Fundamentals of Ecology

Week 7, Ecology Lecture 4

Cara Brook

February 16, 2023

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- <u>Source-sink theory</u> describes how some subpopulations within a metapopulation act as ‘sources’ where births outpace deaths, while others act as ‘sinks’ where deaths outpace births.
- The term ‘<u>ecological trap</u>’ describes a species’ preference for poor quality habitat. When sinks outnumber sources, metapopulation dynamics can actually drive a population to extinction as individuals flock to these traps.

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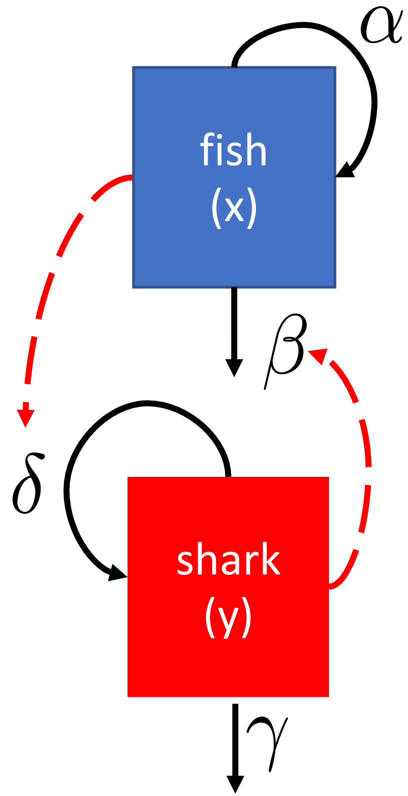
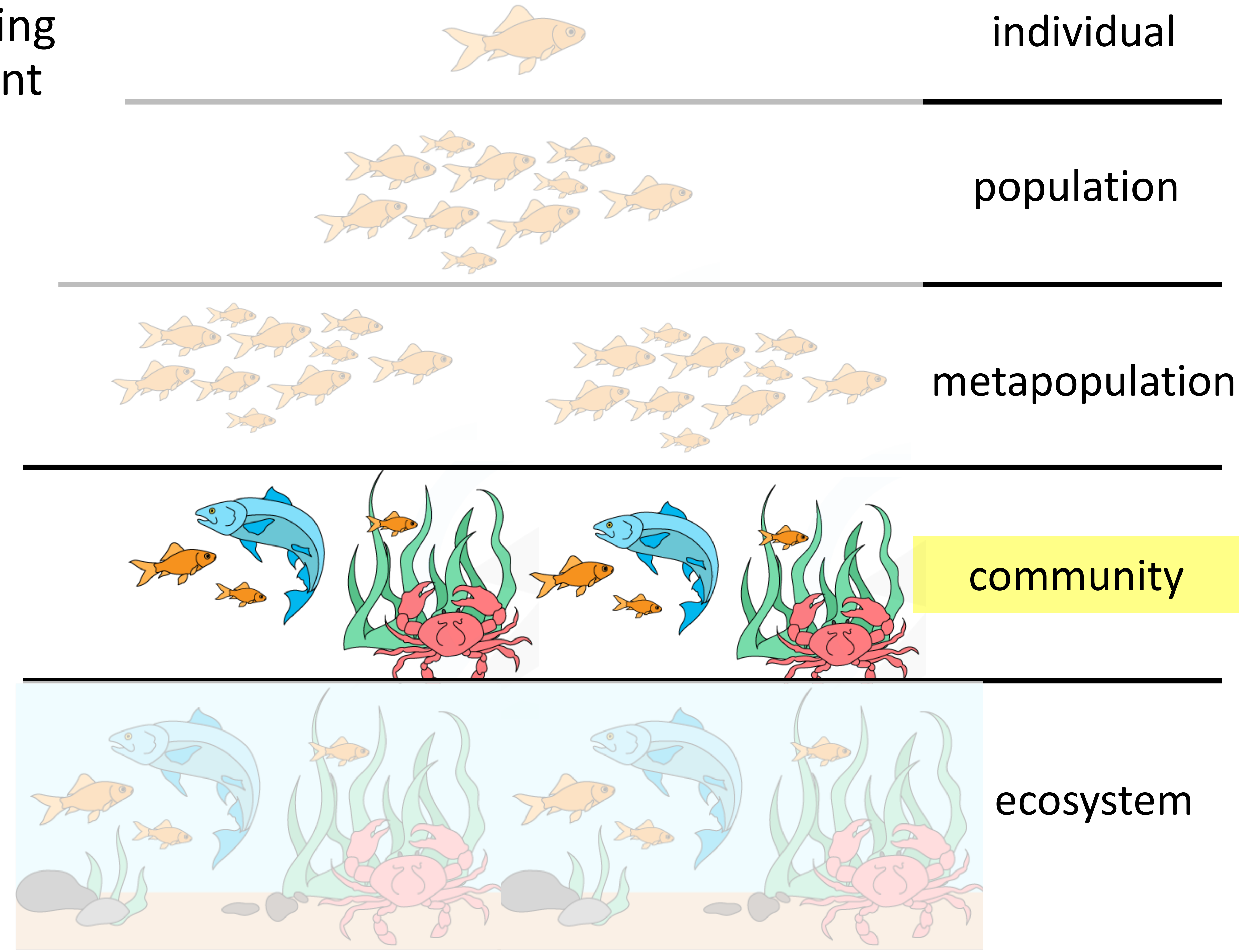
- <u>Trophic cascades</u> occur when species indirectly interact across 3 trophic levels. We discussed several famous examples: Pisaster, CA sea otter, Yellowstone wolf, wildebeest

Community = interacting populations of different species



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



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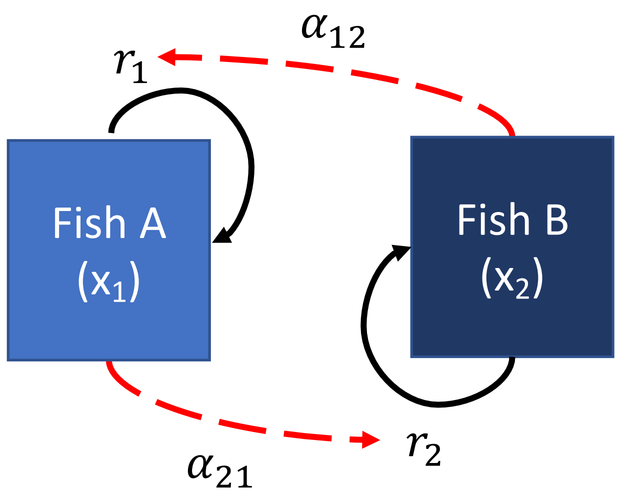

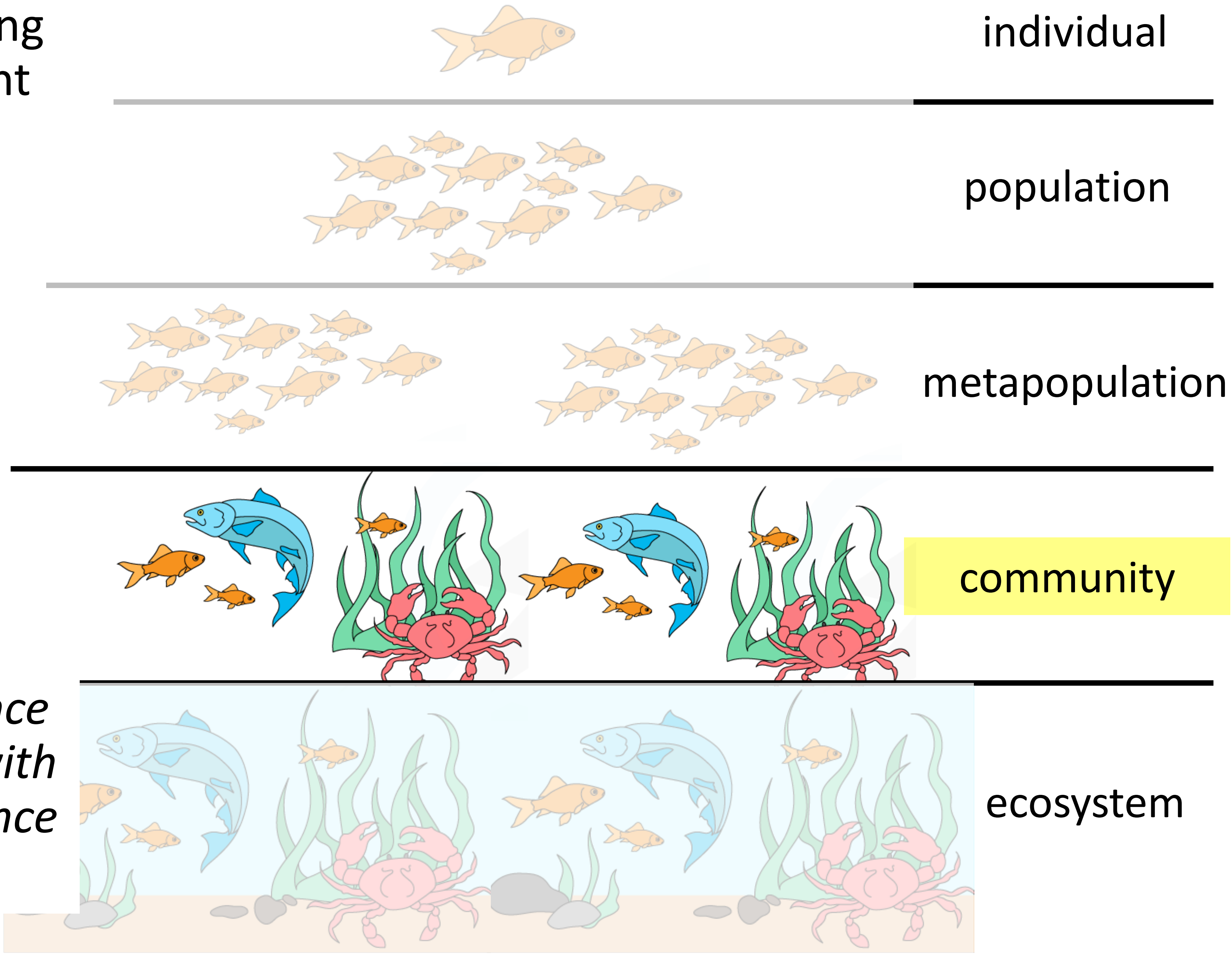

*How does the abundance of **fish species A** vary with changes in the abundance of **fish species B**?*

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

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

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intraspecies competition of species 2

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

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

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

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Four equilibria at:

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

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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.

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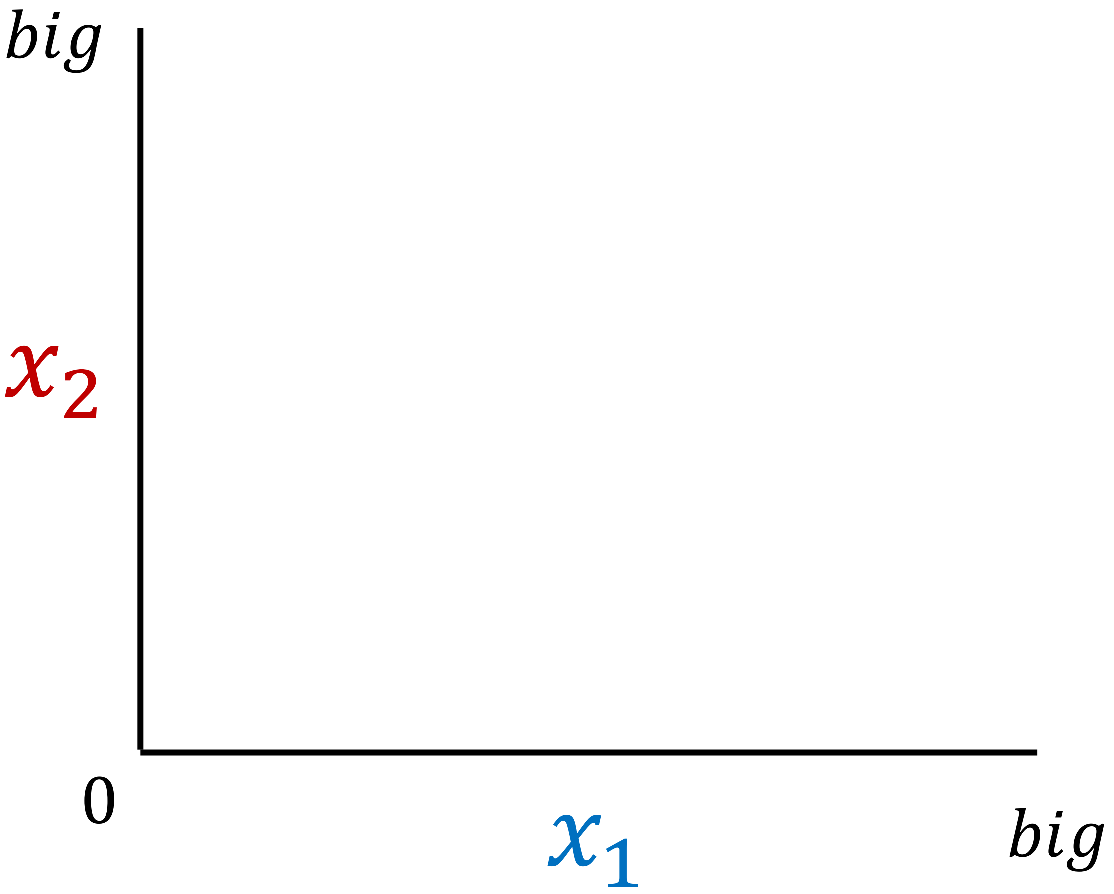

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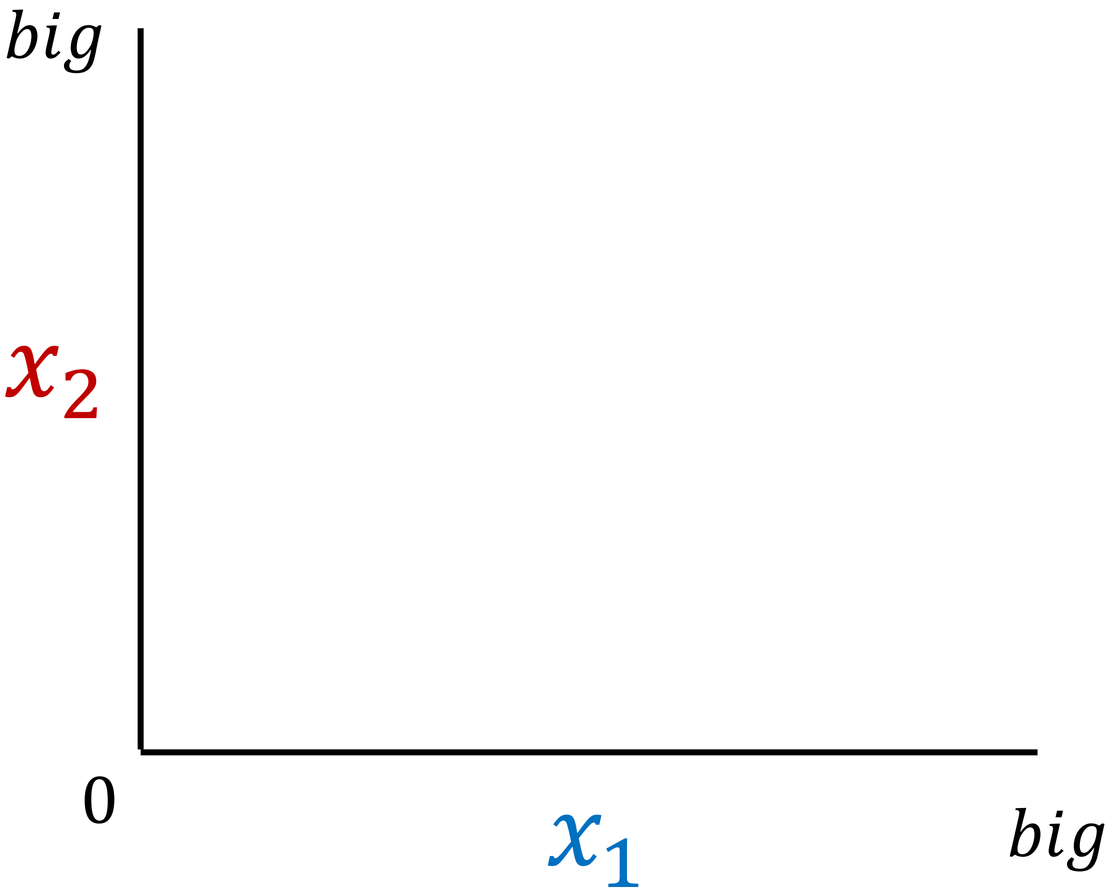

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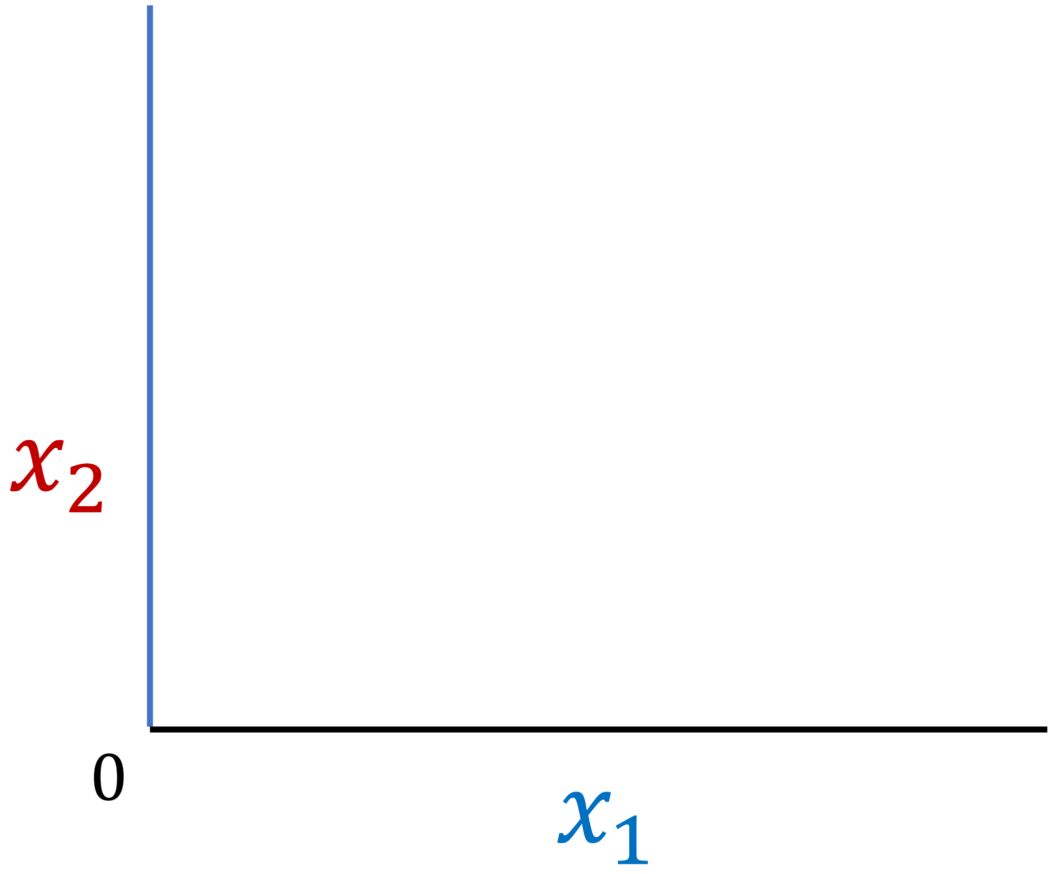

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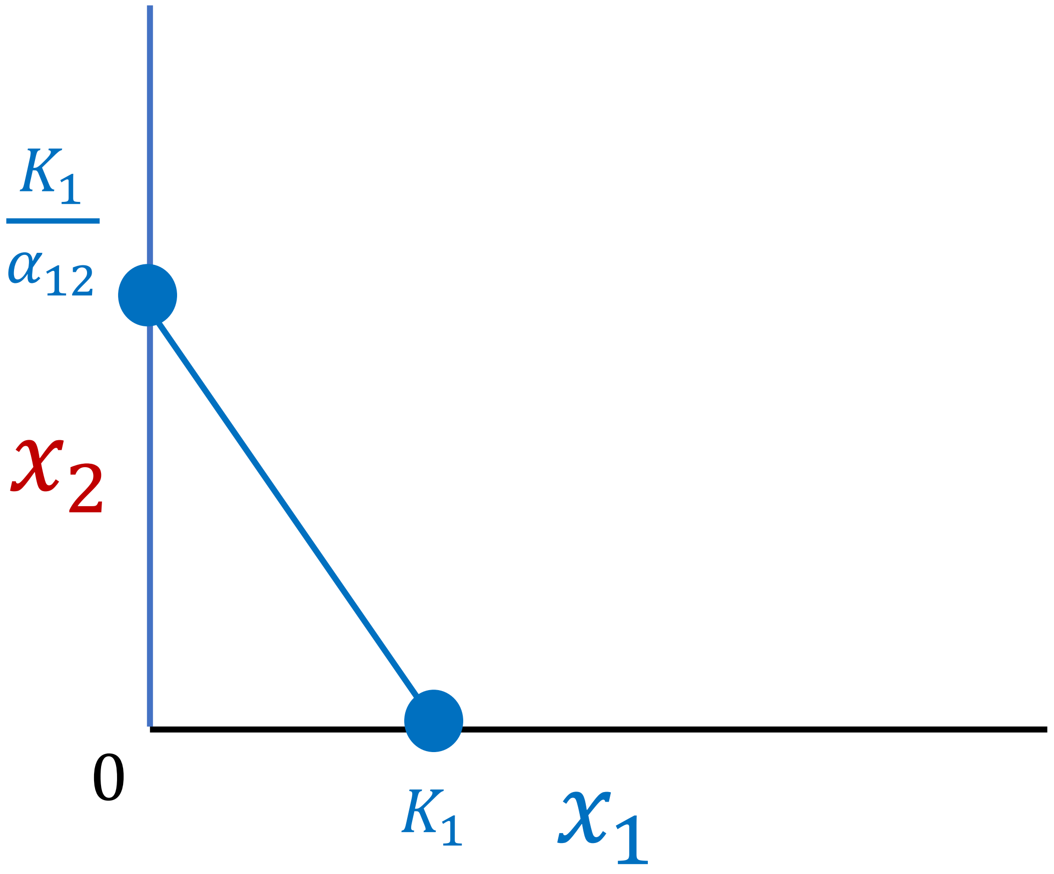
first nullcline at $x_1 = 0$

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



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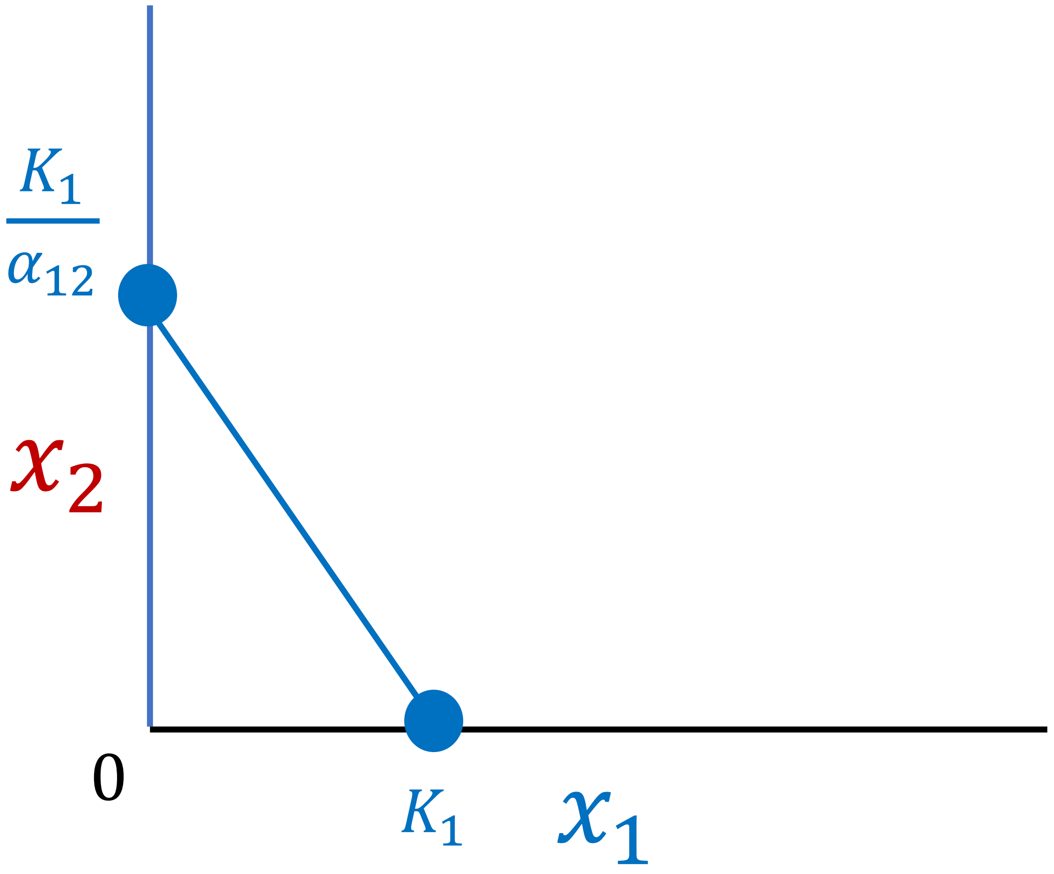

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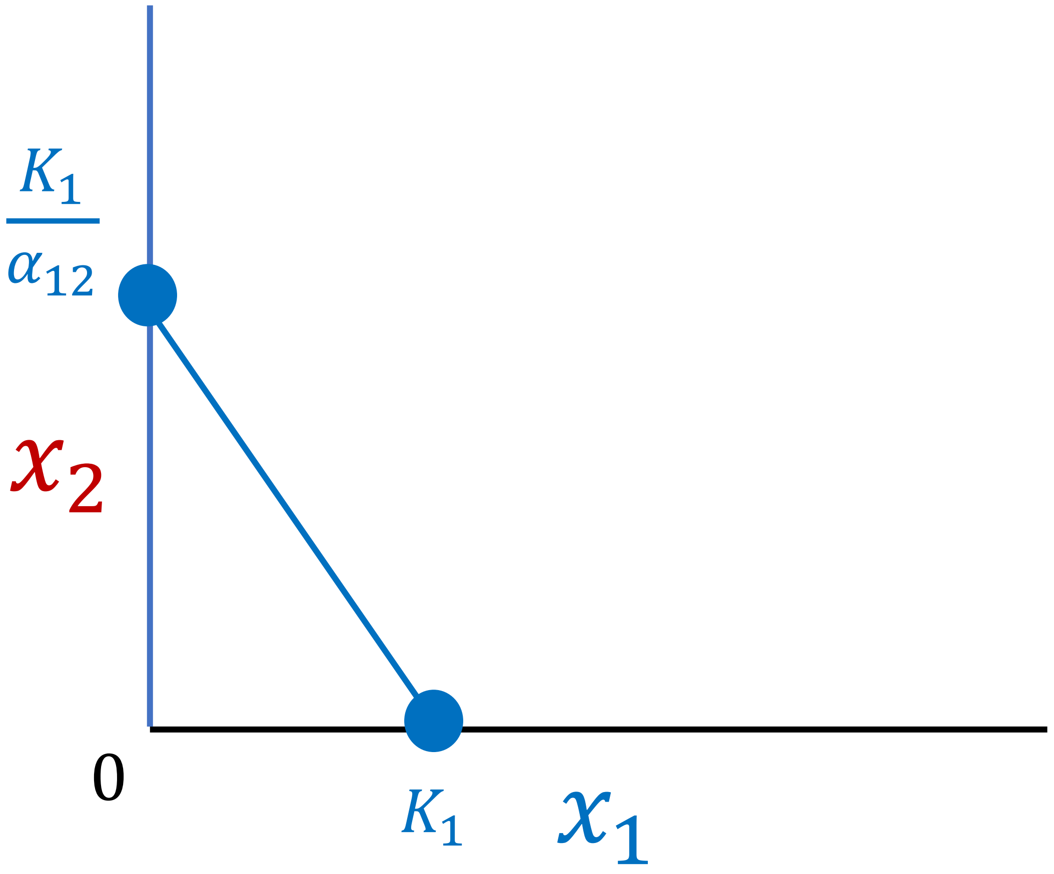

