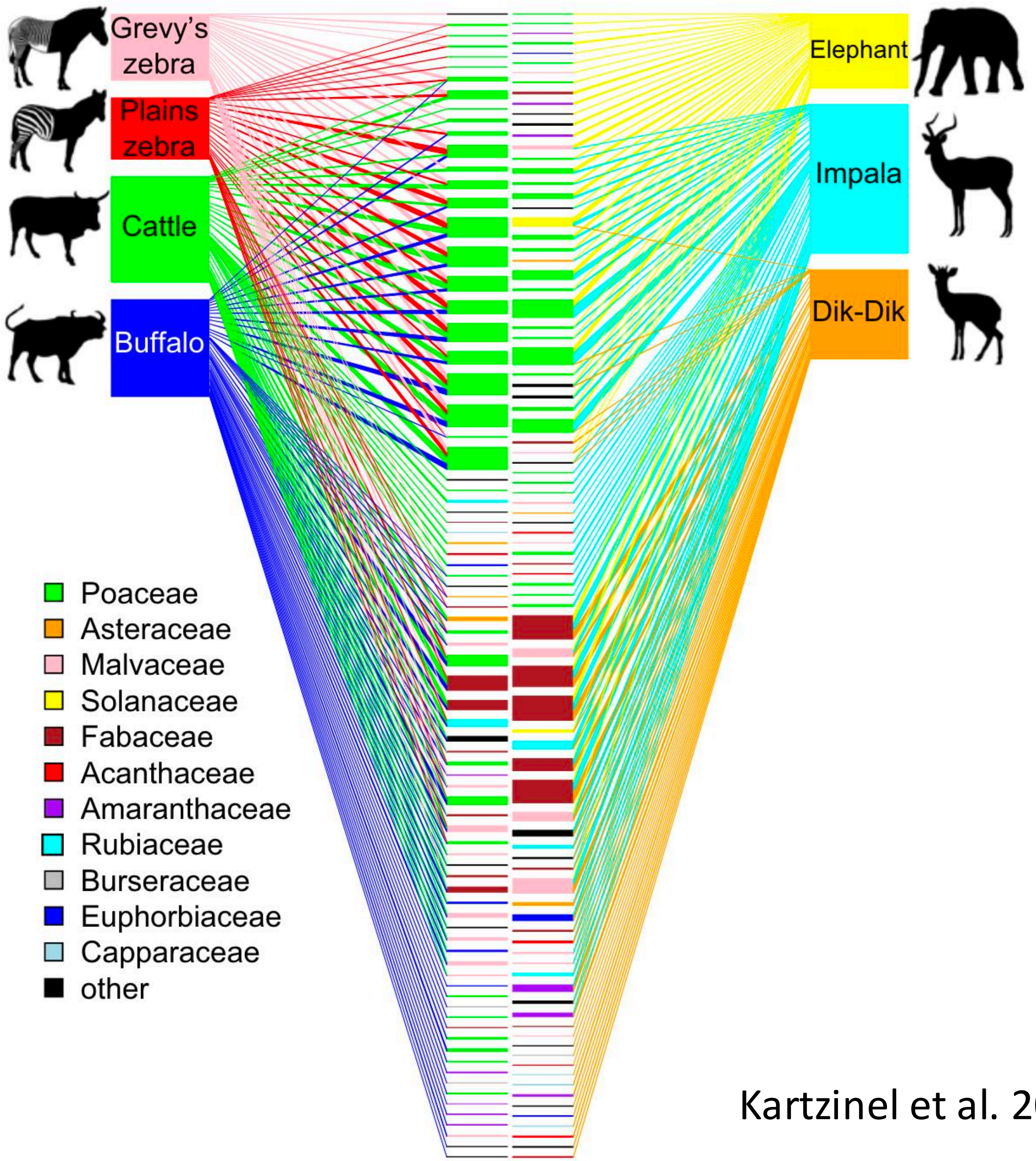
Character displacement forces niches apart.

Grant & Grant 2006. *Science.*

Niche partitioning enables organisms to avoid competitive exclusion

Often 10-25 large mammalian herbivores coexisting in the same African savanna!