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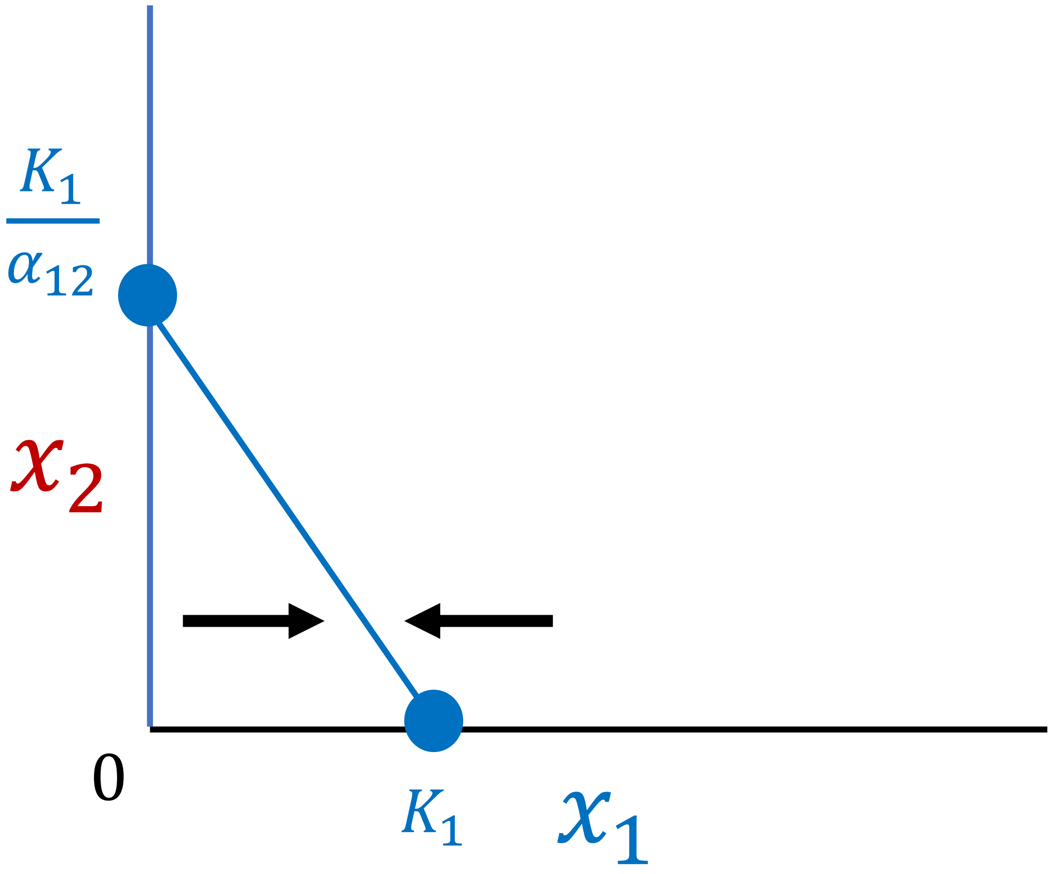

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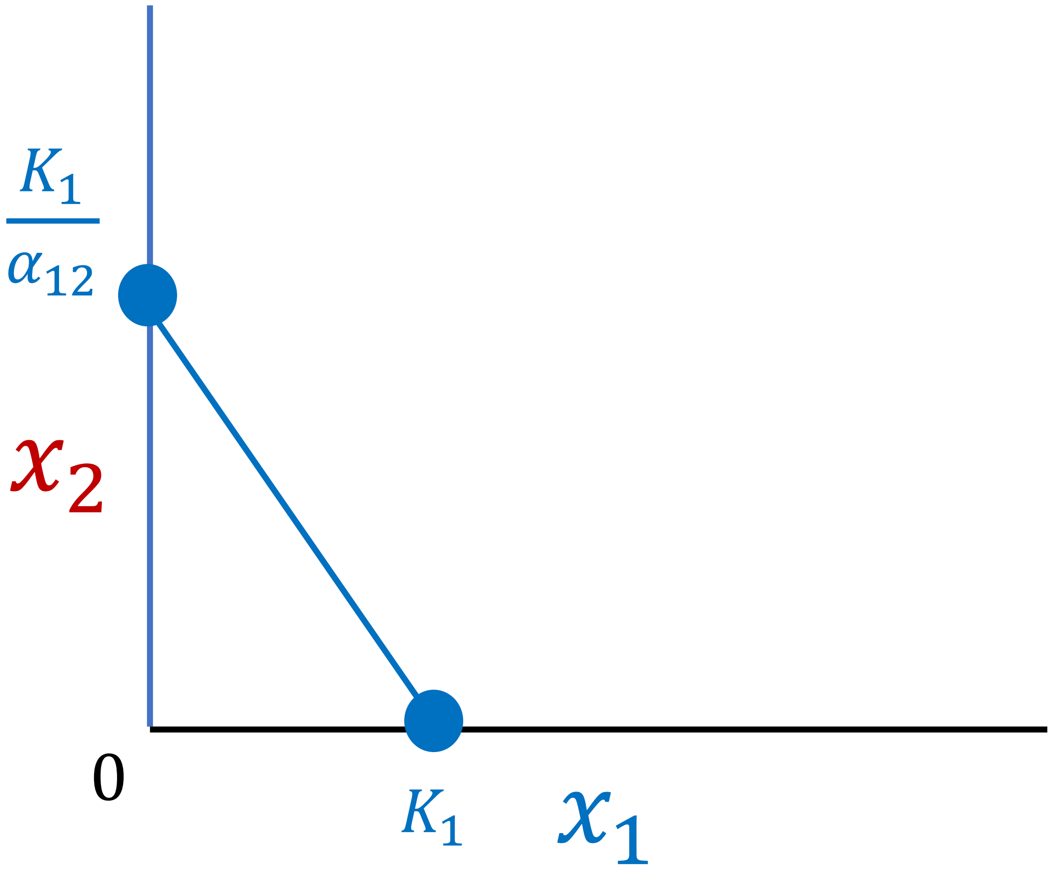

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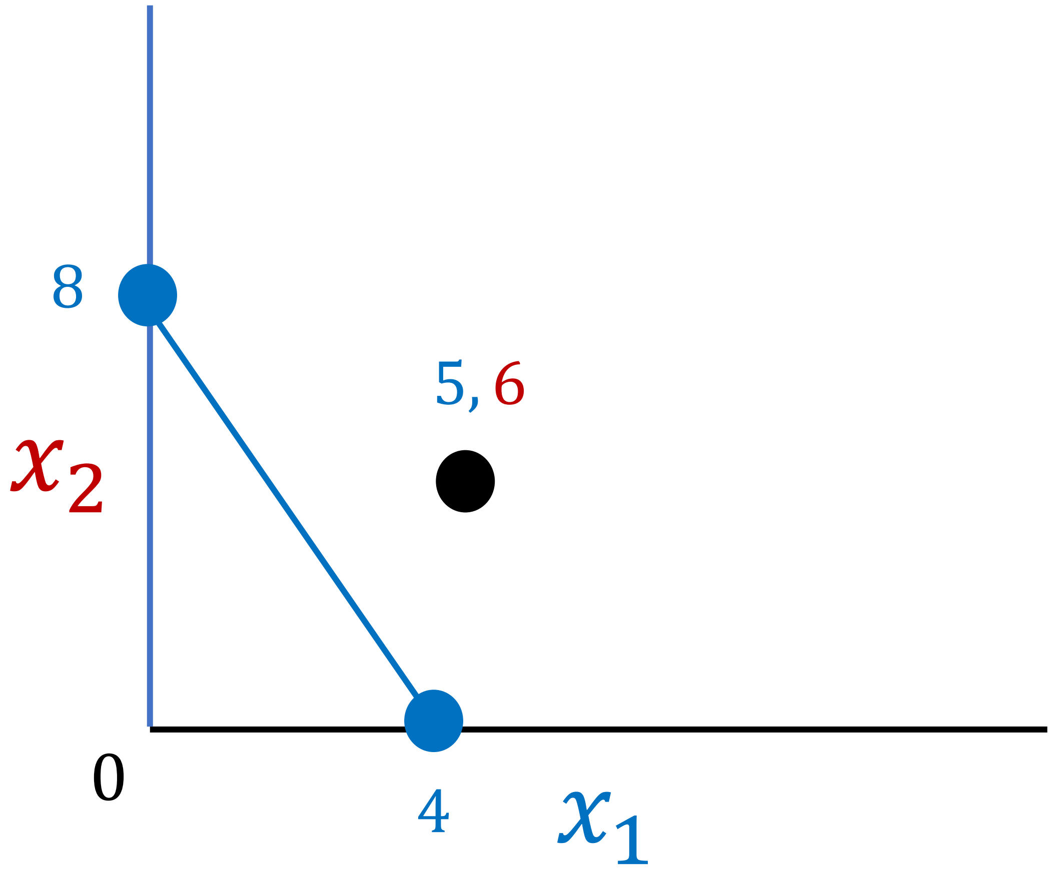

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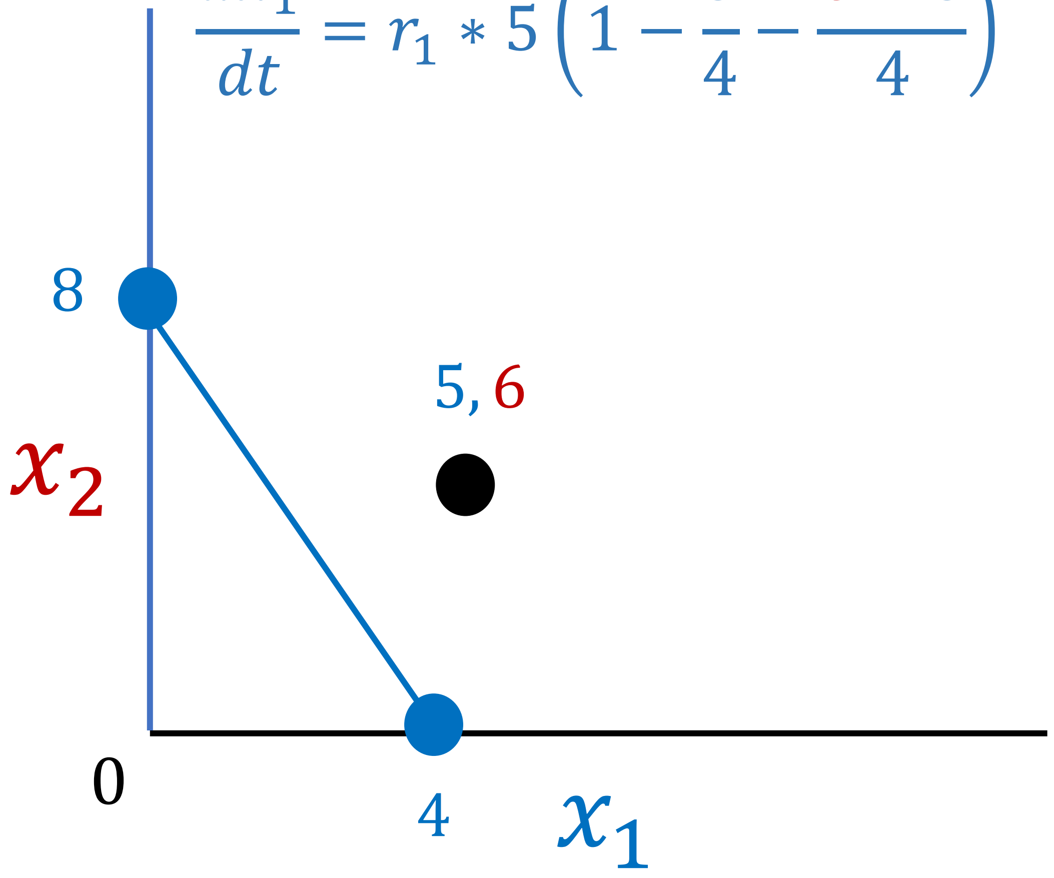

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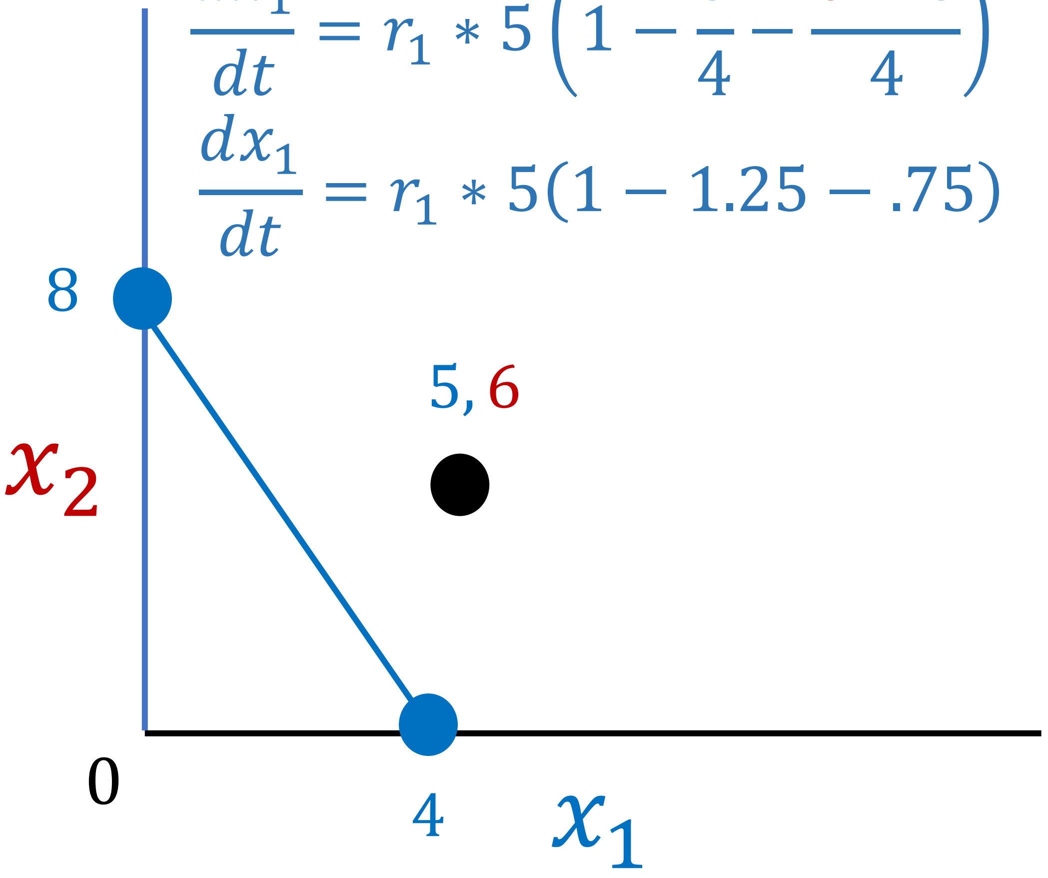

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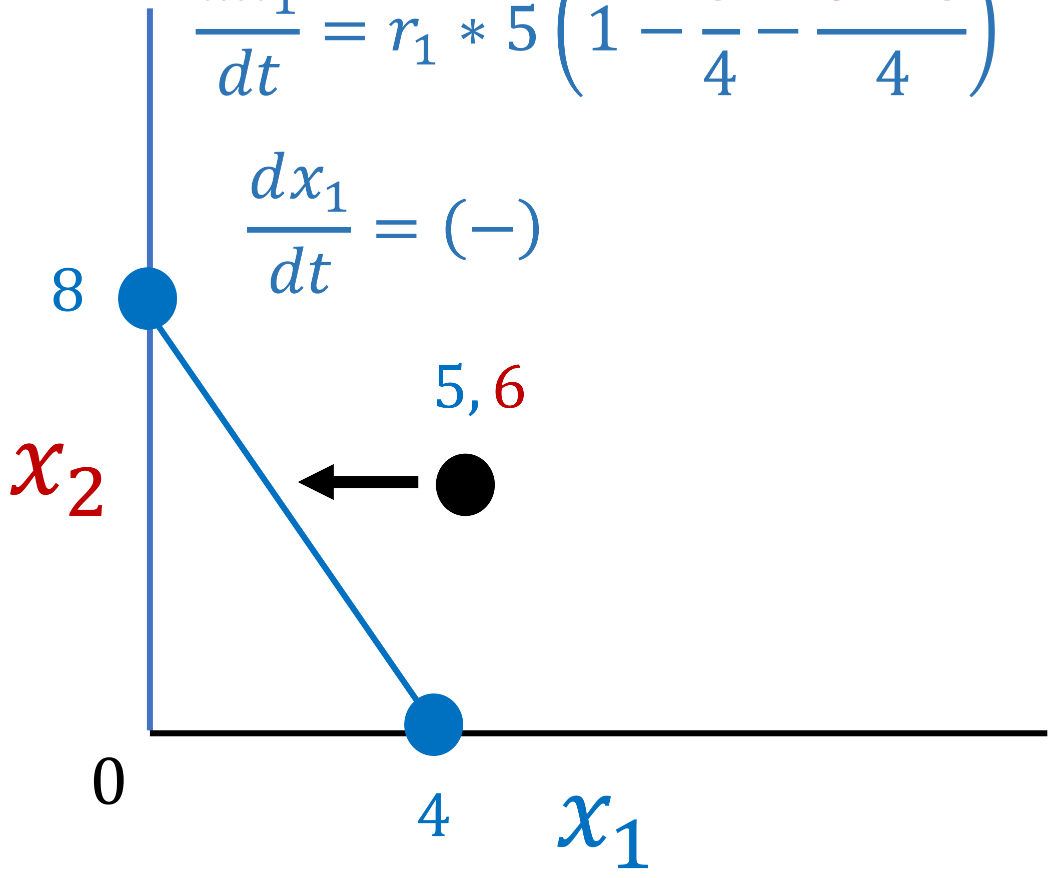

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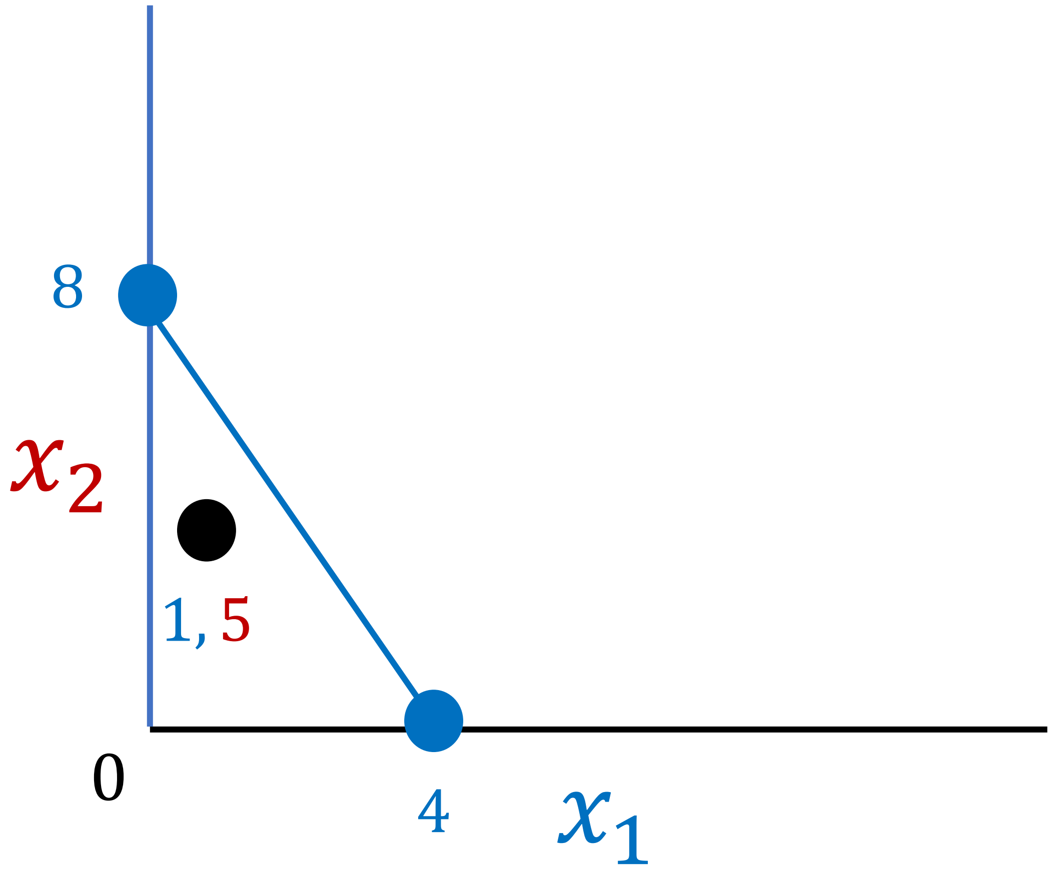

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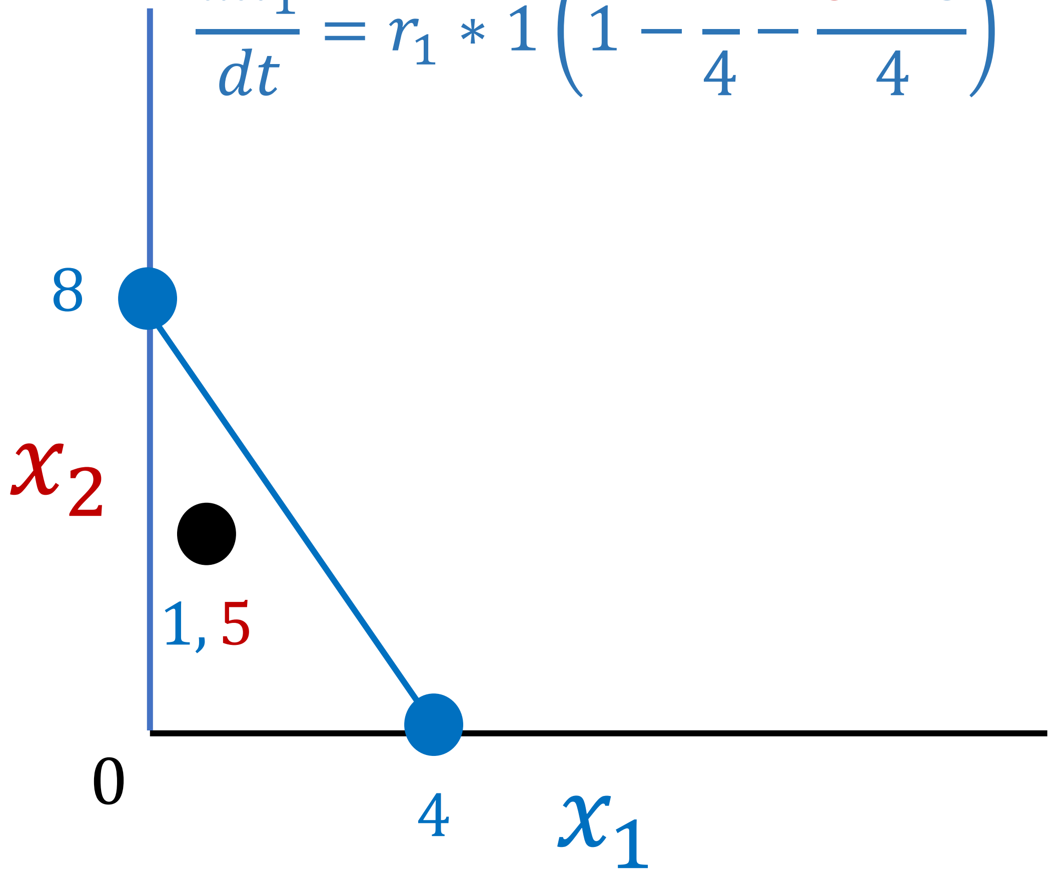

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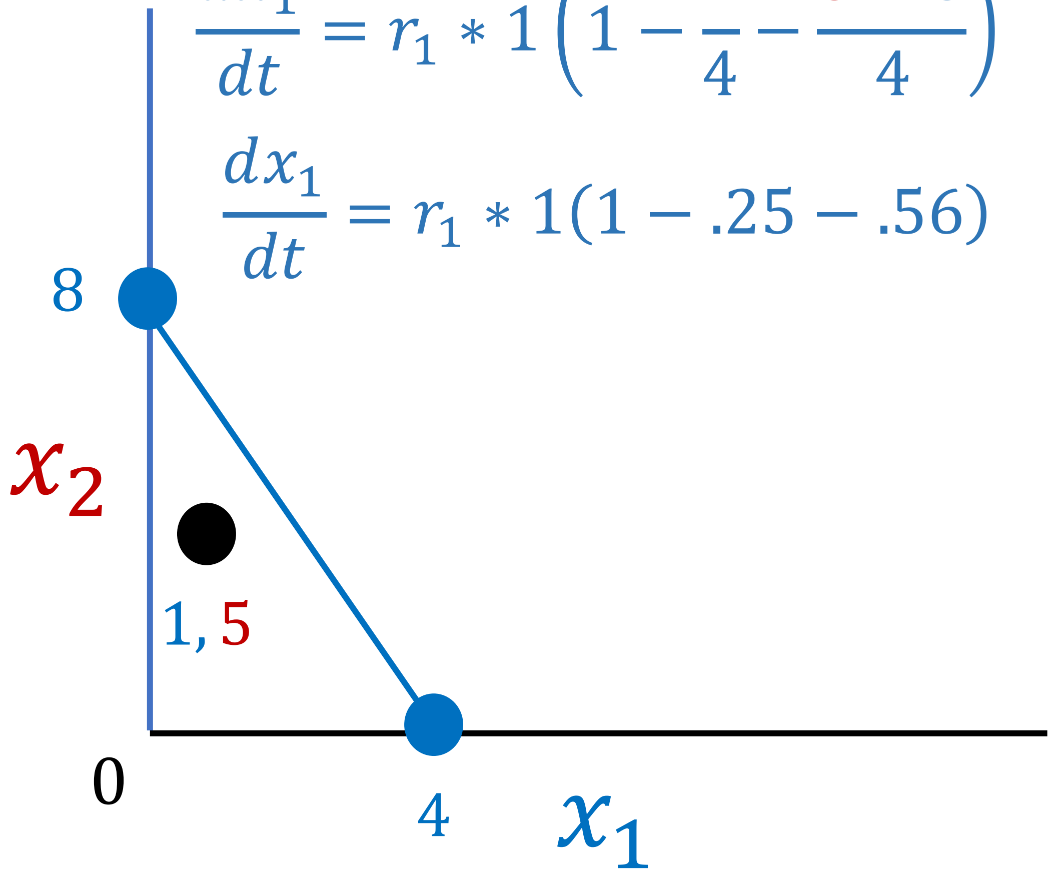
- You can also test it by solving $\frac{dx_1}{dt}$ for different values!
- $K_1 = 4 \,; \alpha_{12} = .5$

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

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

$$\frac{dx_1}{dt} = r_1 * 1(1 - .25 - .56)$$



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

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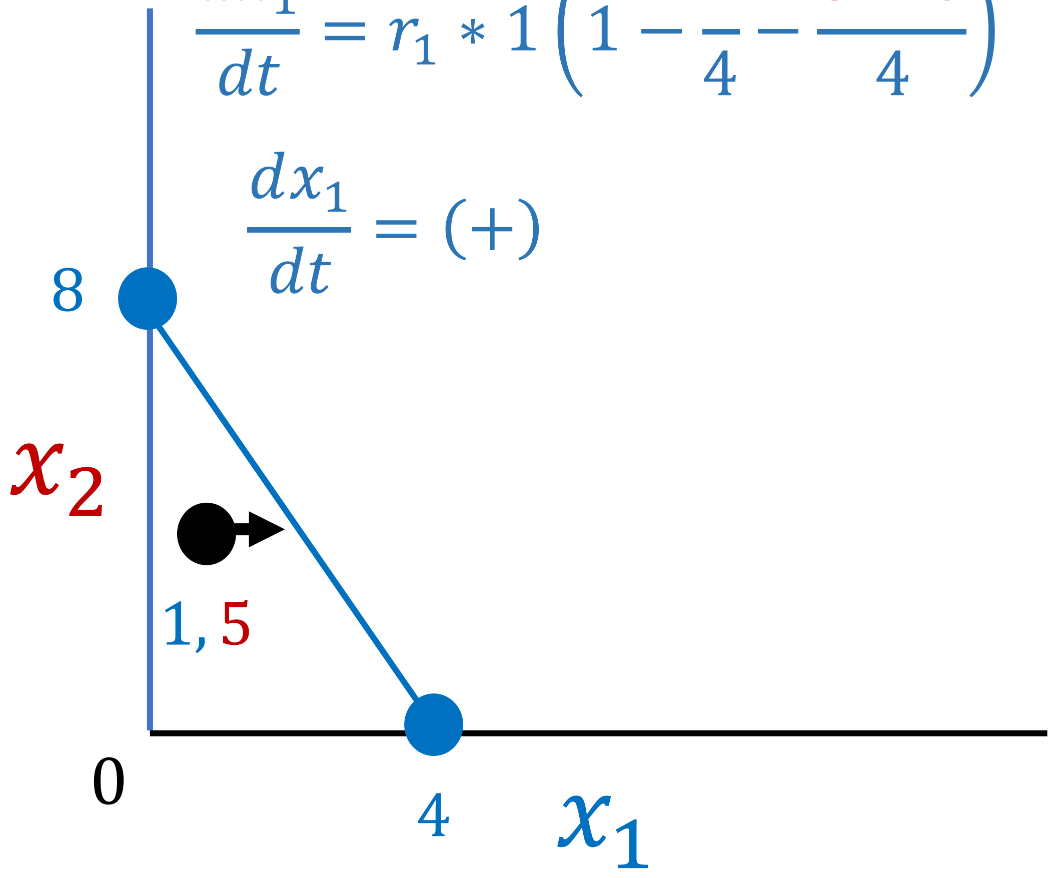
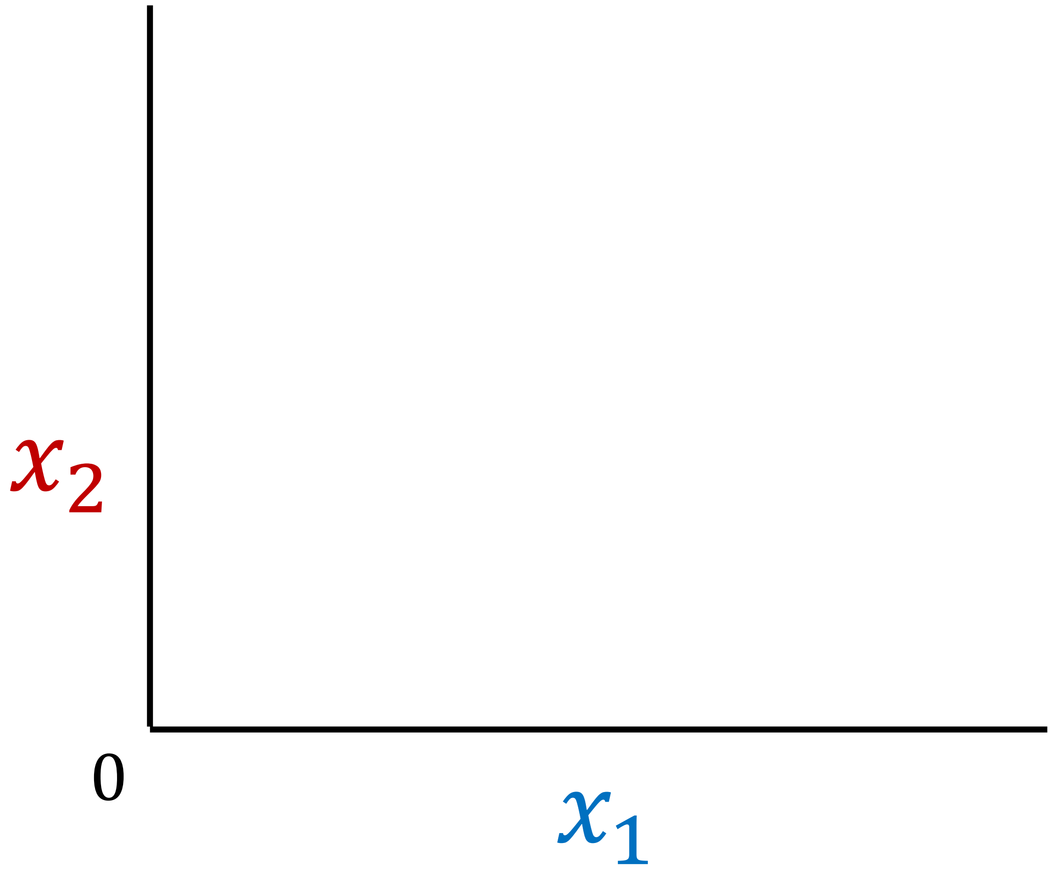


Nullclines (or **isoclines**) of the **Lotka-Volterra competition model**

These are the lines that correspond to the conditions when one species is not changing!

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



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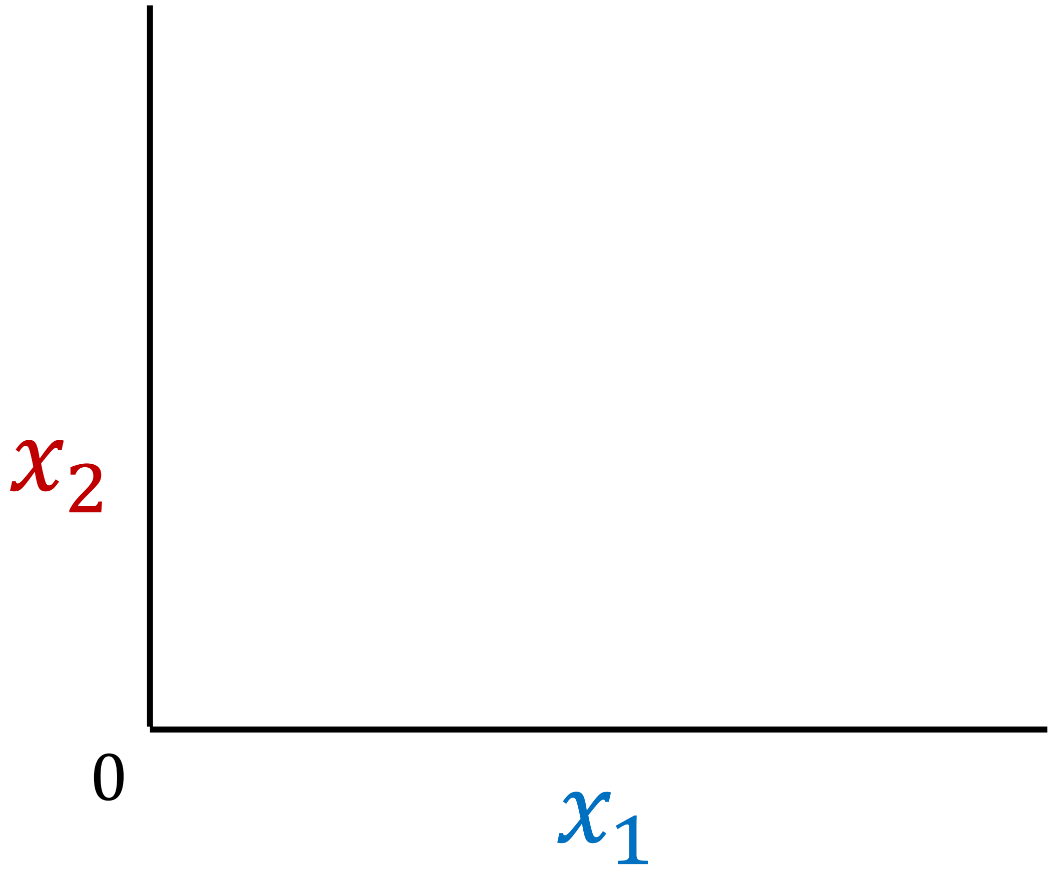

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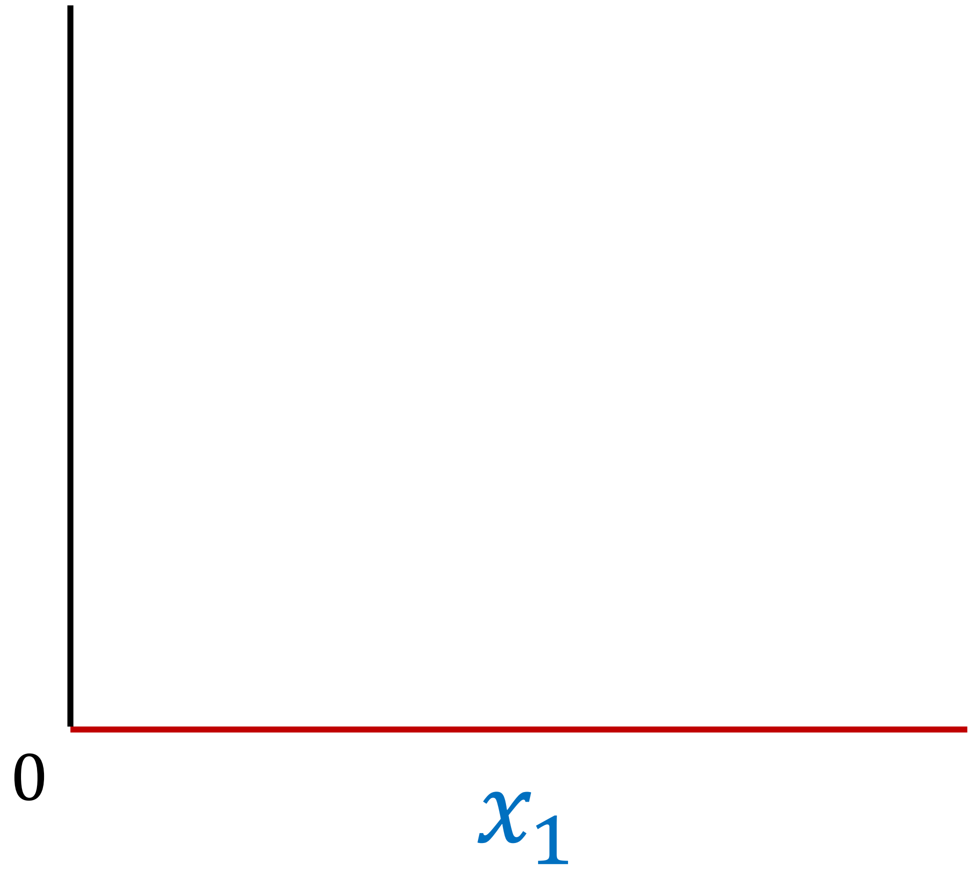

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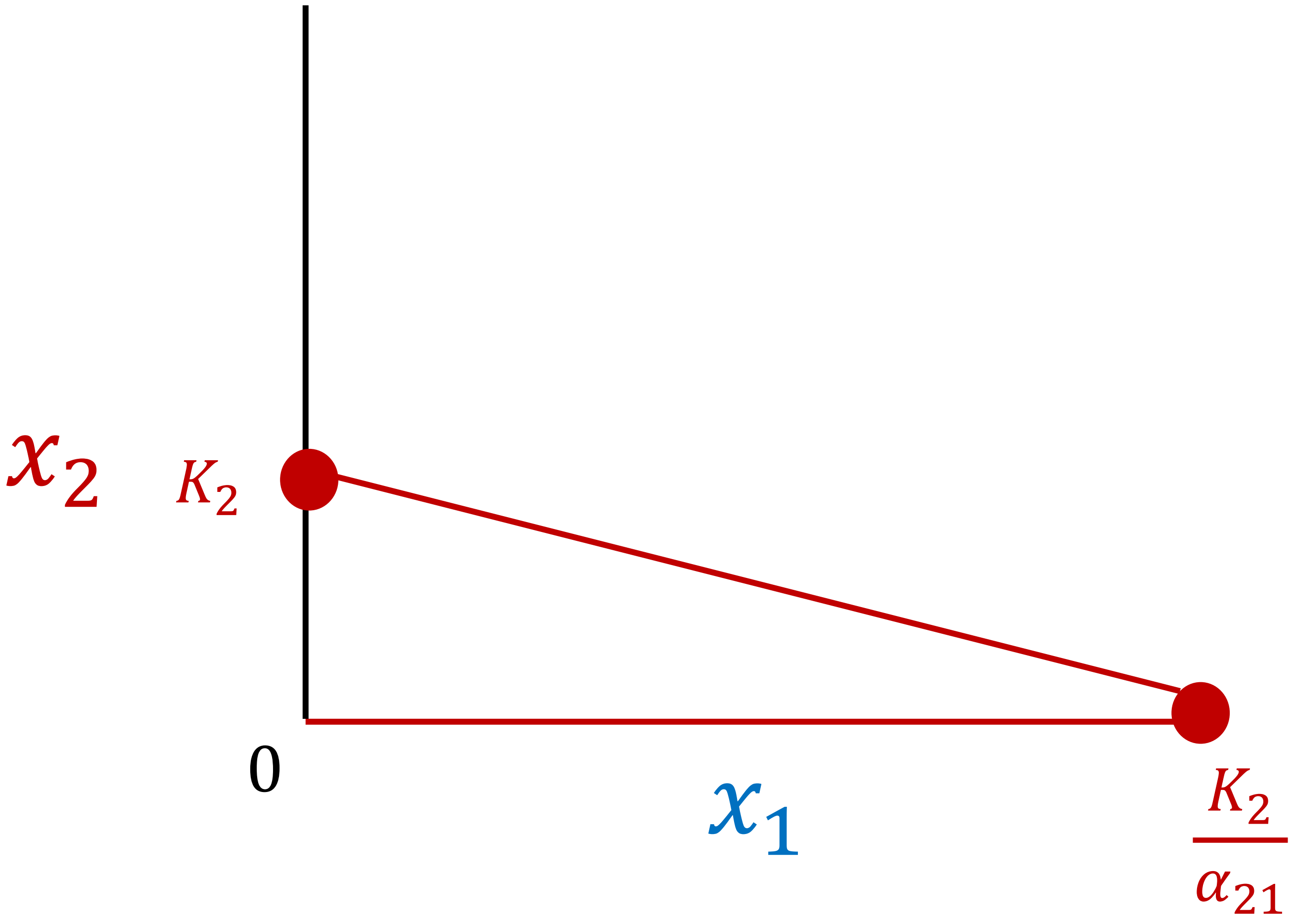
first nullcline at $x_2 = 0$

second nullcline at $x_2 = -\alpha_{2a} x_1 + K_2$



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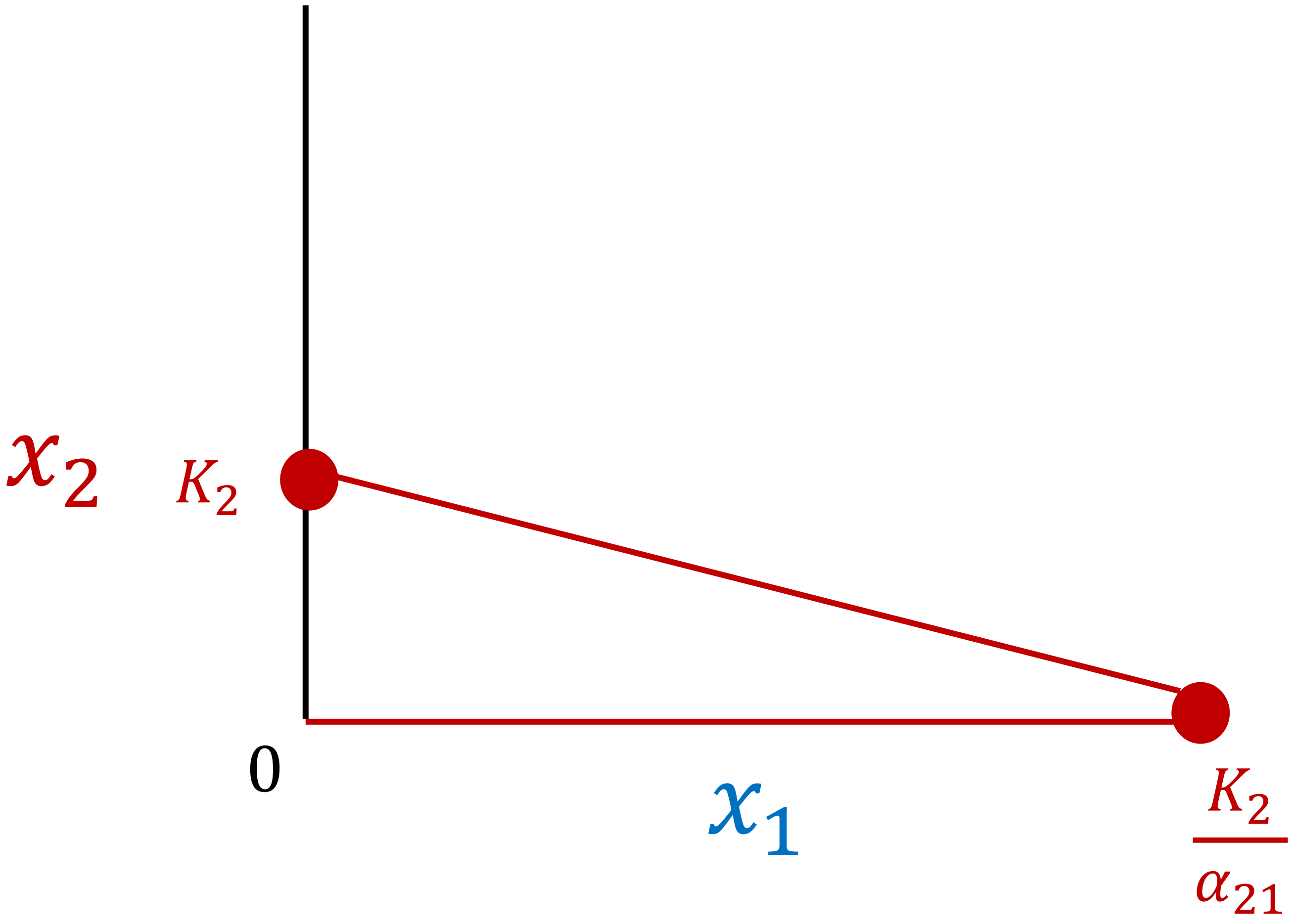

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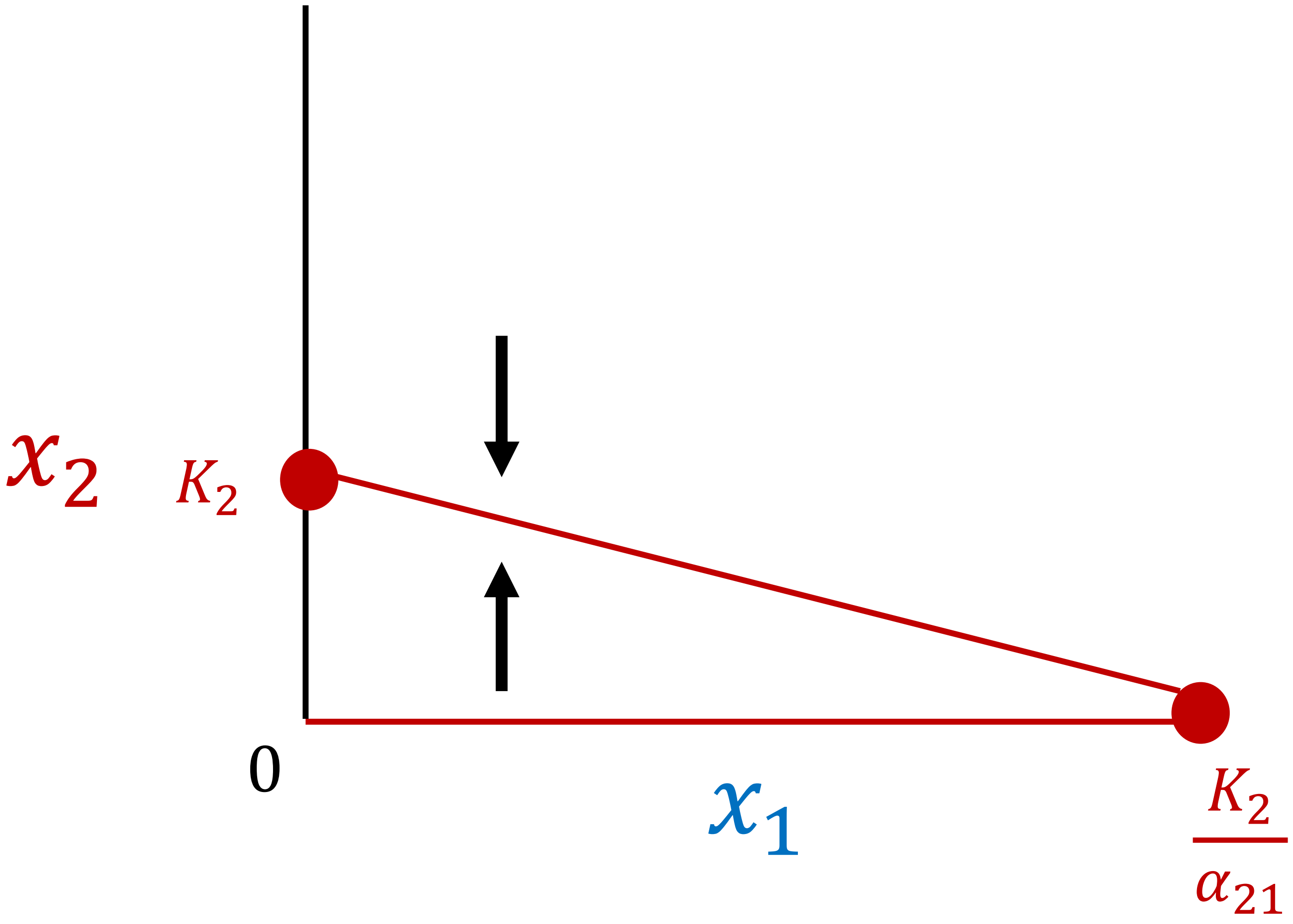

Nullclines (or isoclines) of the Lotka-Volterra competition model

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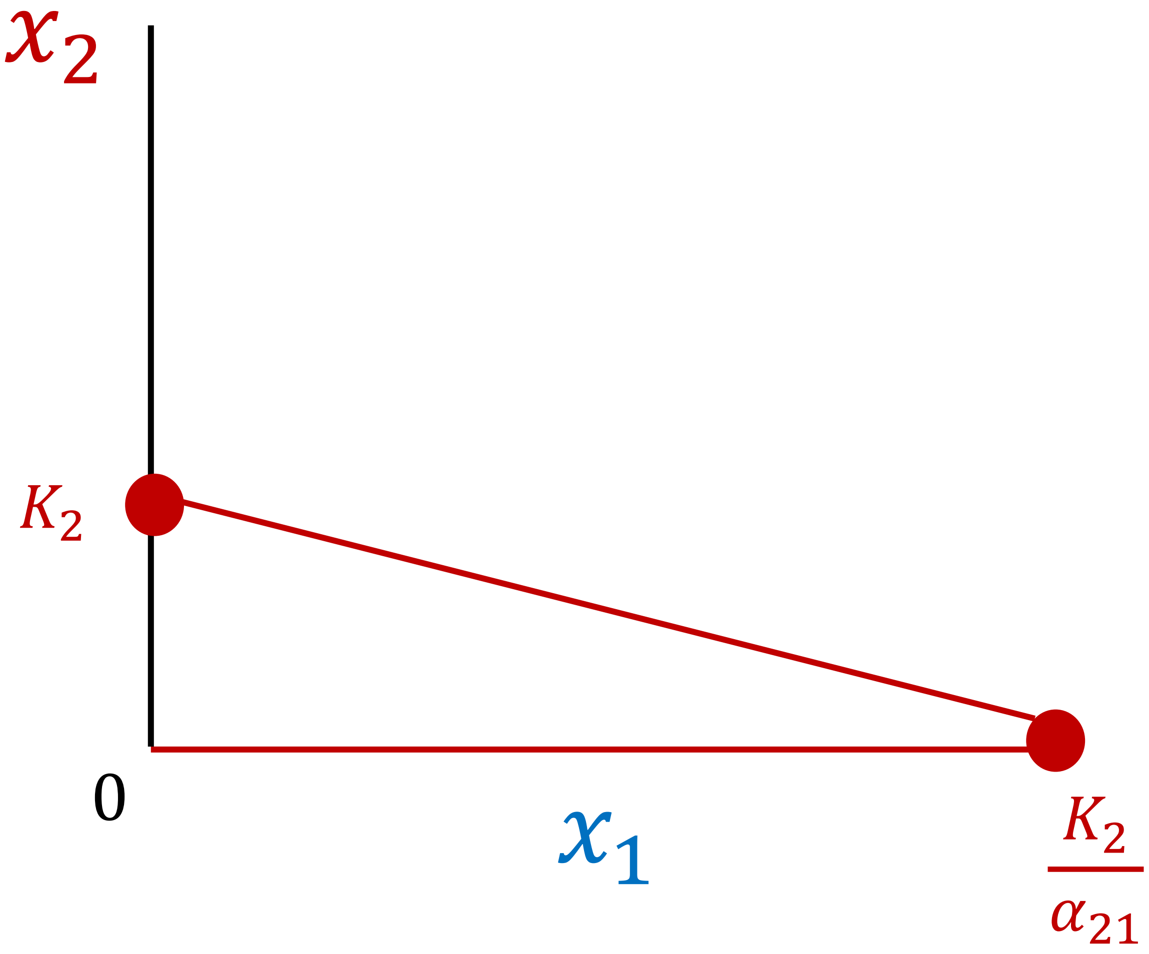