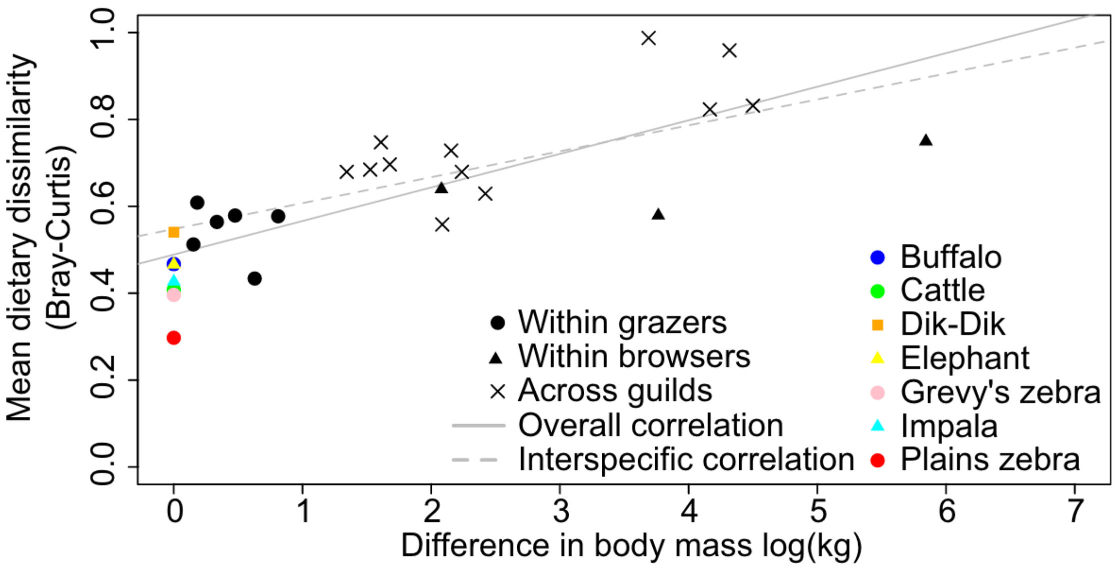


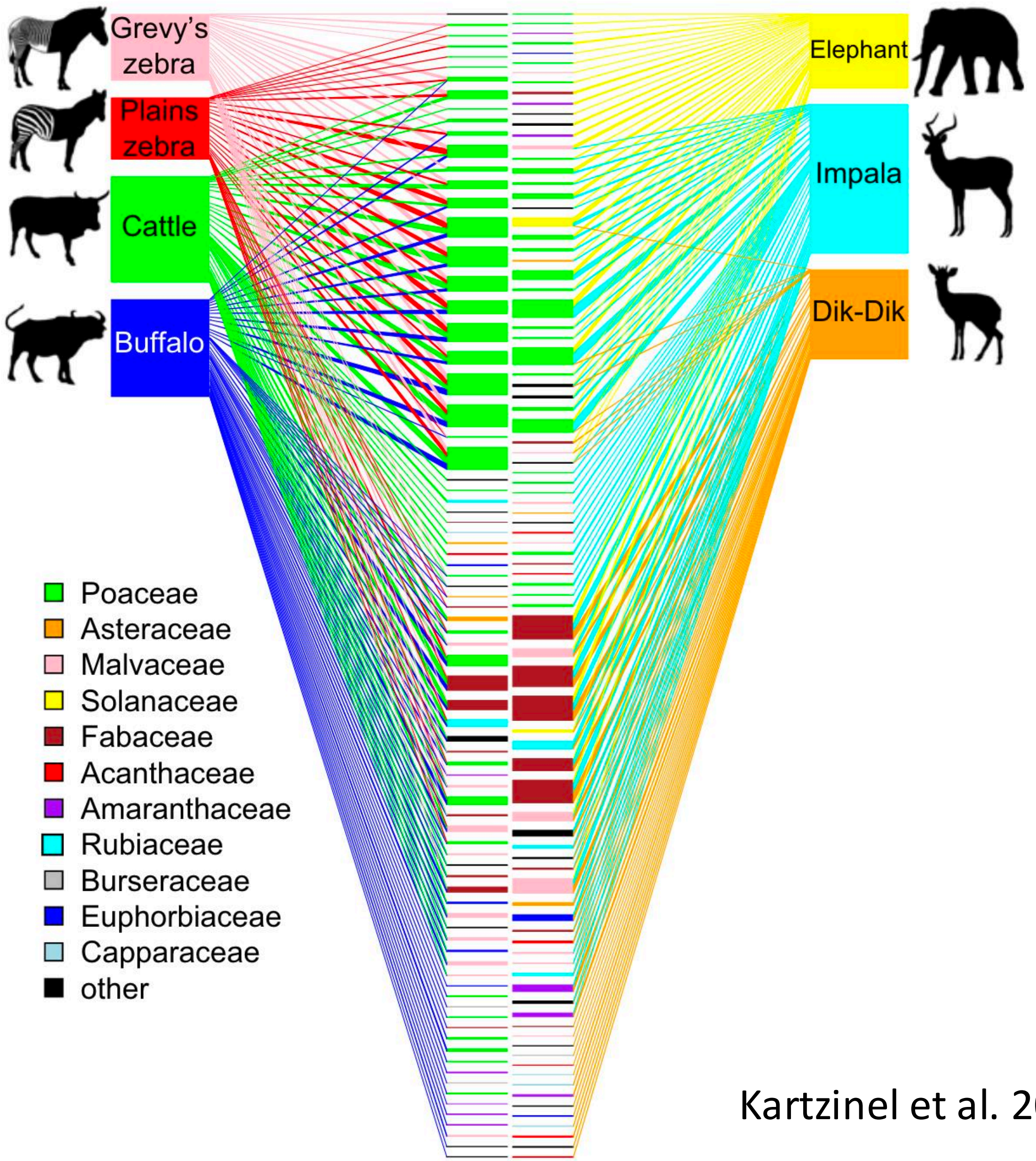


Kartzinel et al. 2015. *PNAS.*

Niche partitioning enables organisms to avoid competitive exclusion

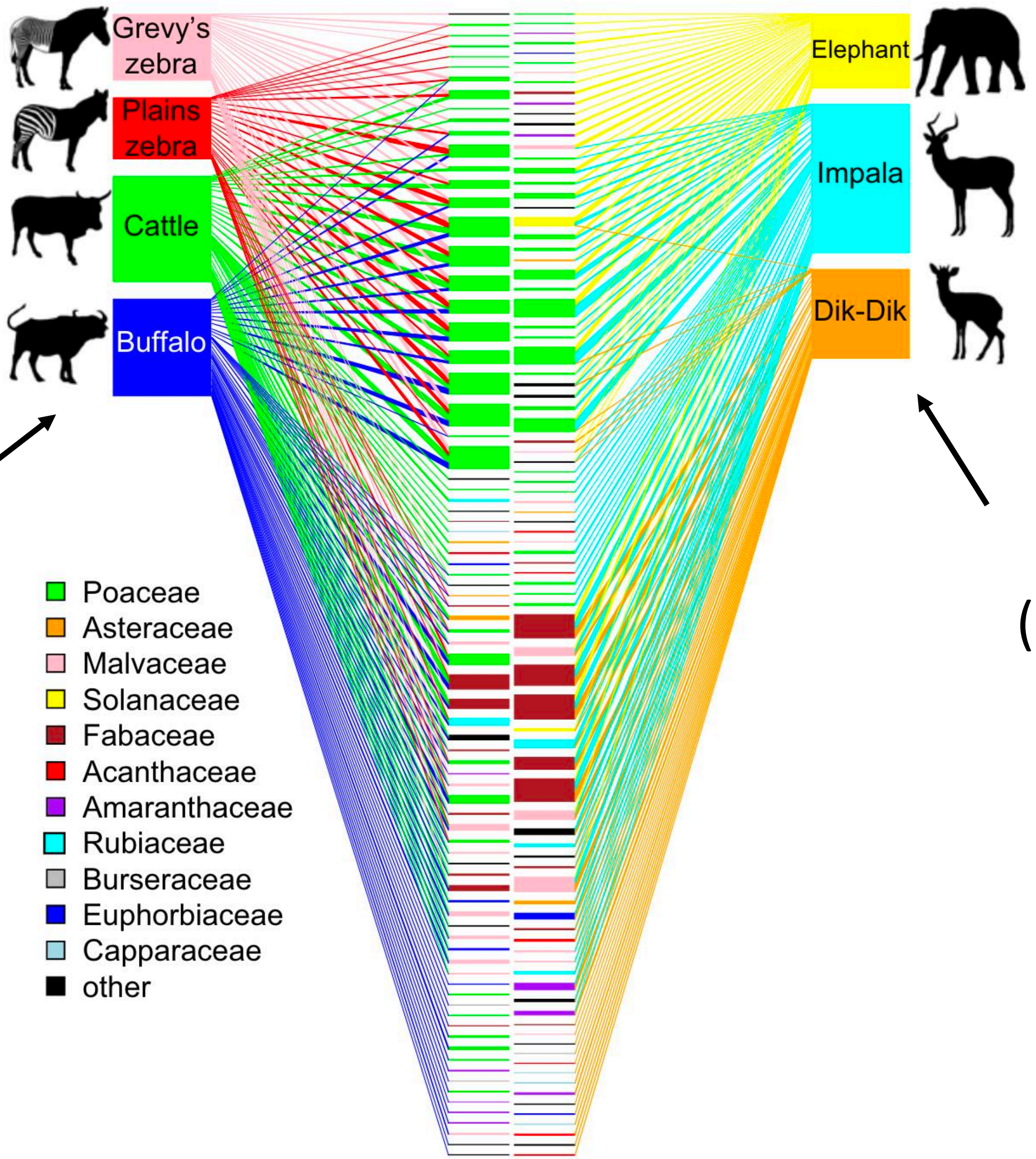
Dietary overlap is higher in similar-sized mammals





Kartzinel et al. 2015. *PNAS.*

Consumer resource partitioning in the African savanna



Grazer (generalist)

Browser (specialist)

Kartzinel et al. 2015. *PNAS.*