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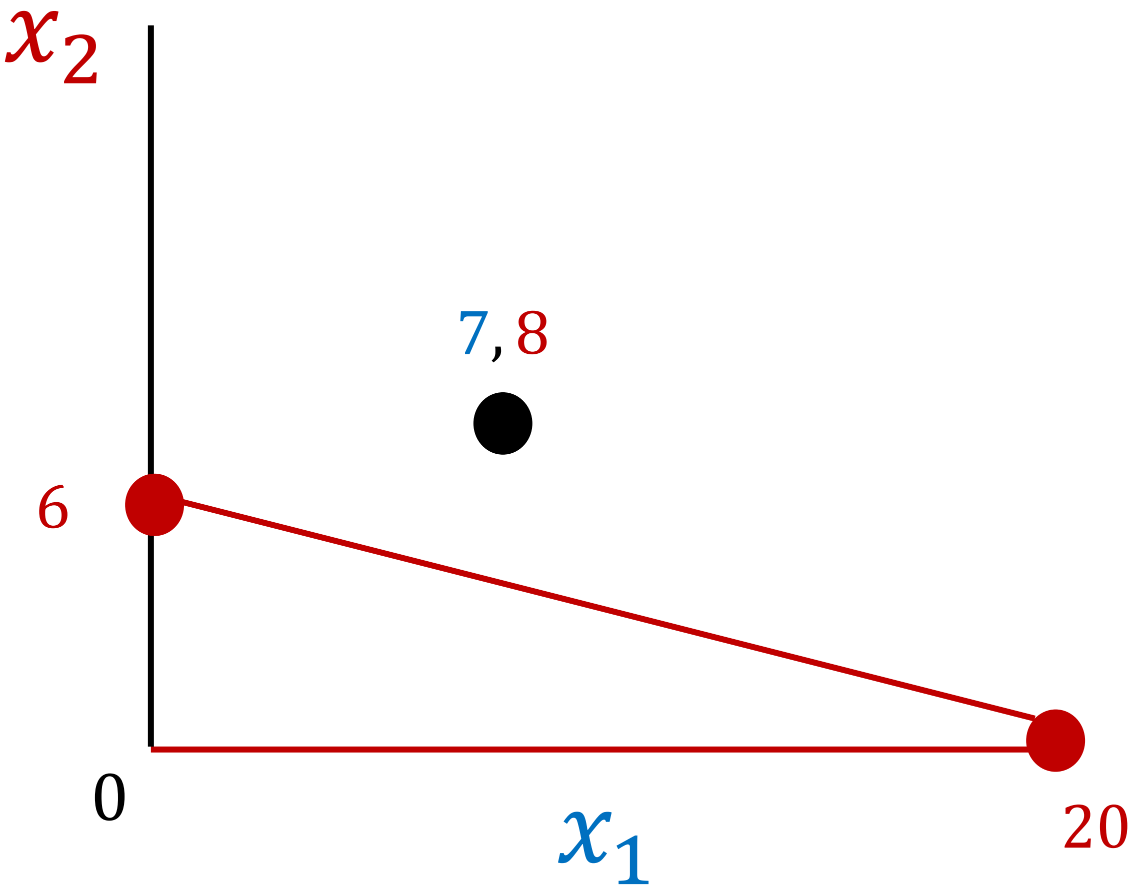

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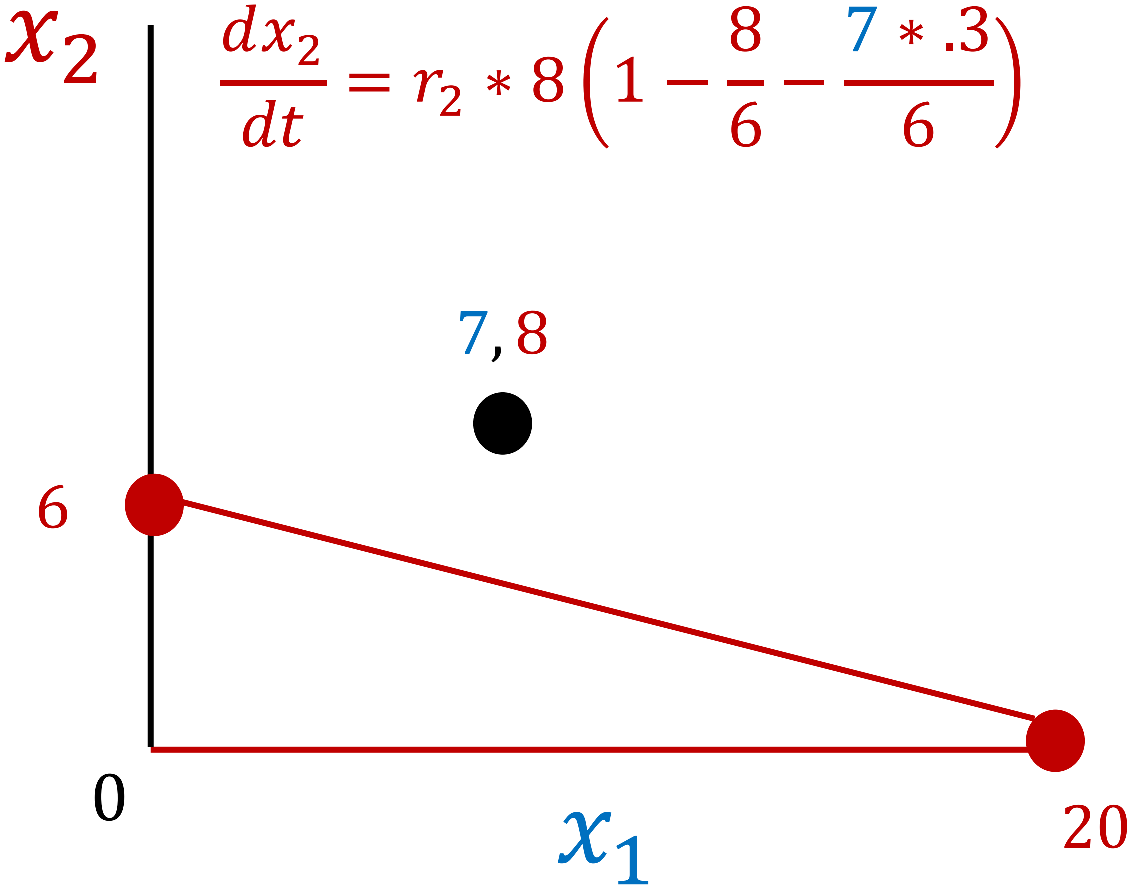

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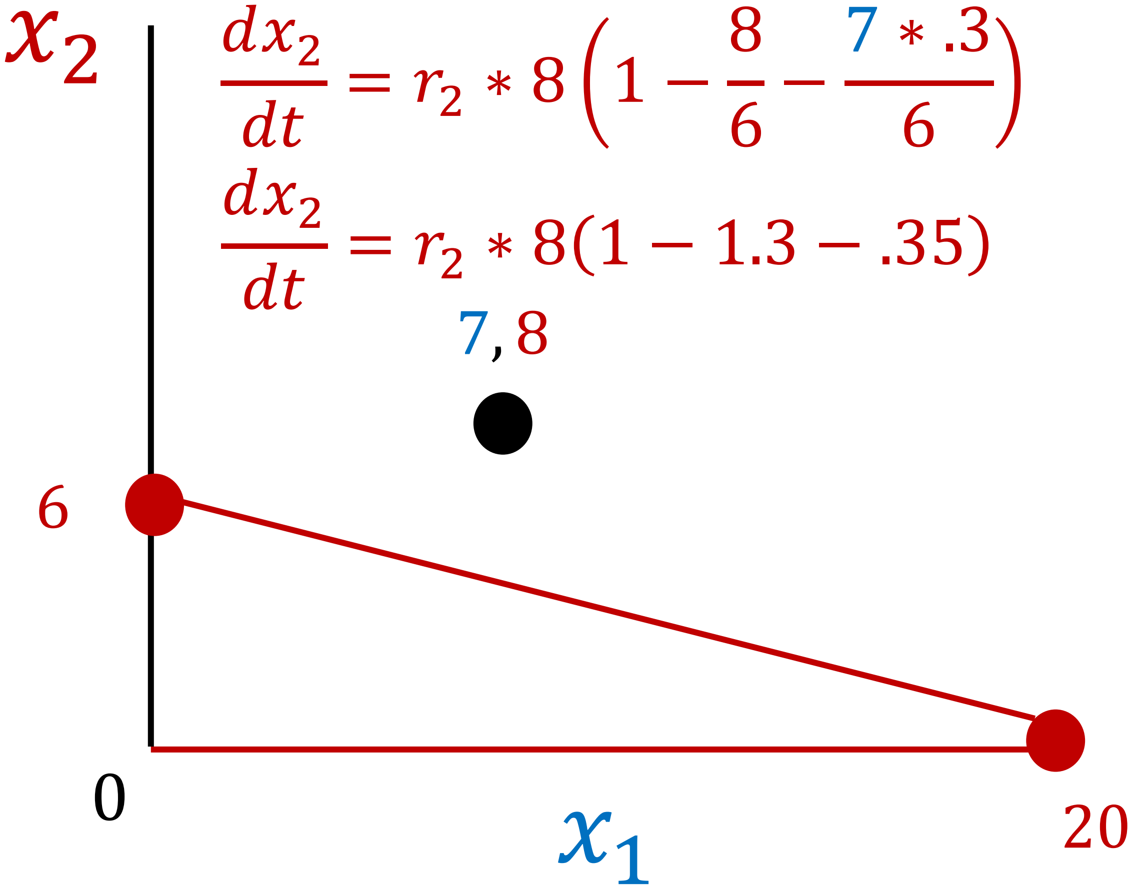

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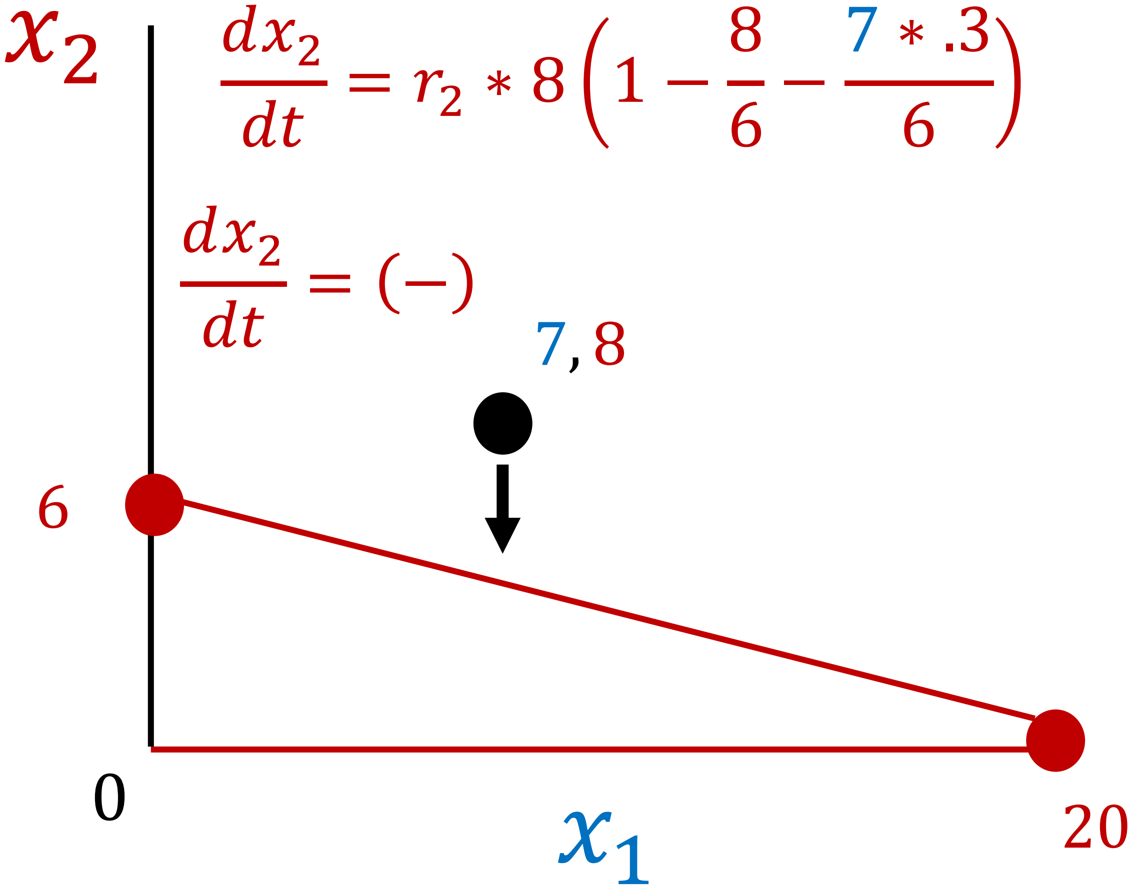

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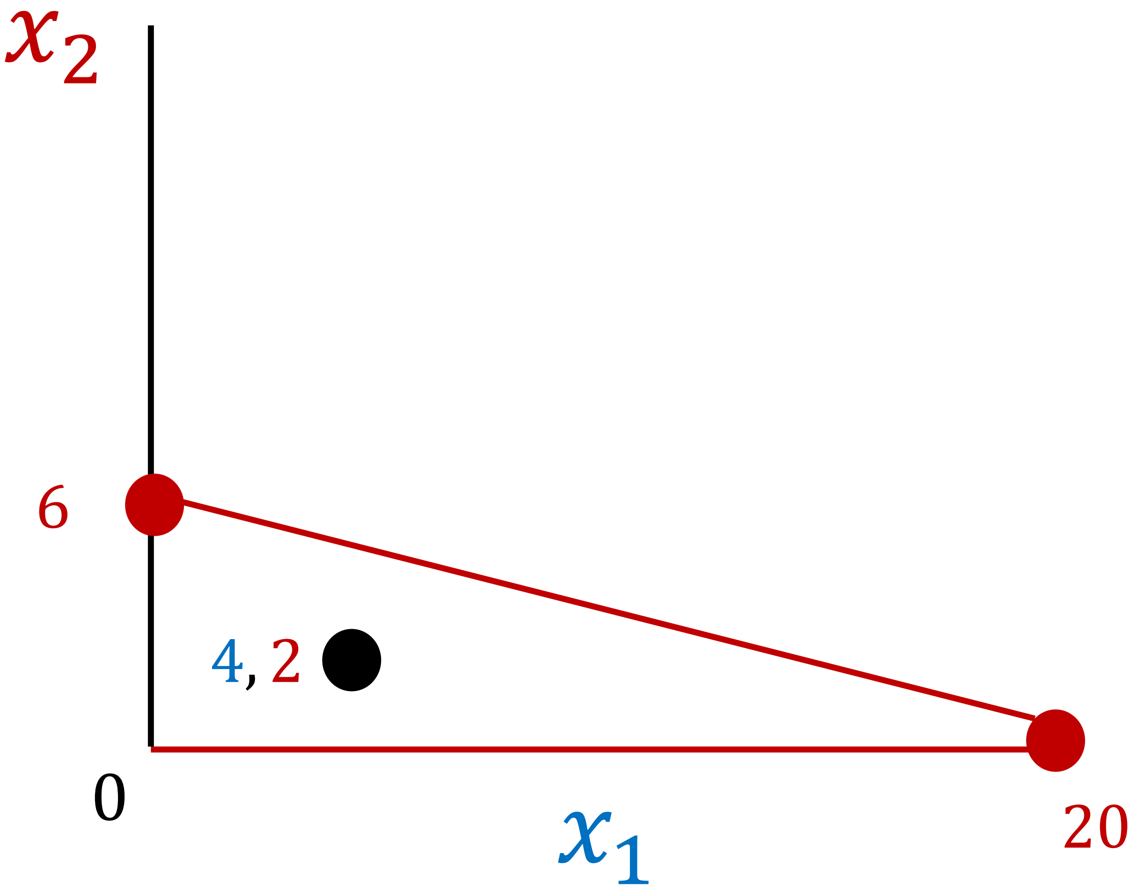

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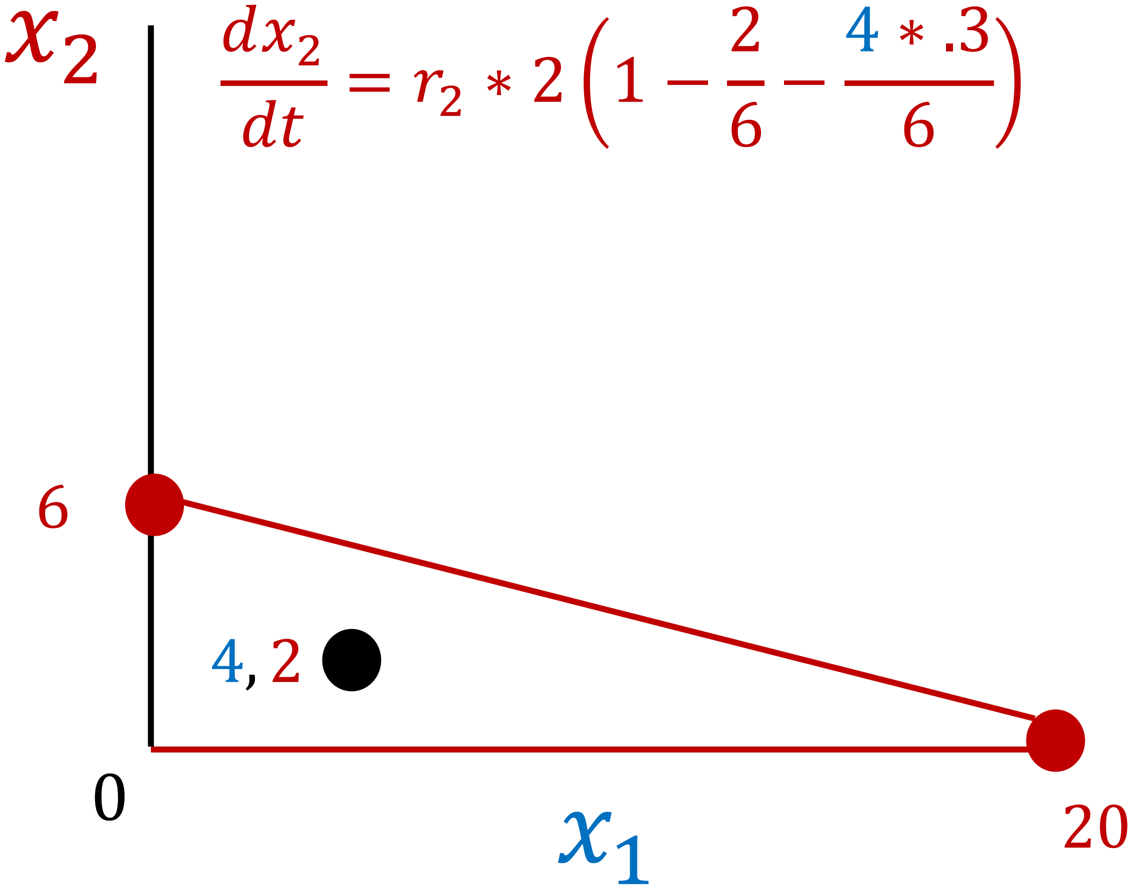

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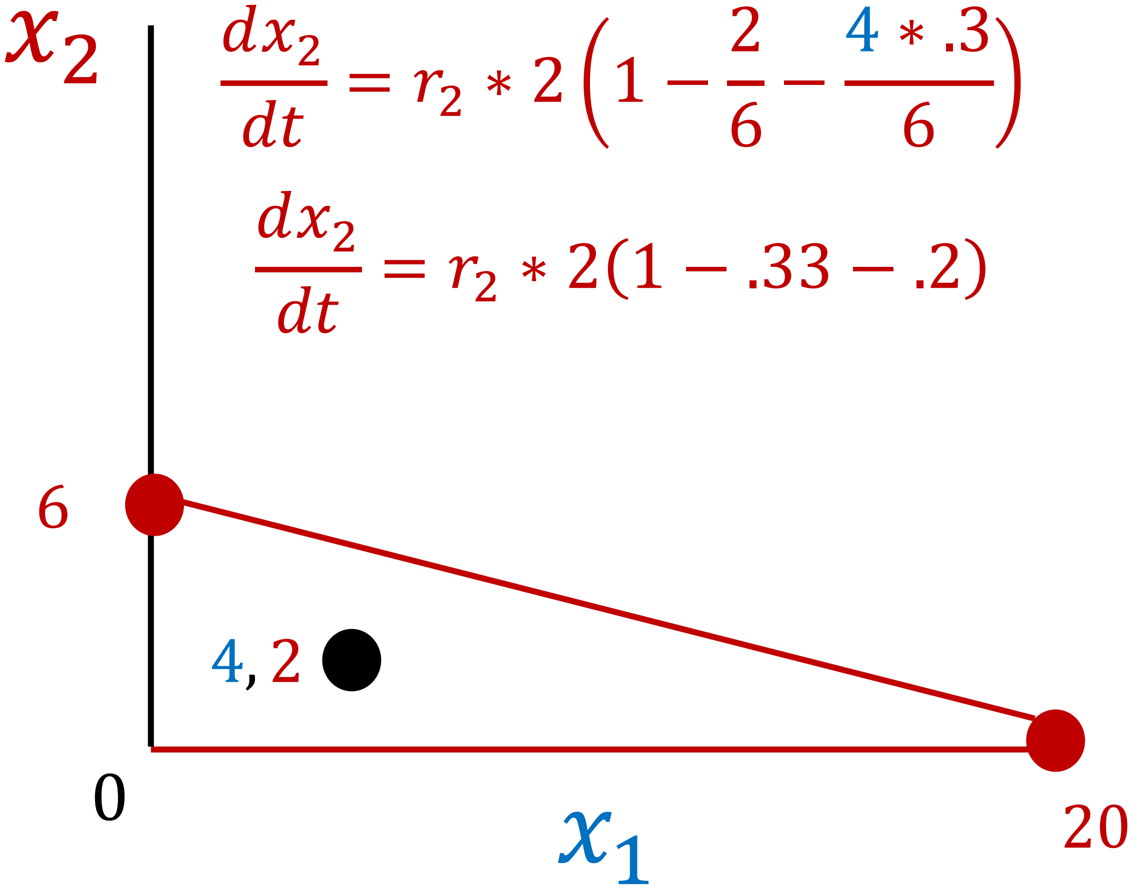

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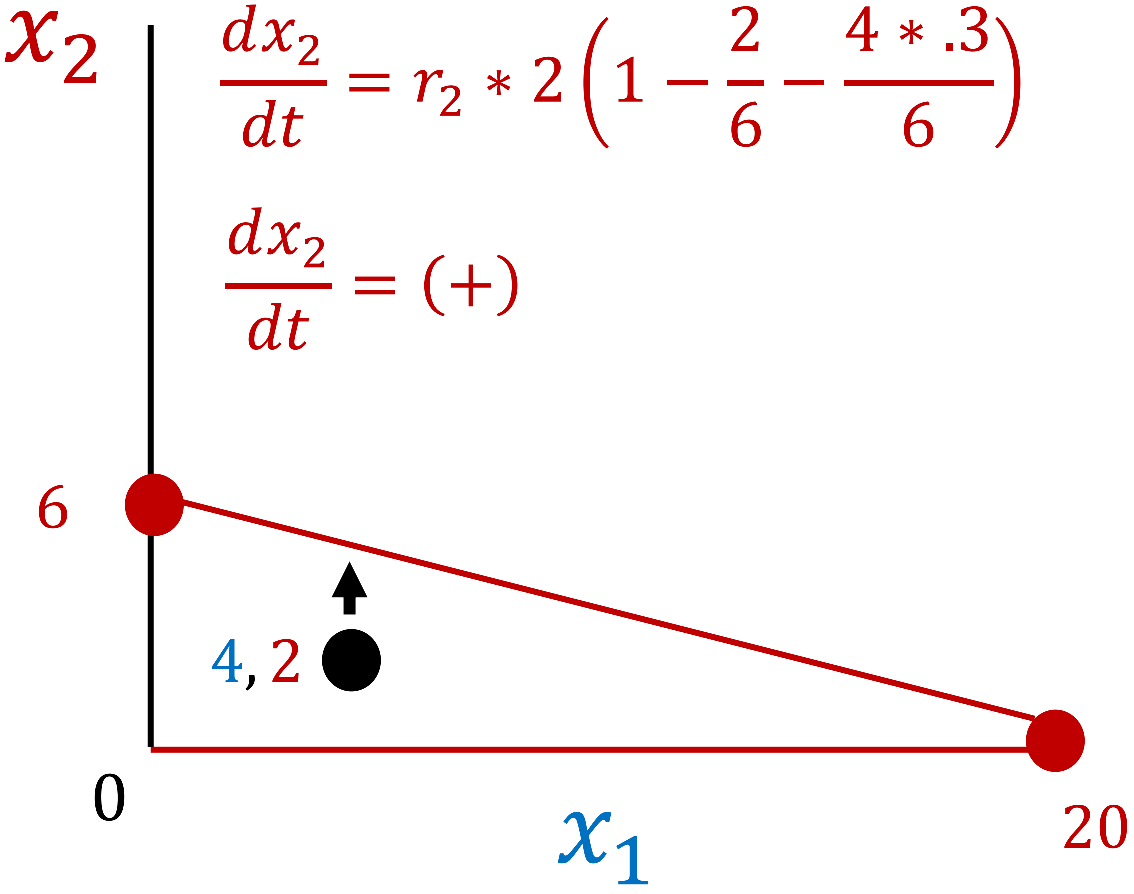
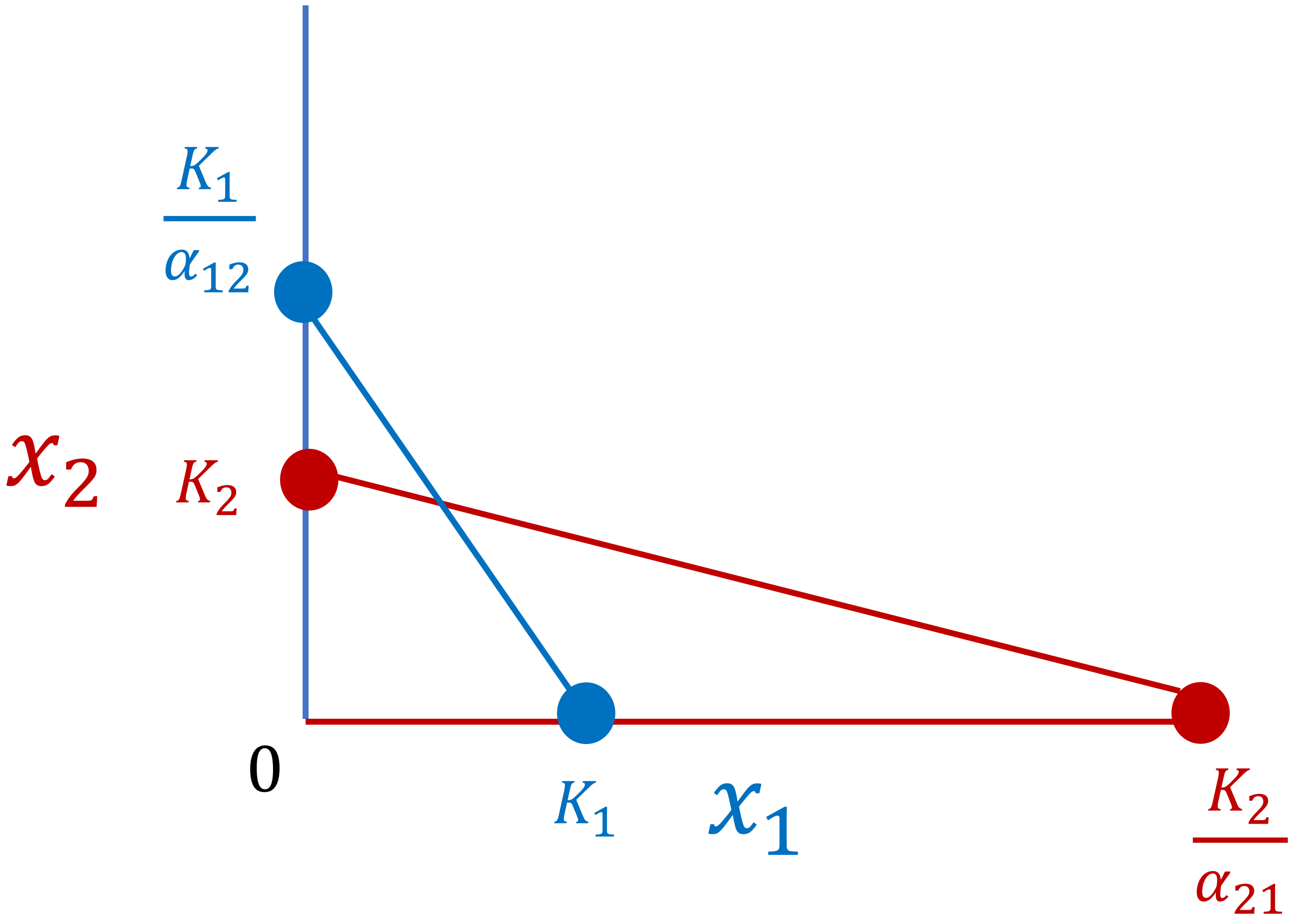
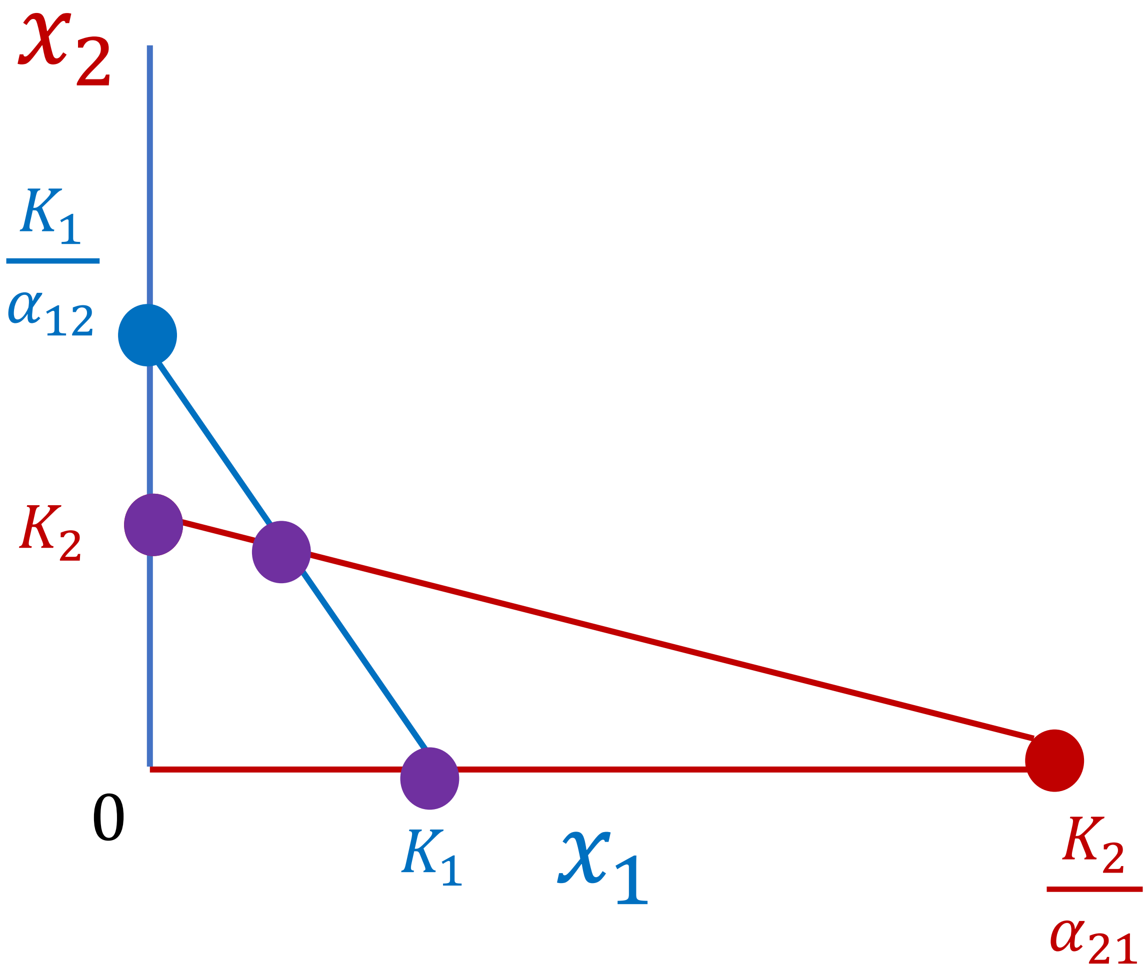


Given different combinations of x_1 and x_2 what is the outcome of competition?



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.



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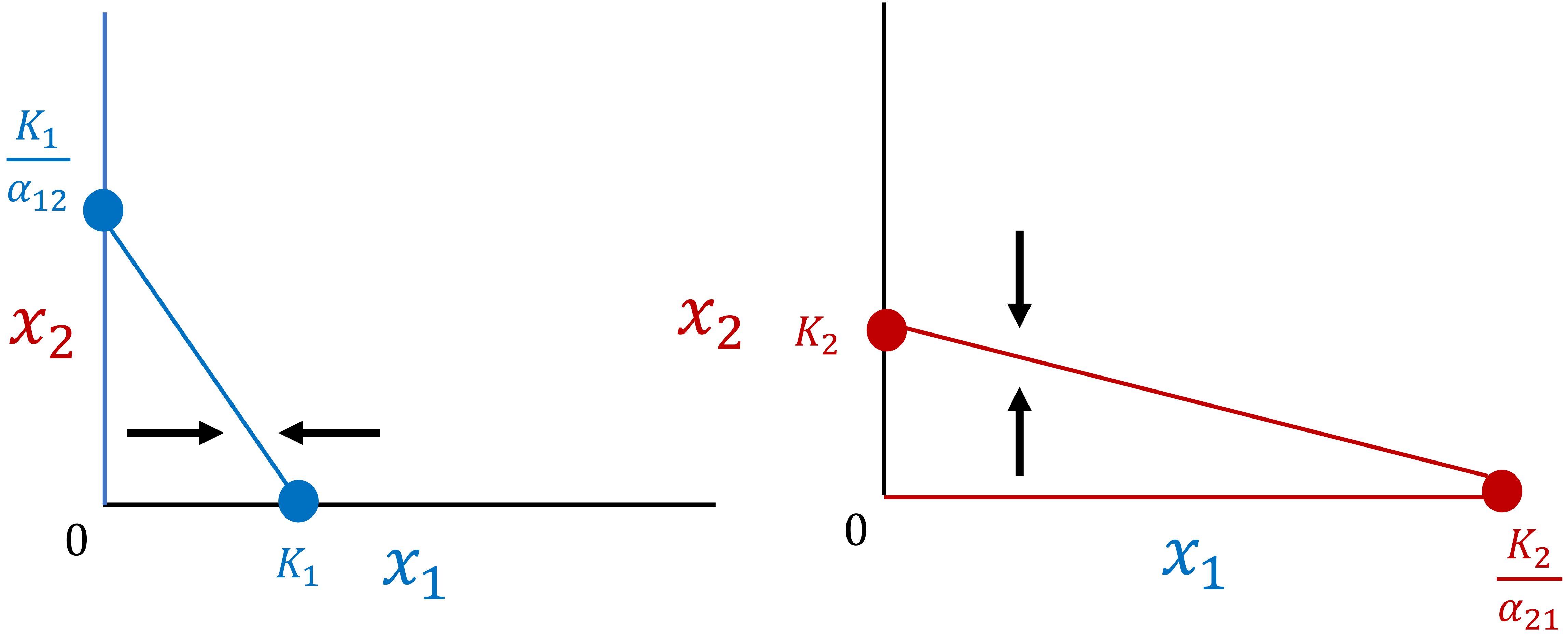

We can use vector addition from the individual nullclines to determine the outcome of competition.

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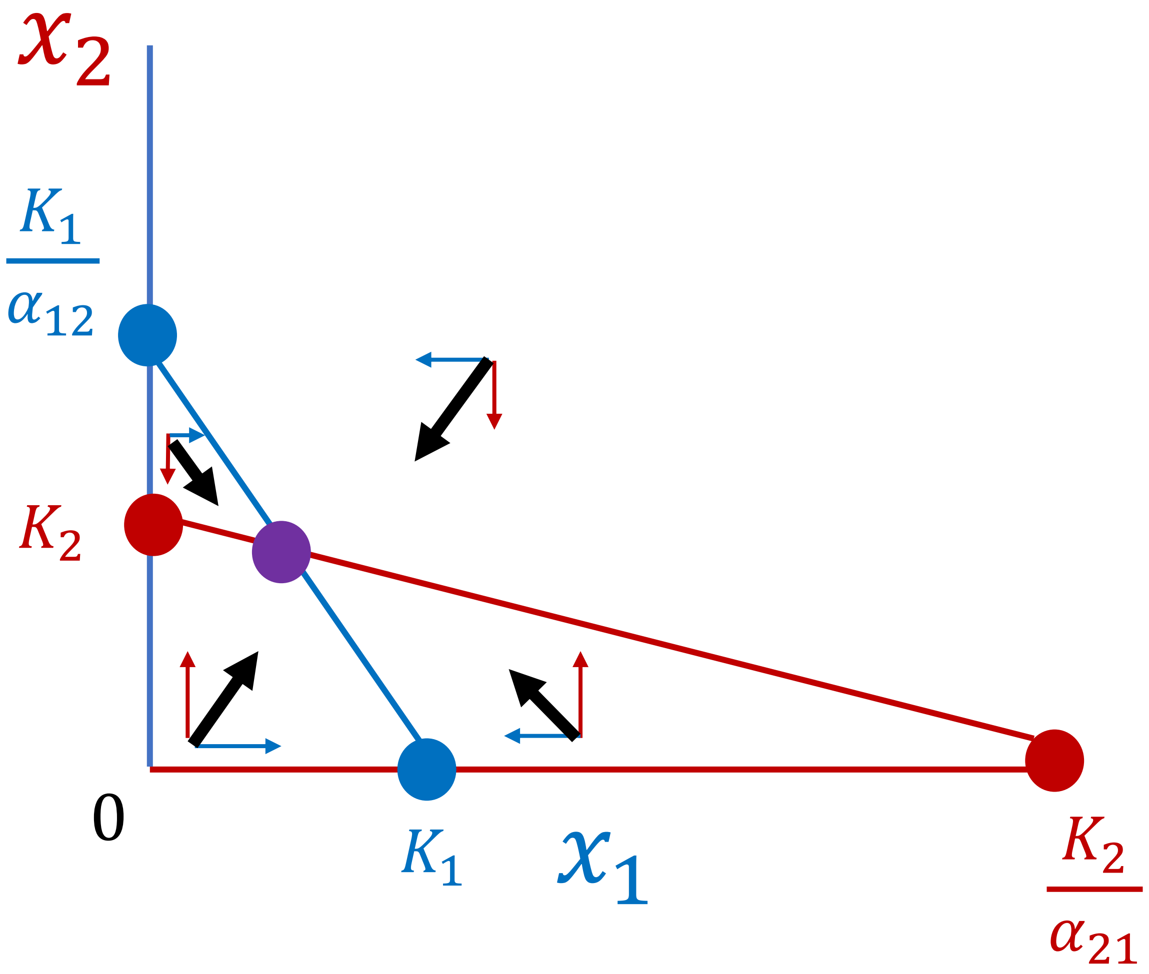
We can use vector addition **in each quadrat** from the individual nullclines to determine the outcome of competition.



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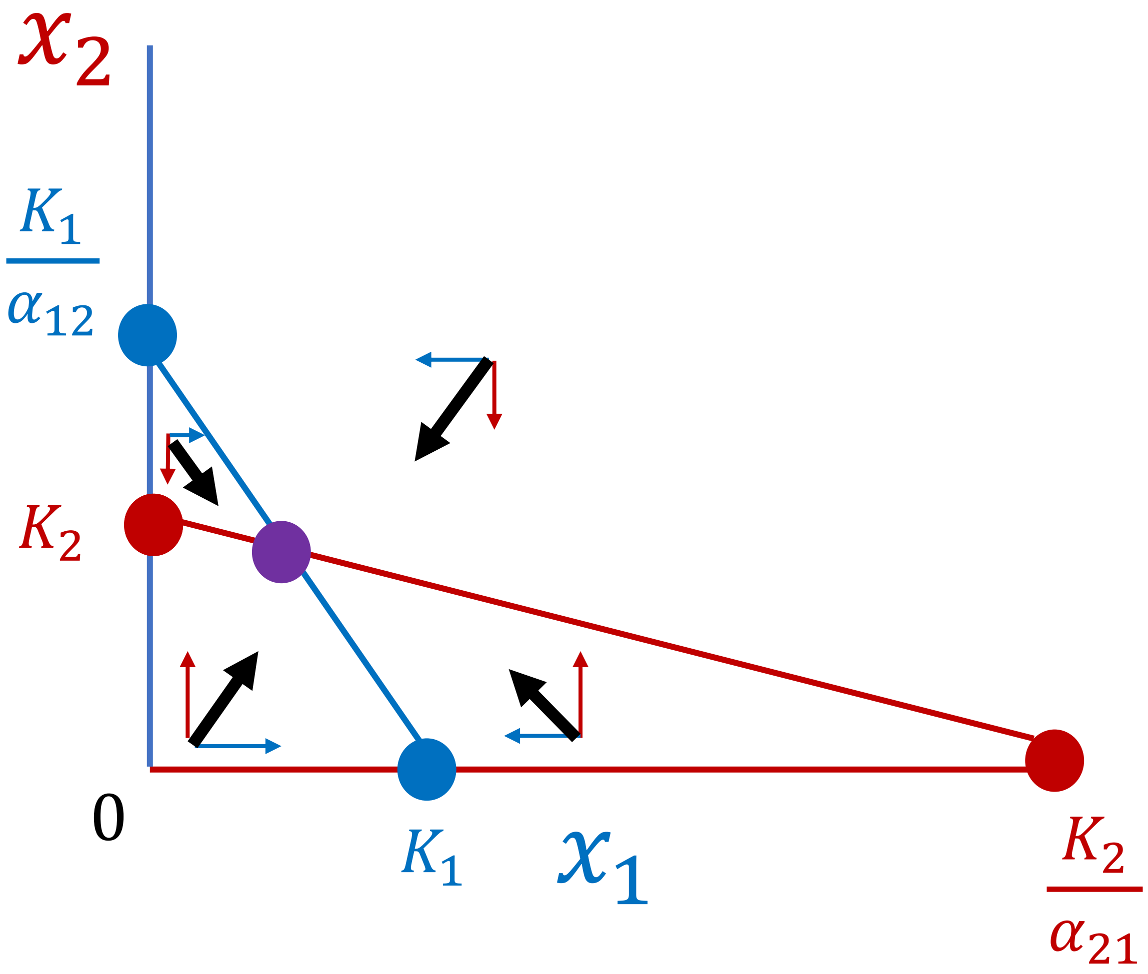
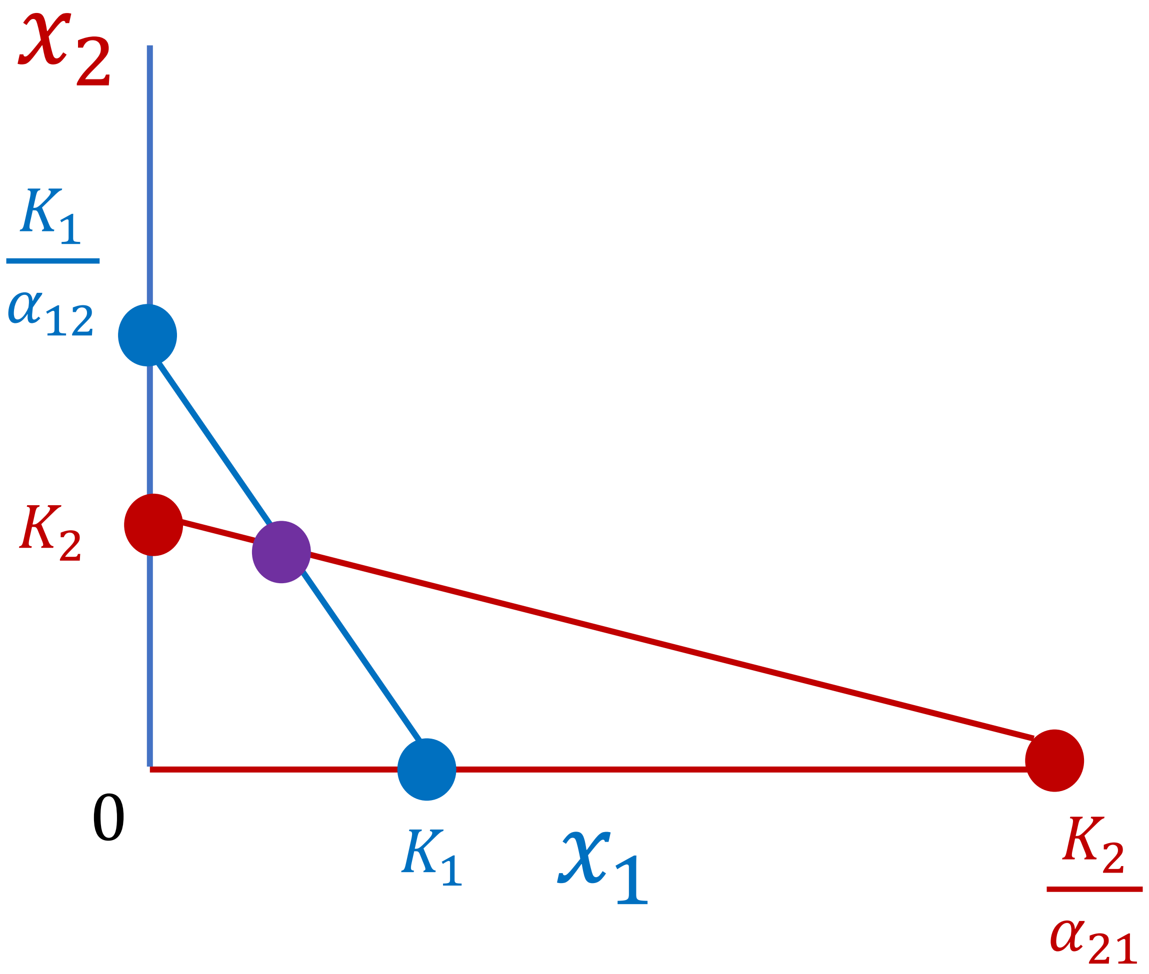
This configuration is a **stable equilibrium**, indicating **stable coexistence** at:

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



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).



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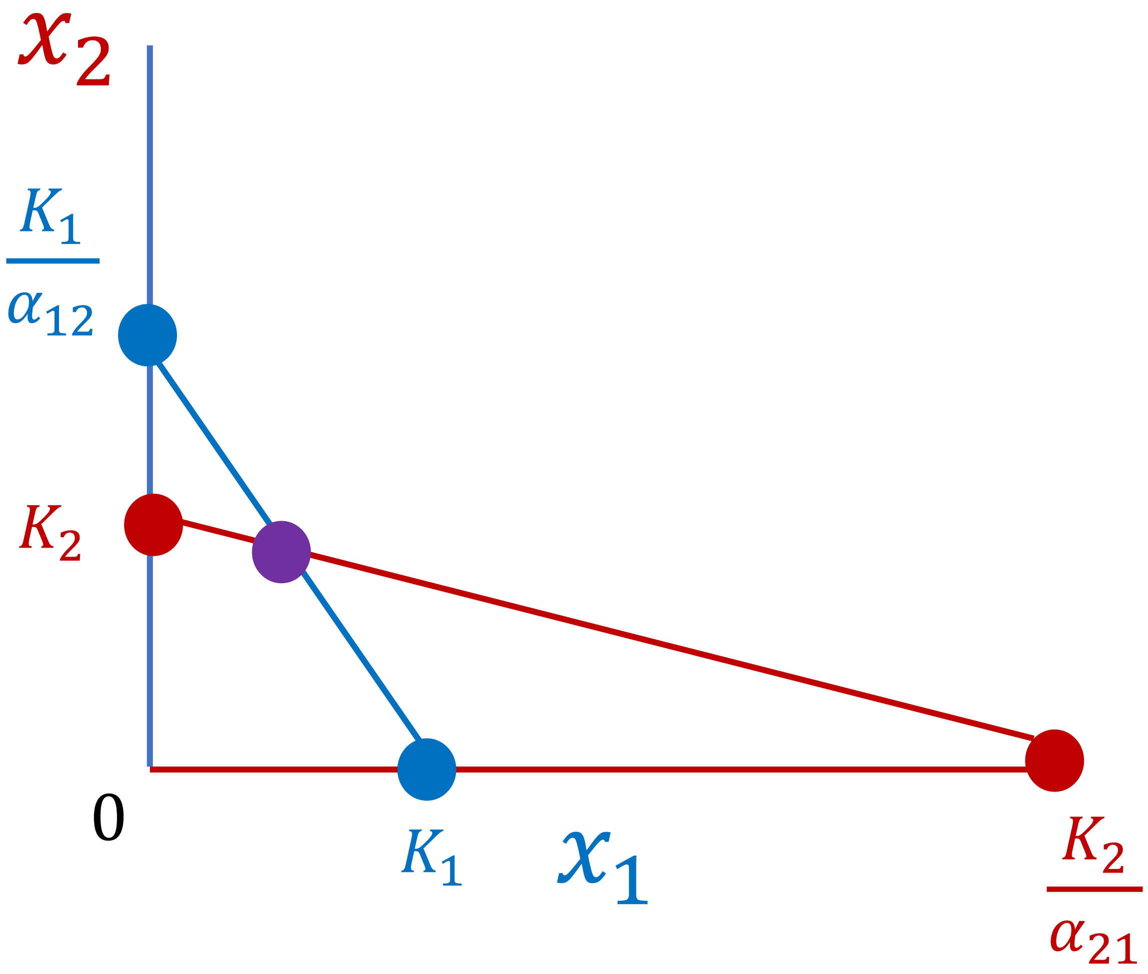
We can solve $\frac{dx_2}{dt}$ at different combinations of x_1 and x_2 to test the direction the x_2 population will move during competition (always along the y-axis).

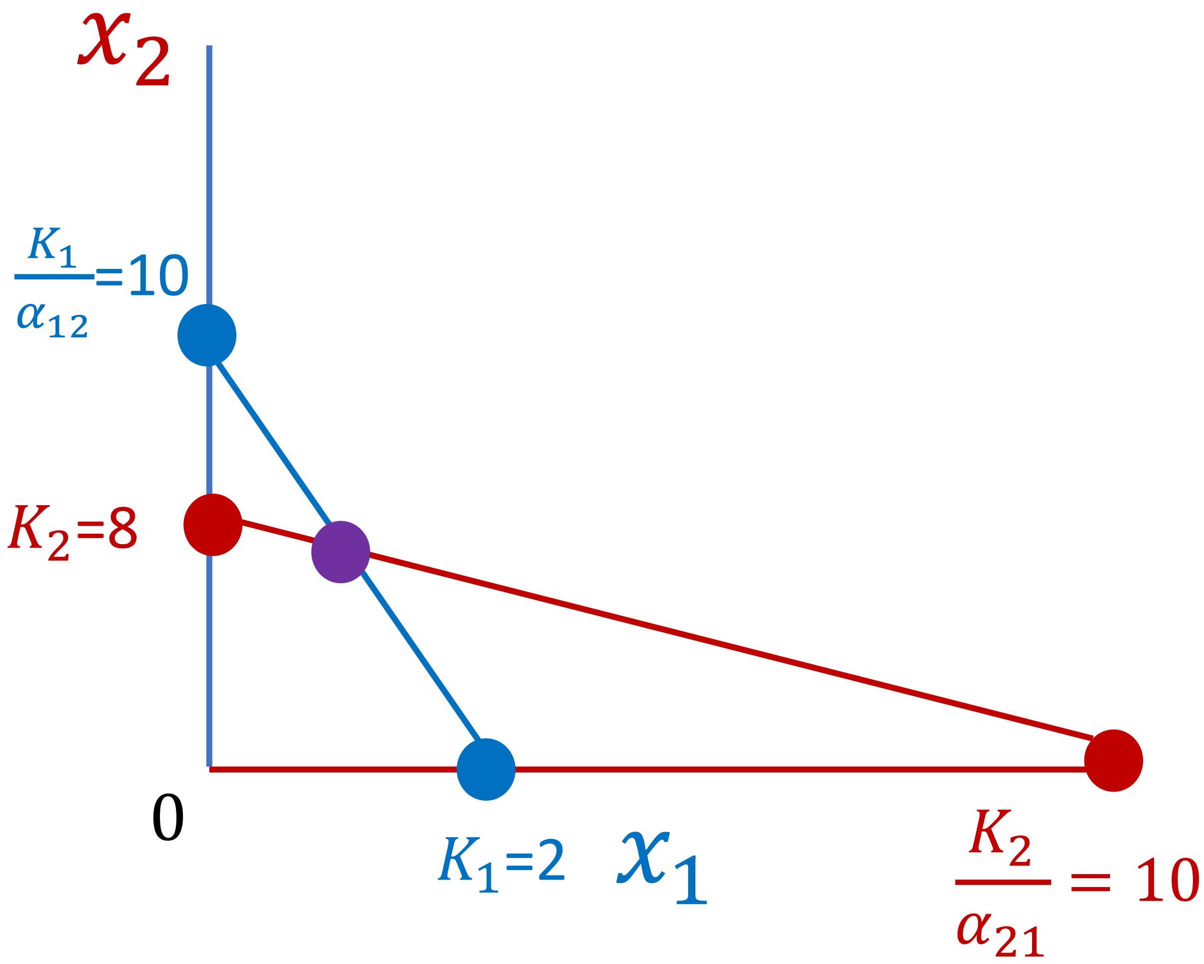


Given different combinations of x_1 and x_2 what is the outcome of competition?

Let's try it!

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

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



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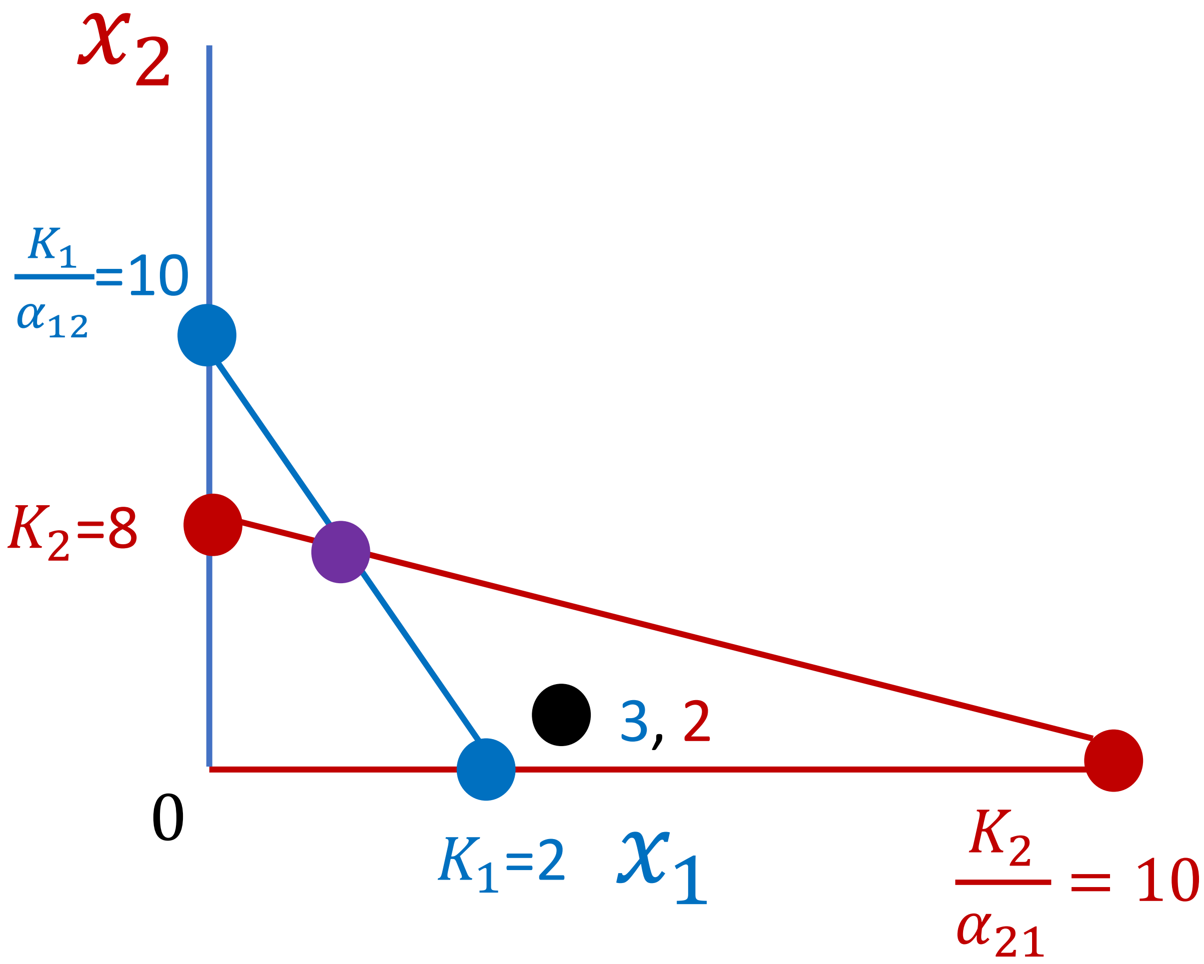

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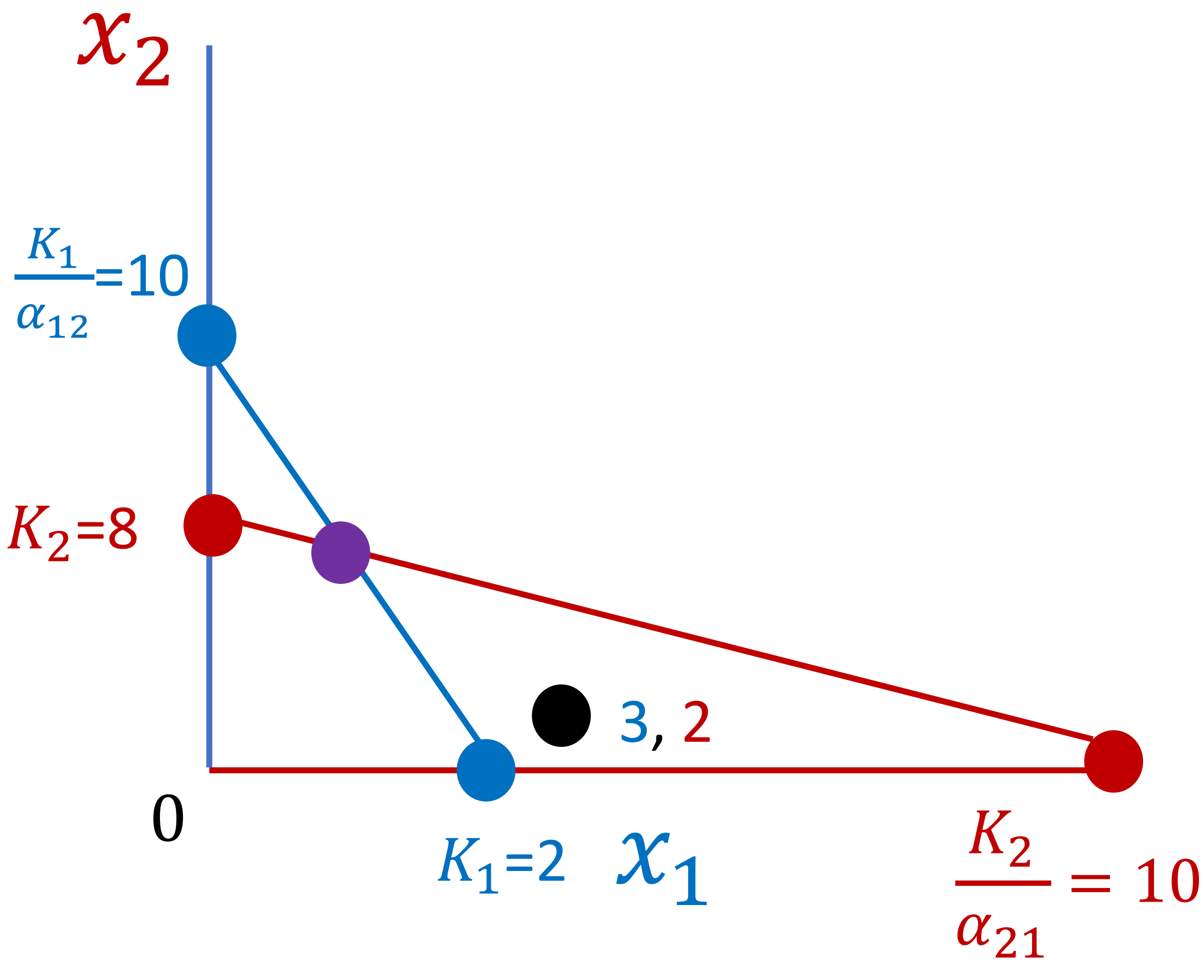

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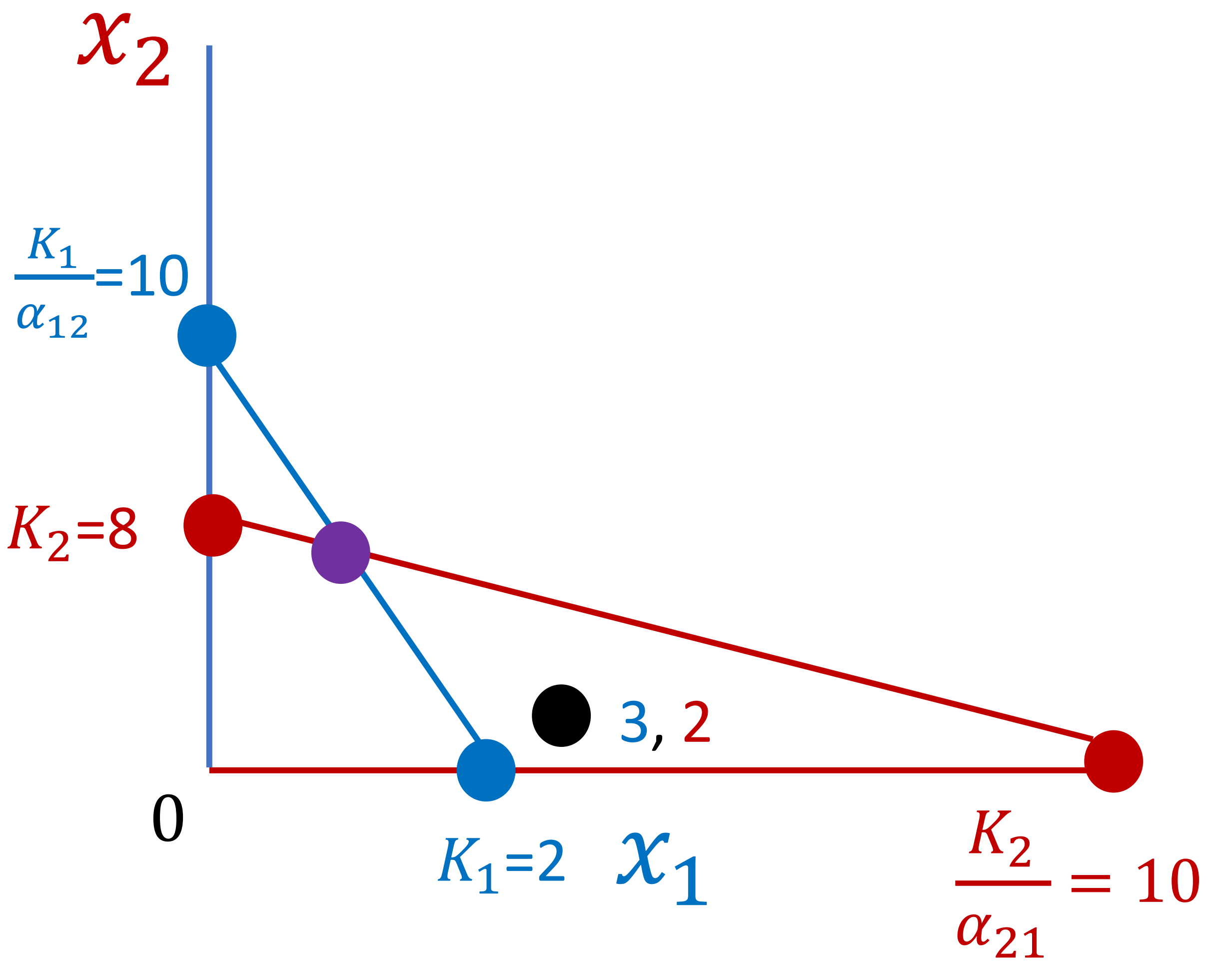

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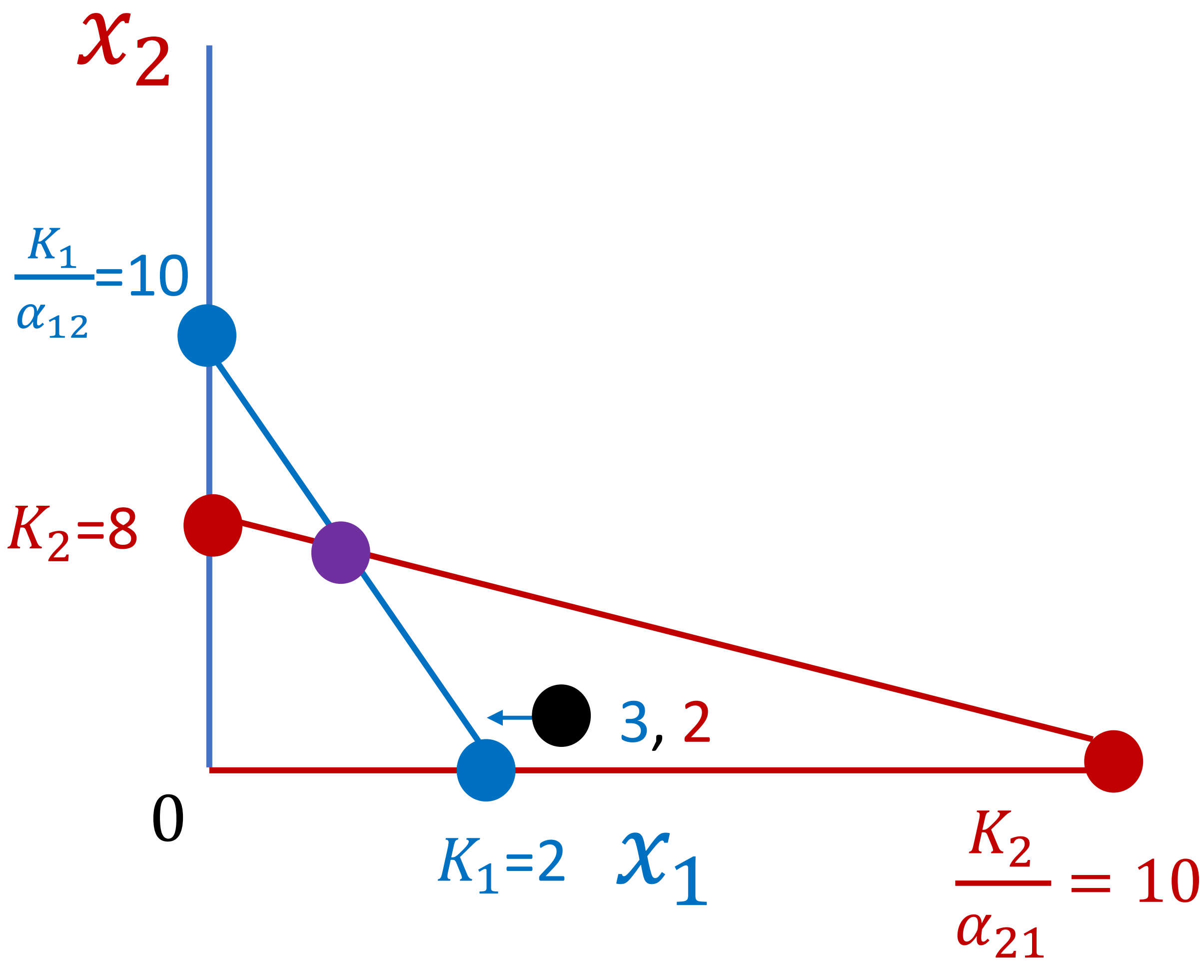

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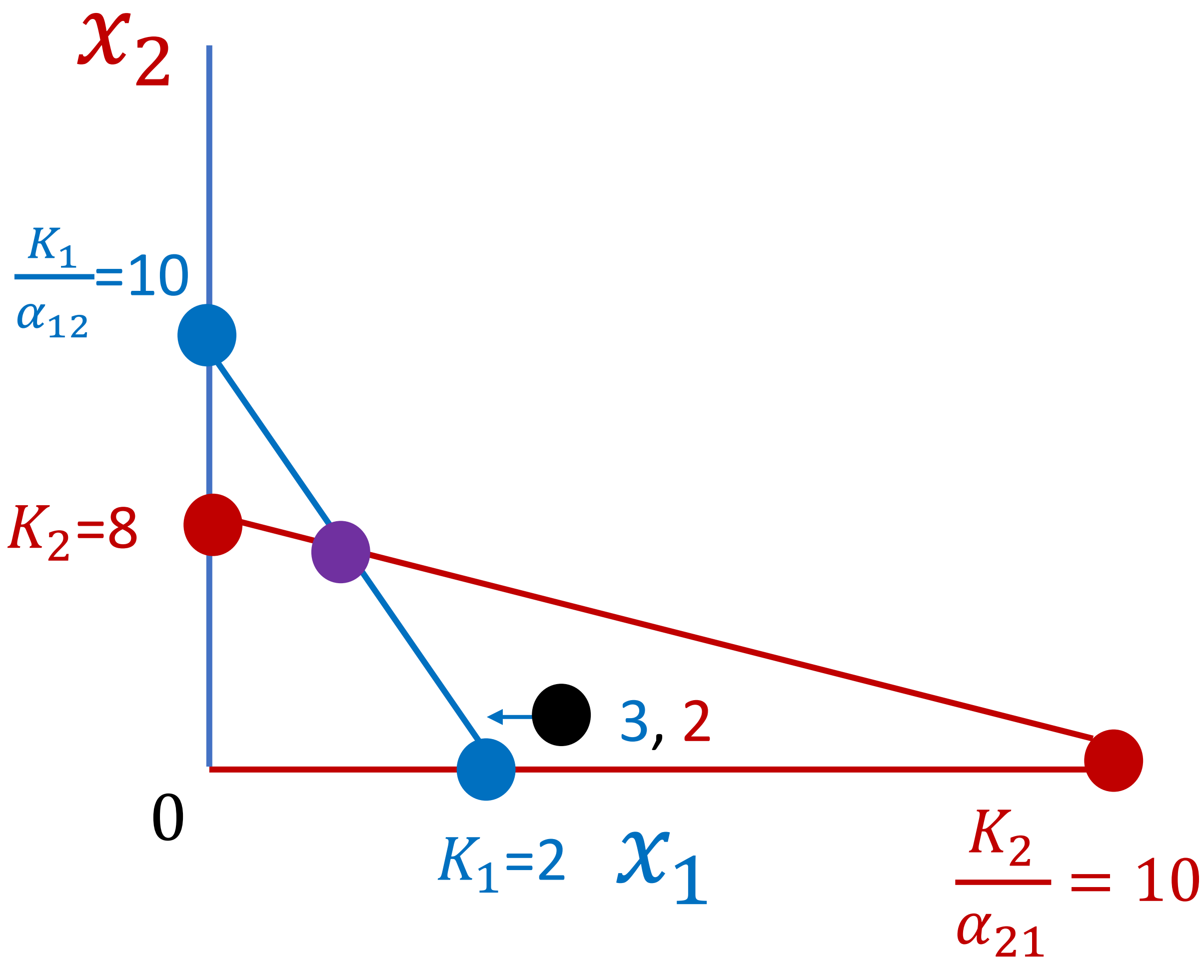

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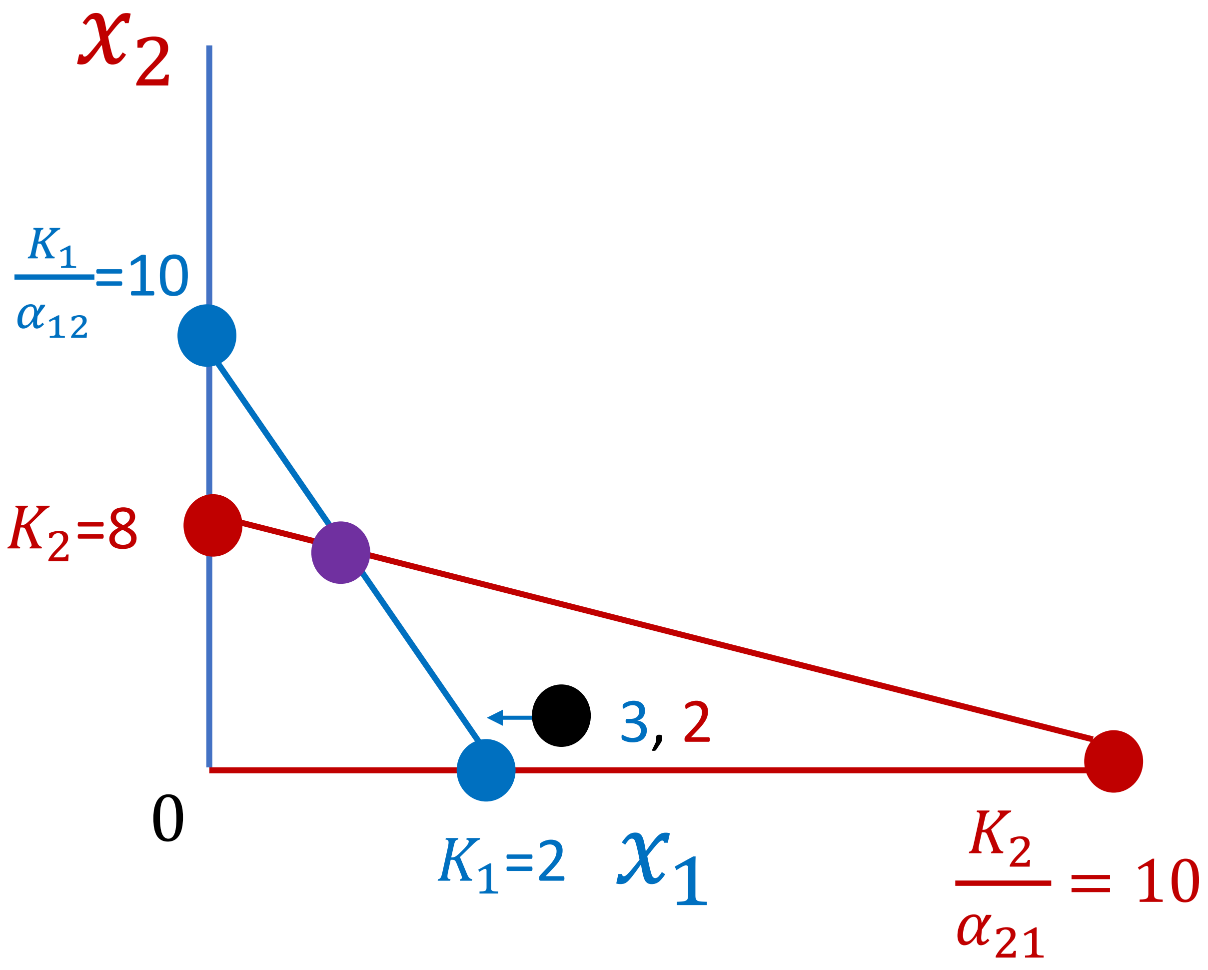

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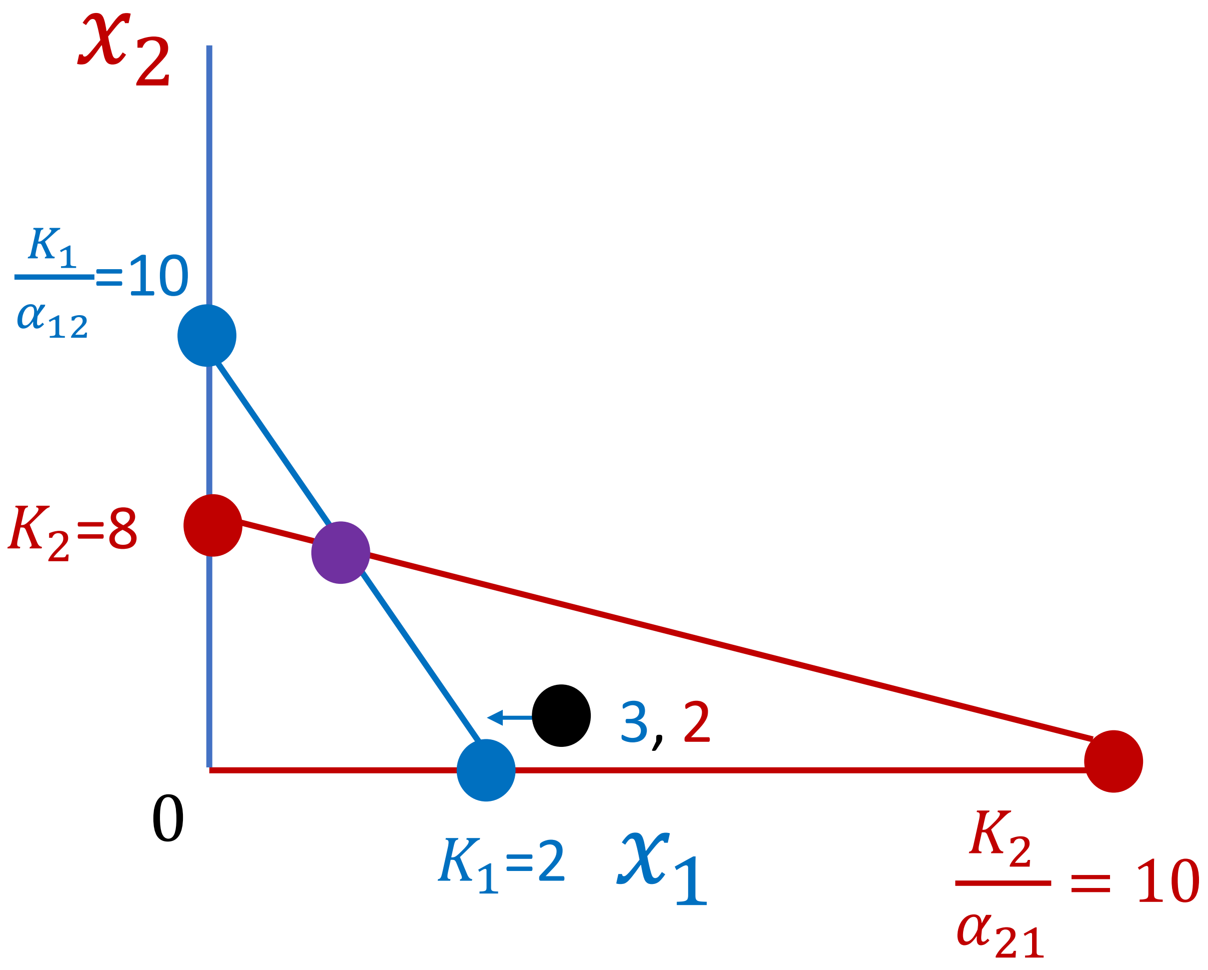

Given different combinations of x_1 and x_2 what is the outcome of competition?

Let's try it!

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

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

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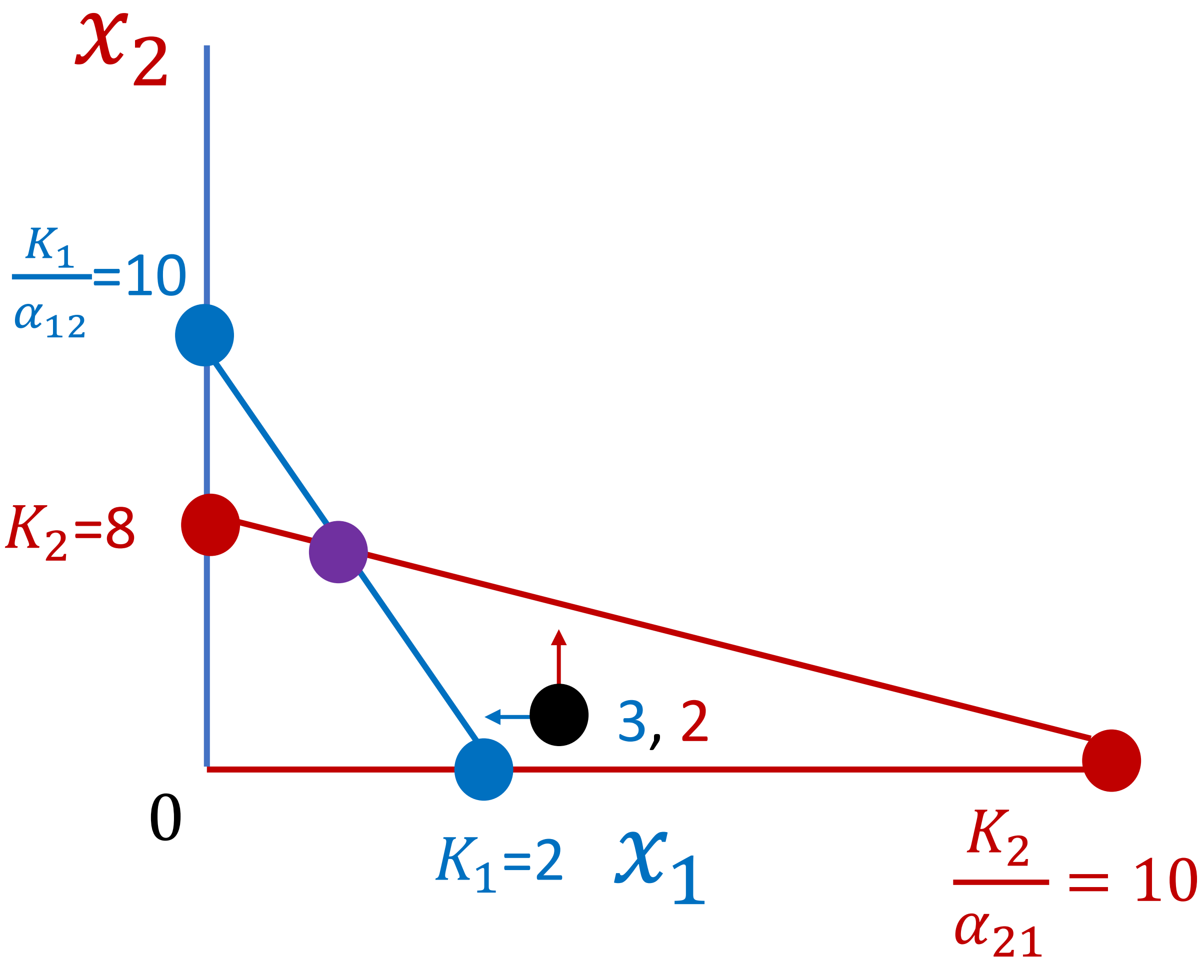

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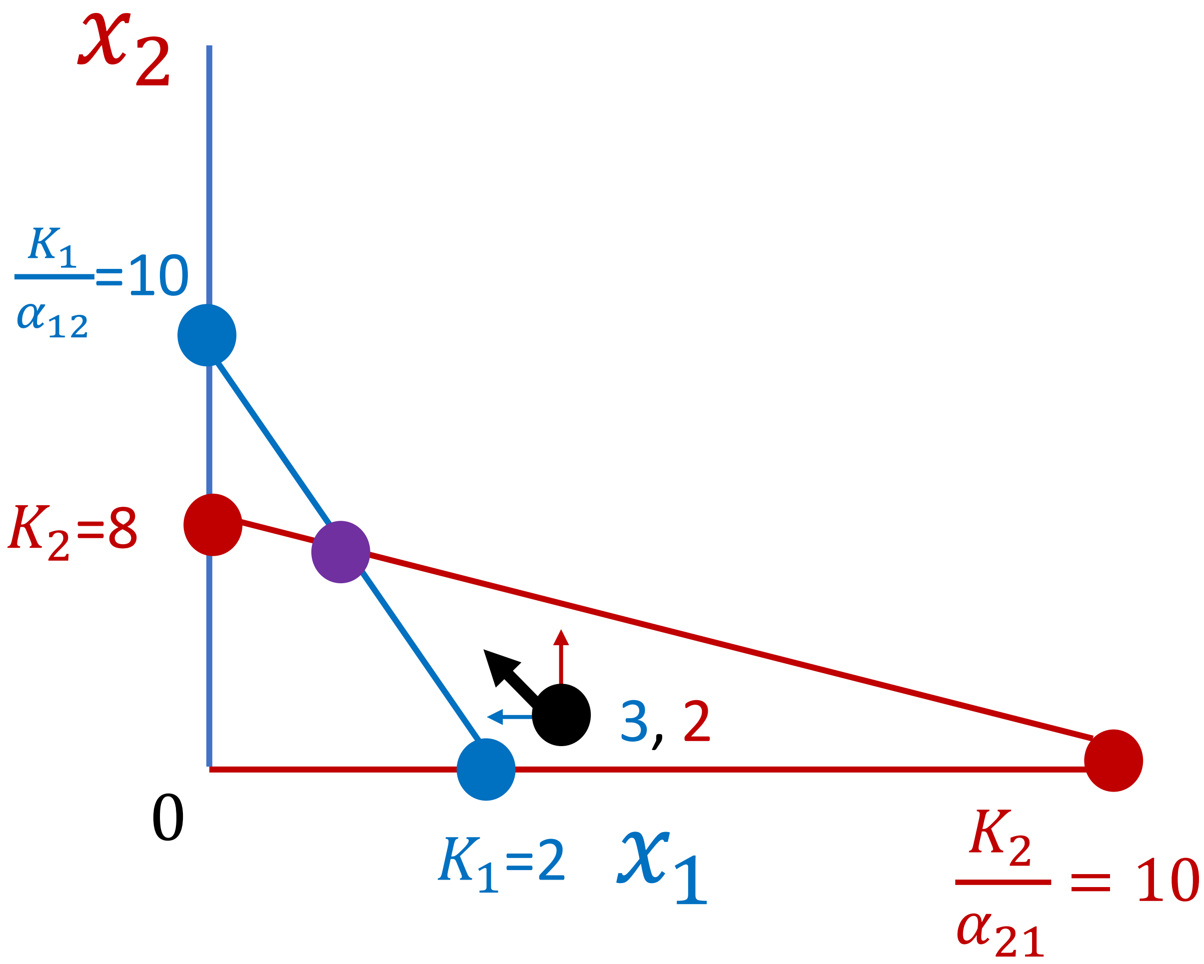
Results replicate graphical approach!

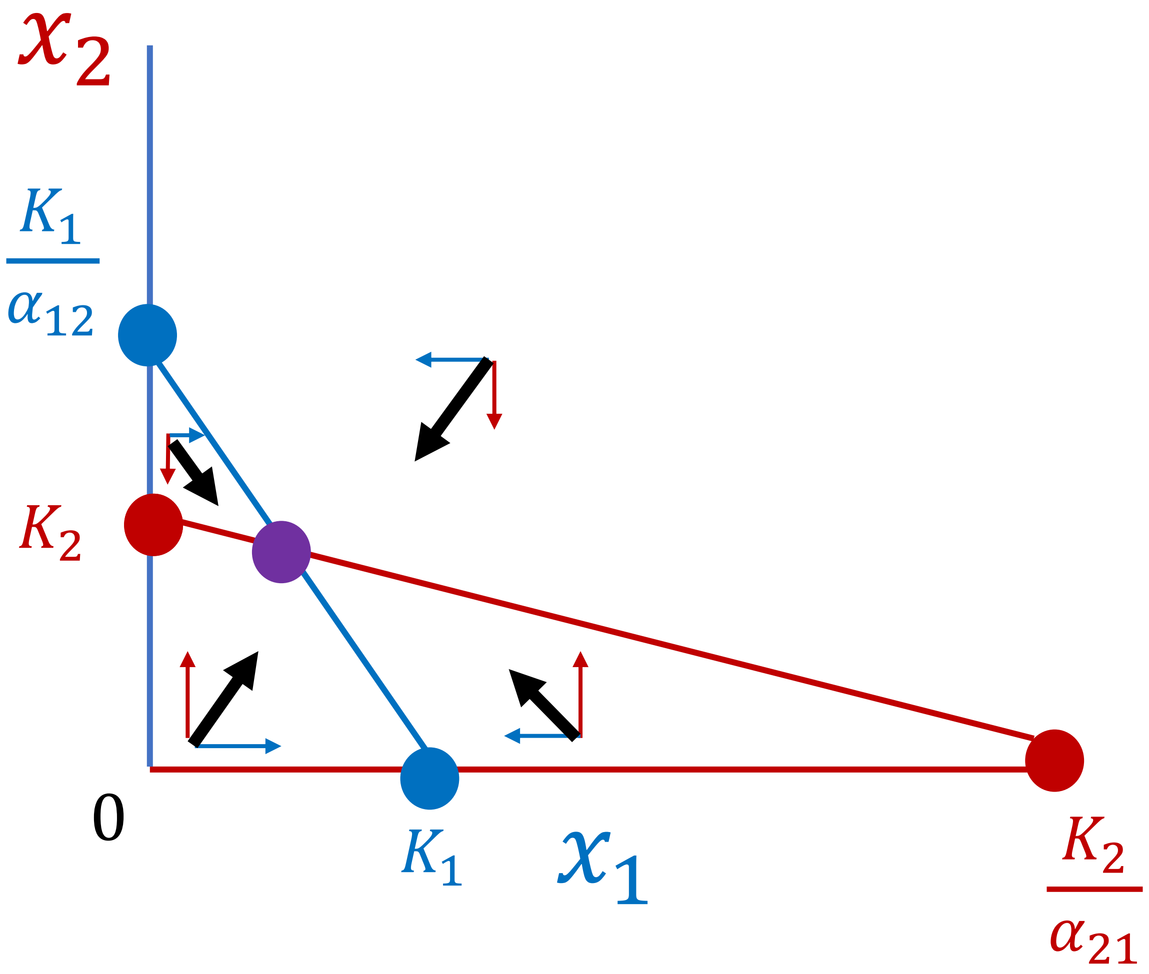


Four possible outcomes for competition

Case 1:

Stable equilibrium, with **coexistence** at:

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



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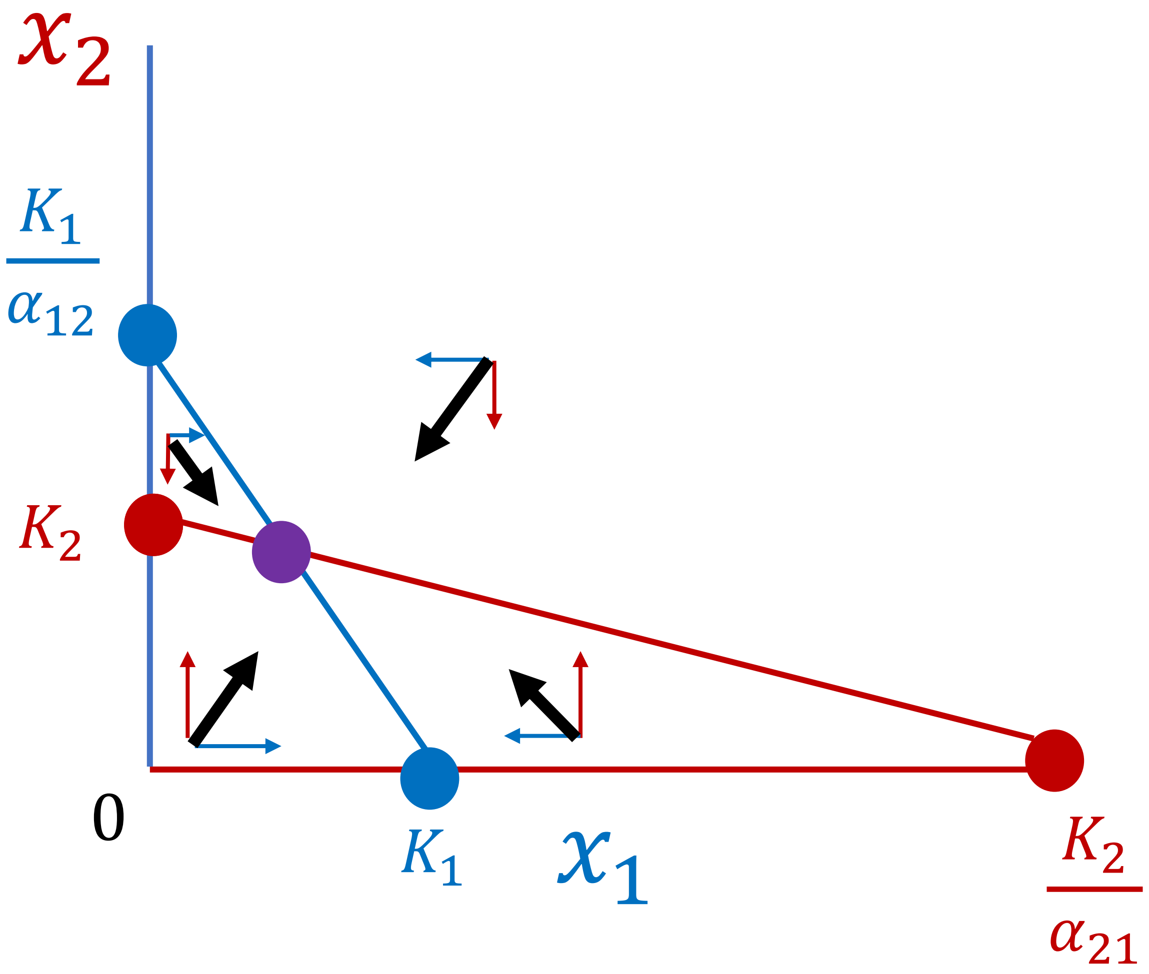
$$(\alpha_{12} * \alpha_{21} < 1)$$



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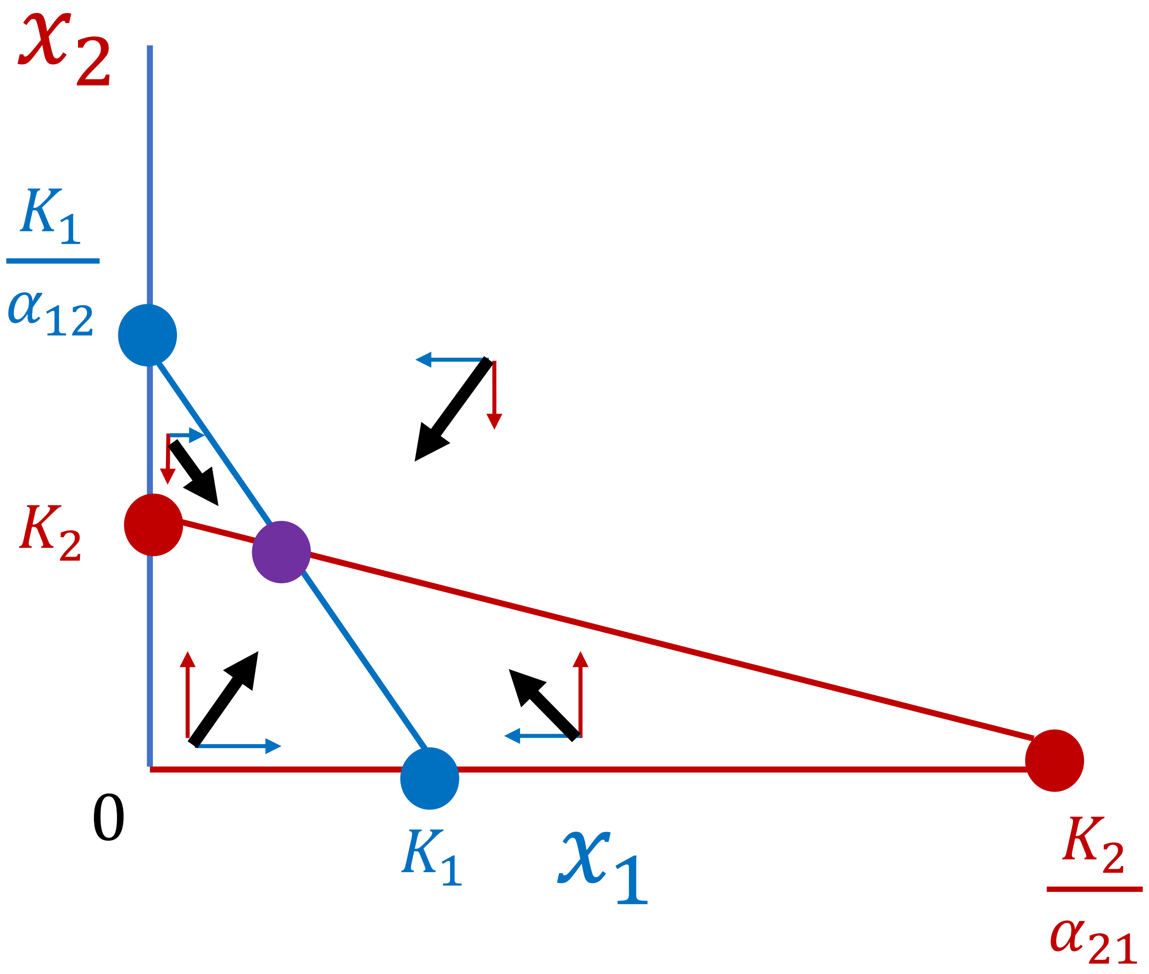
- Species coexist stably but **below carrying capacity** for each individual population.
- **Intraspecific** competition is stronger than **interspecific** competition.



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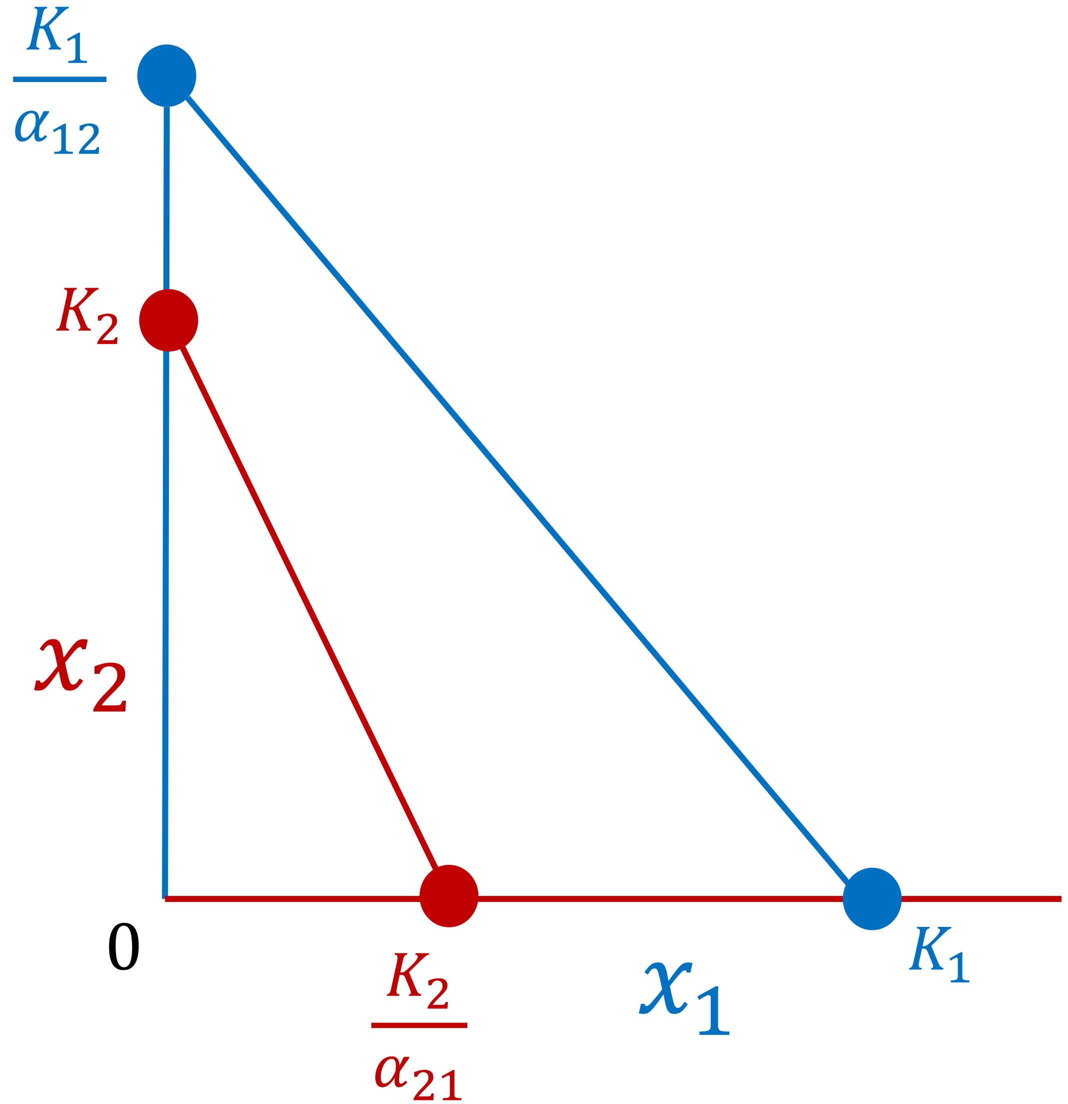
Species 1 outcompetes species 2

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



Four possible outcomes for competition

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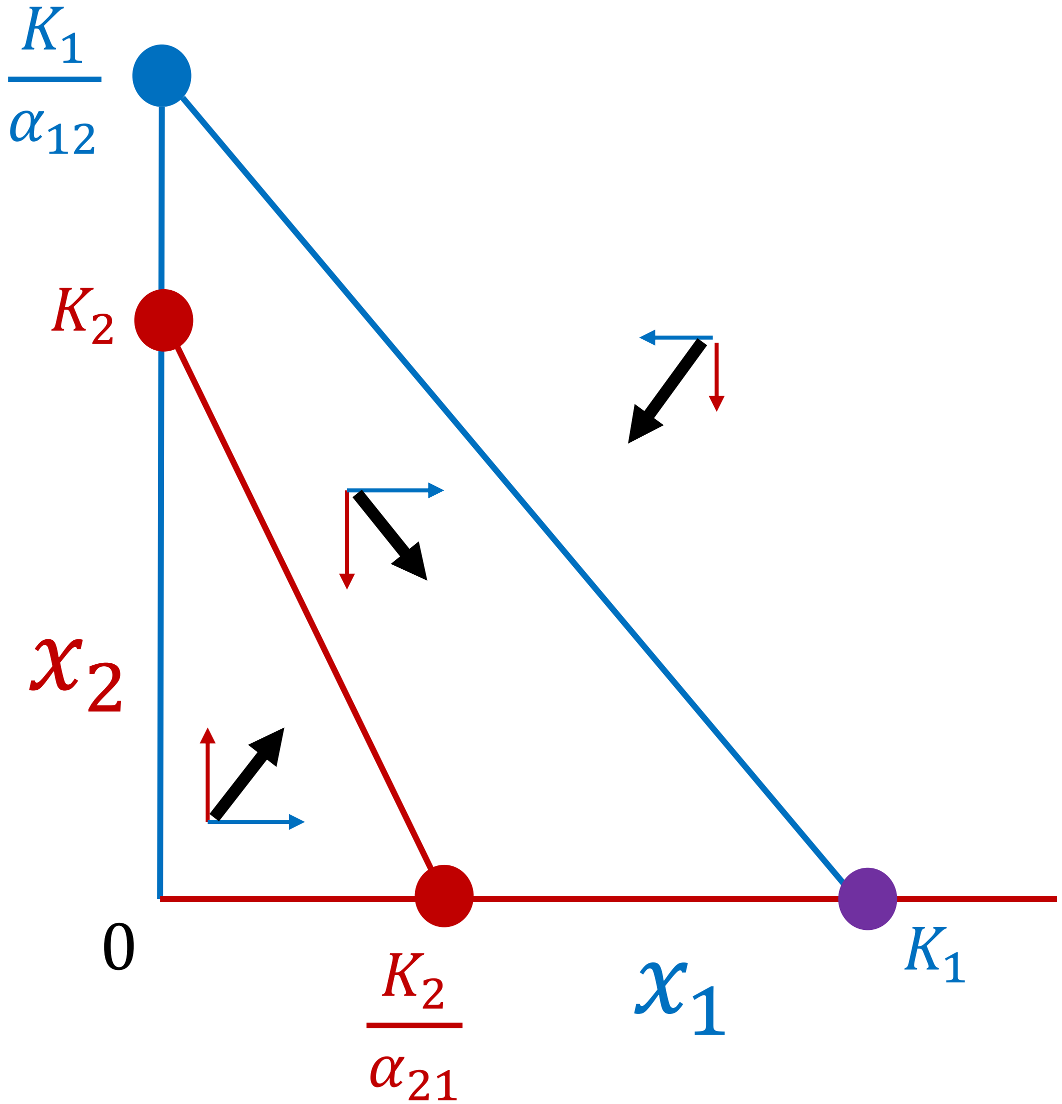
System collapses to equilibrium:

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



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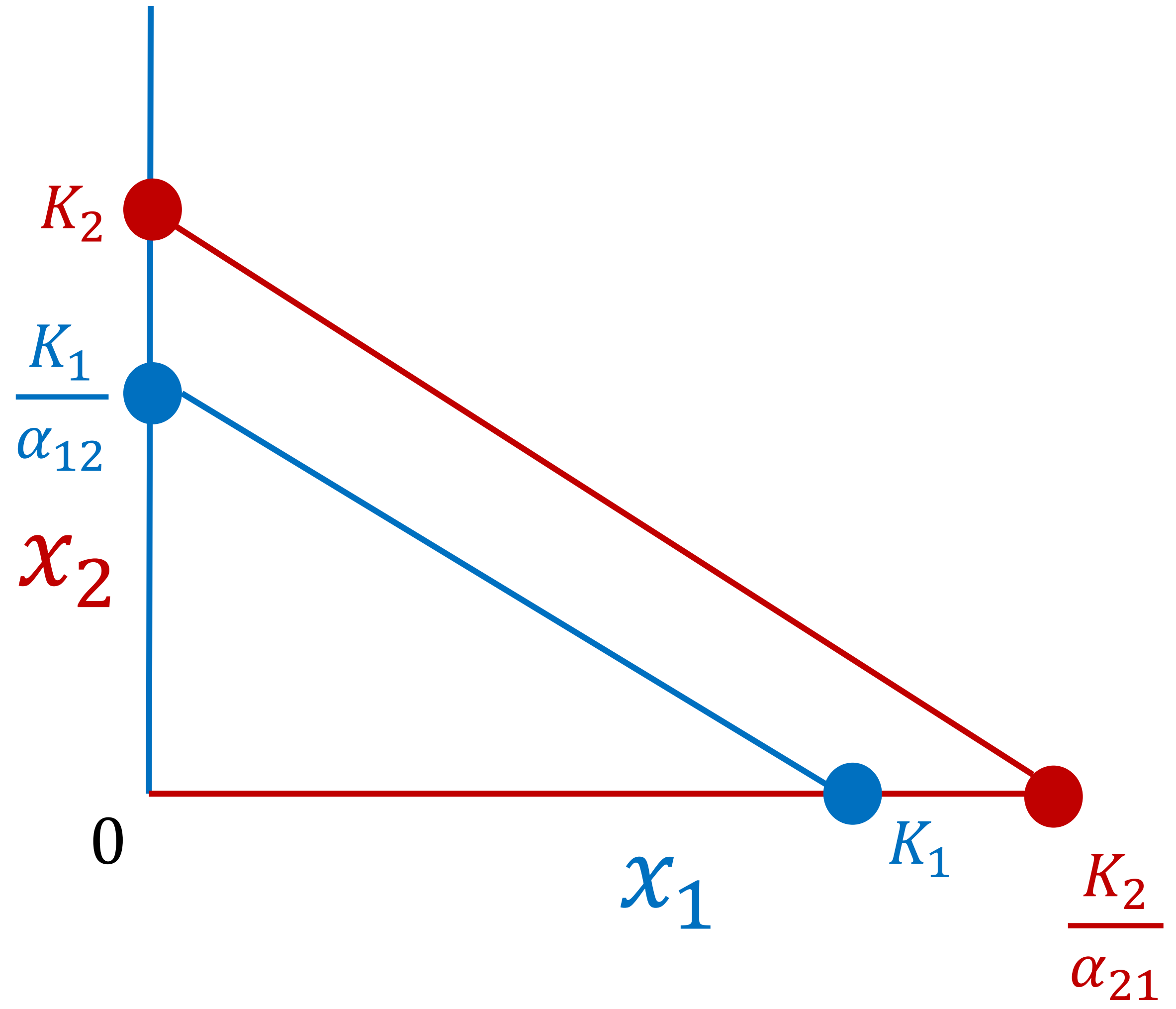

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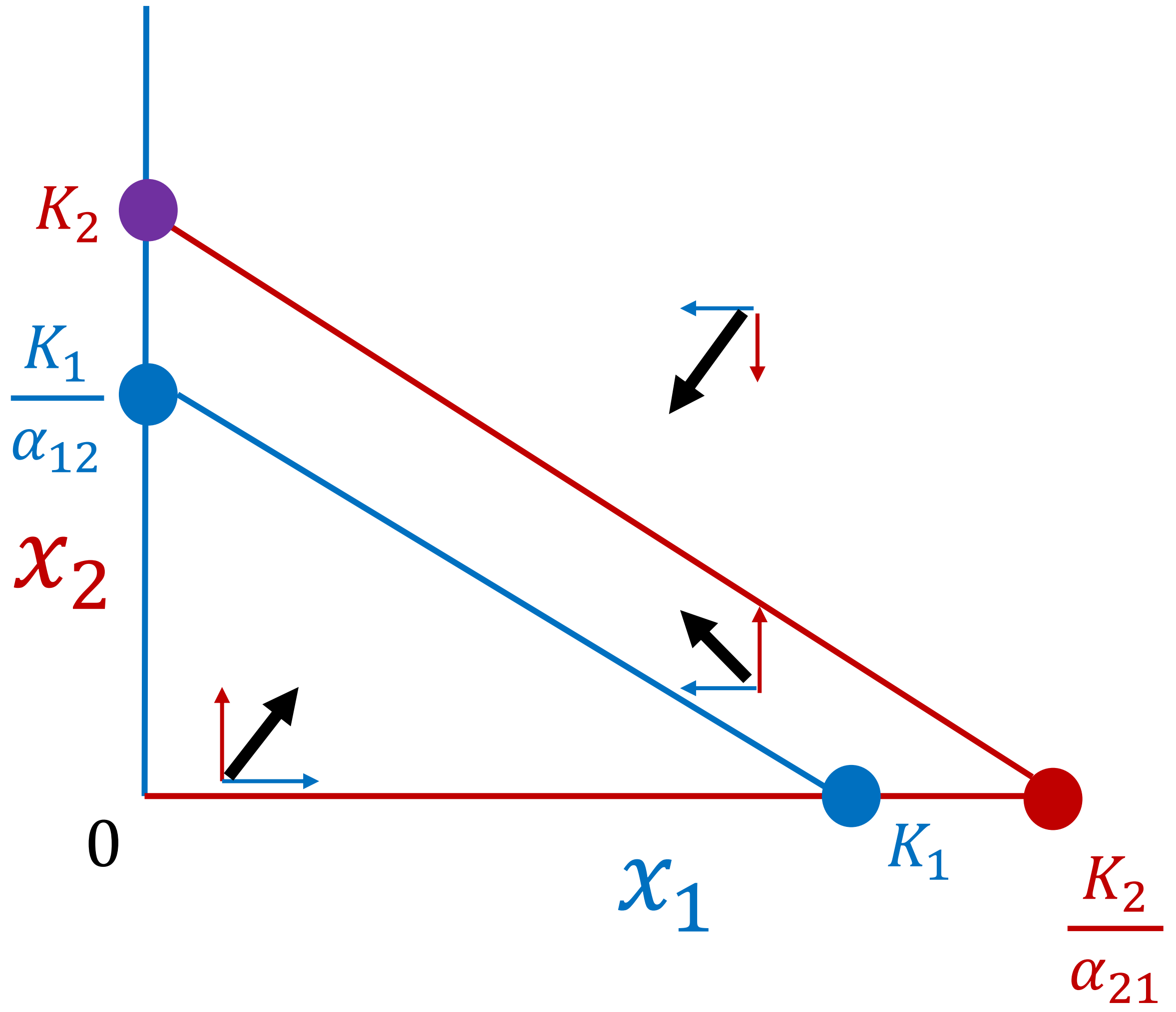
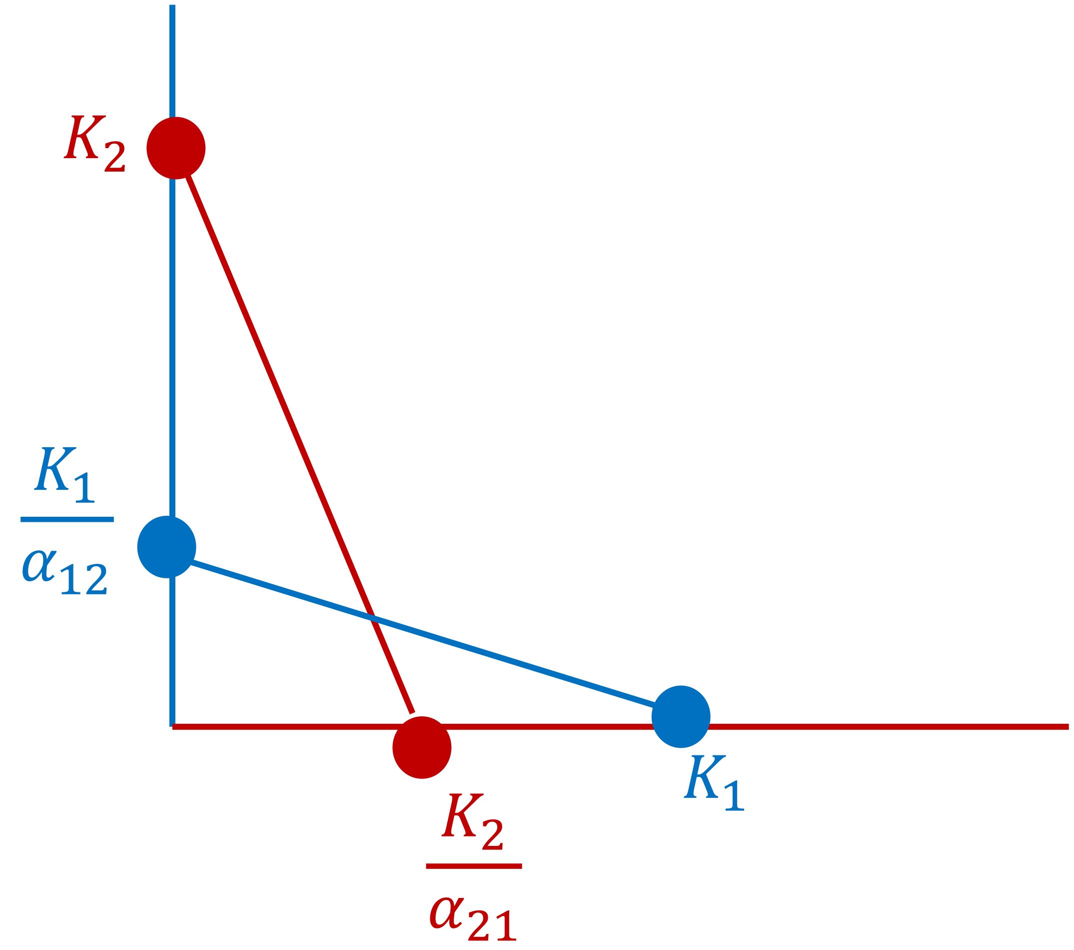


Four possible outcomes for competition

Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.



Four possible outcomes for competition

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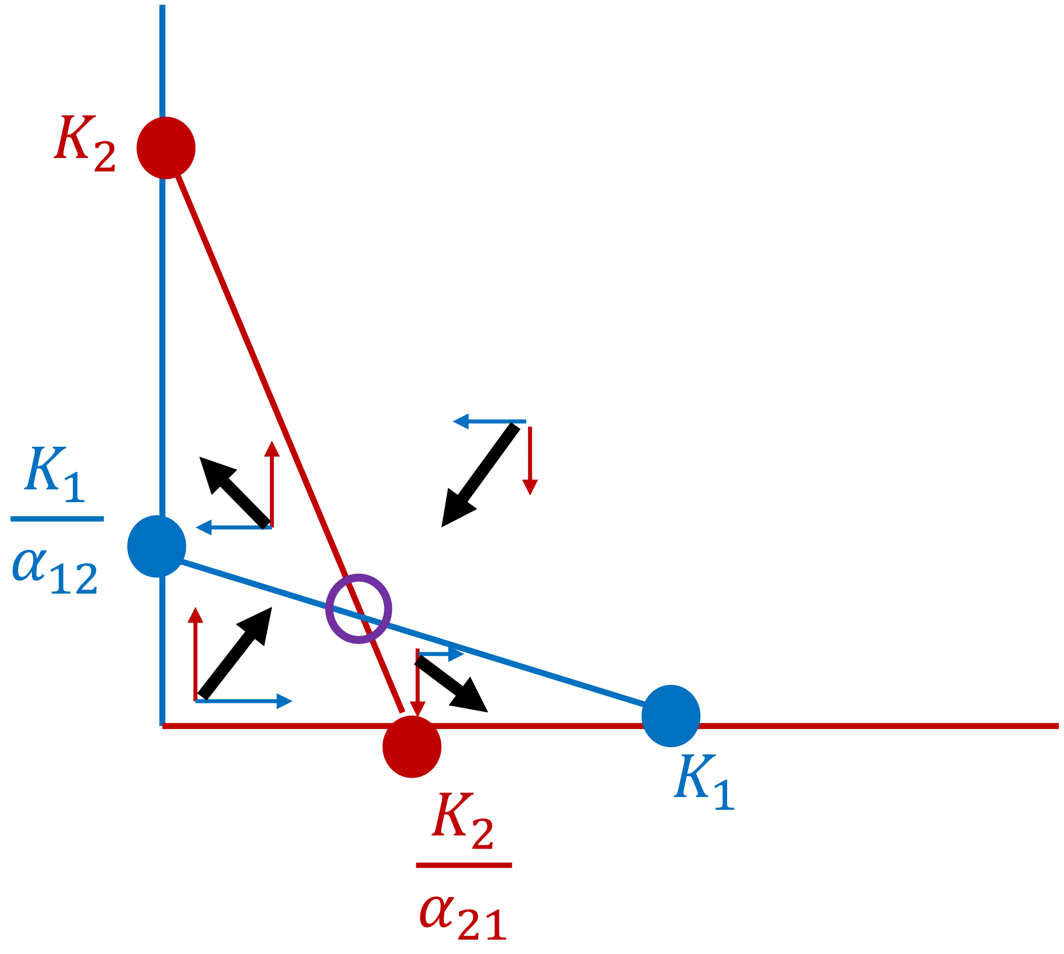
$$\frac{K_1}{\alpha_{12}} < K_2 \;\&\; \frac{K_2}{\alpha_{21}} < K_1$$

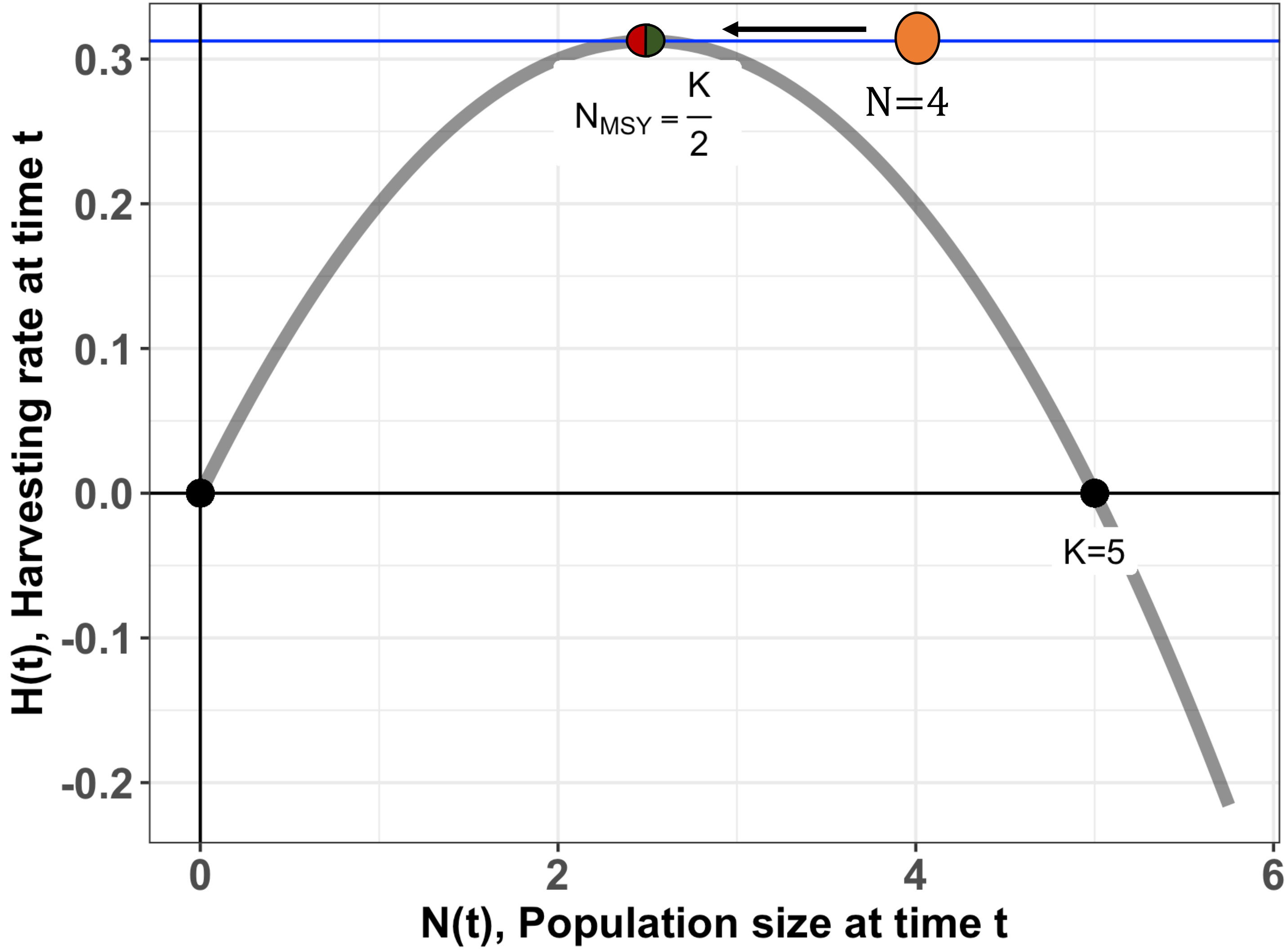
$$(\alpha_{12} * \alpha_{21} > 1)$$

- **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.



Remember MSY, the semi-stable equilibrium:

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



K=5

r=0.25

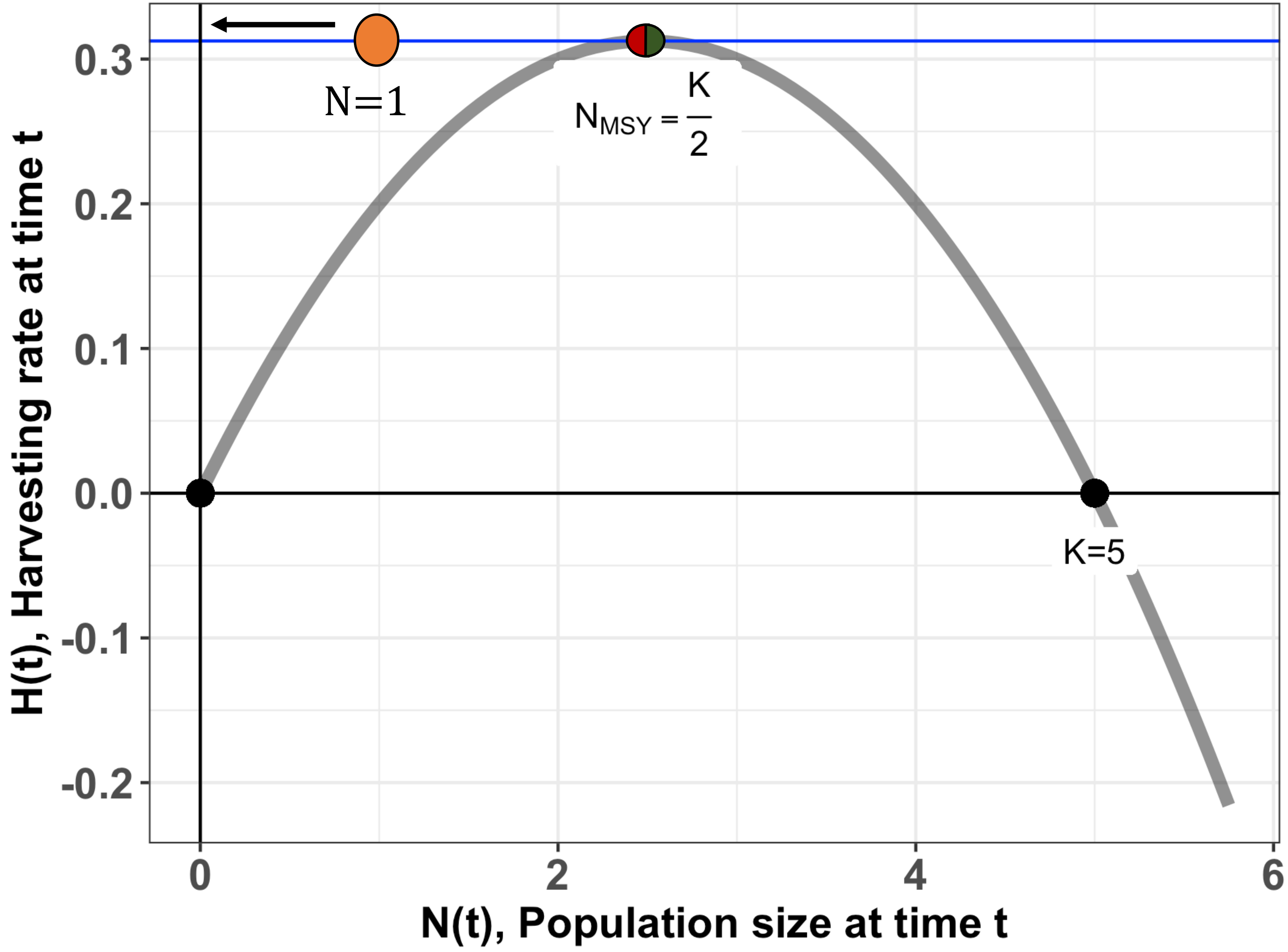
H=.3125

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

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

Remember MSY, the semi-stable equilibrium:

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



K=5

r=0.25

H=.3125

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

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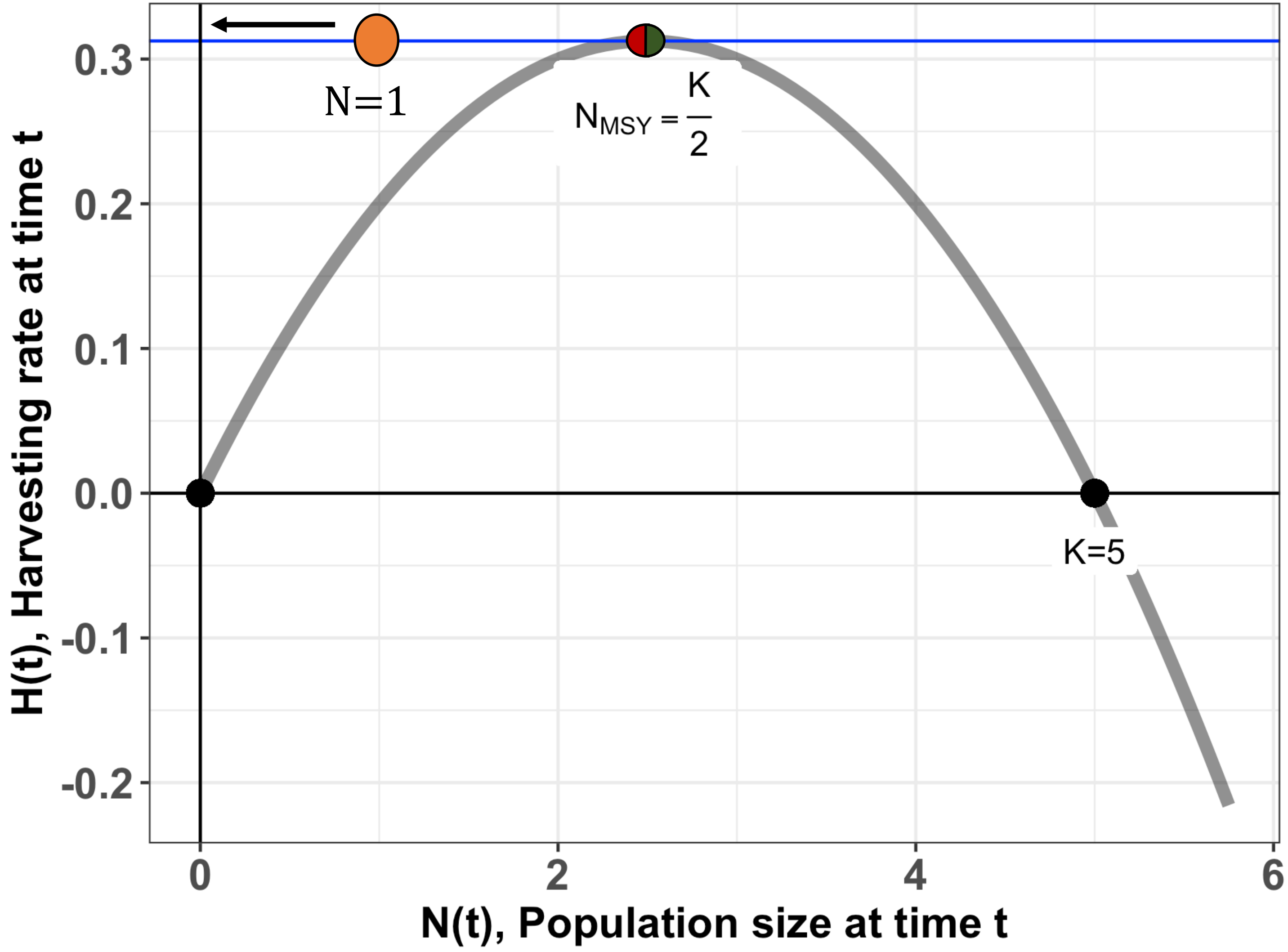


K=5
r=0.25
H=.3125

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

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

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

Four possible outcomes for competition

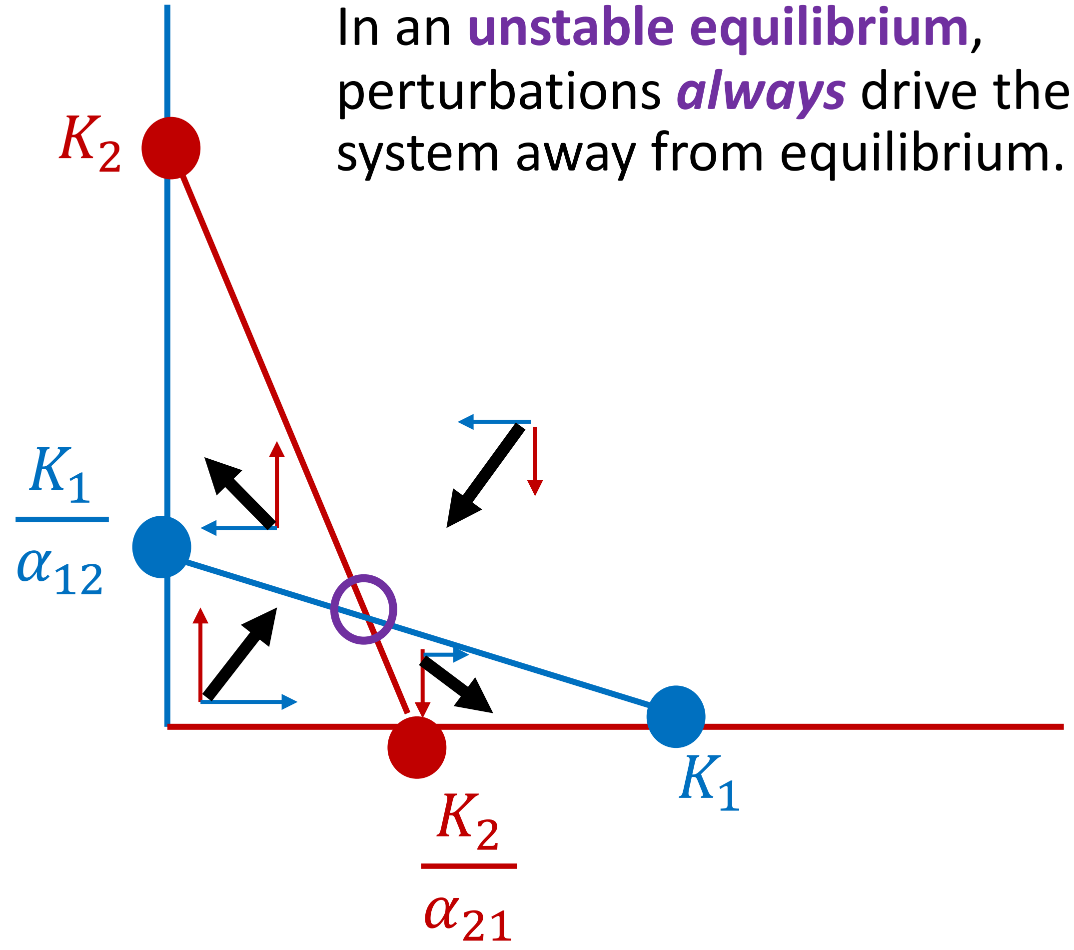
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

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

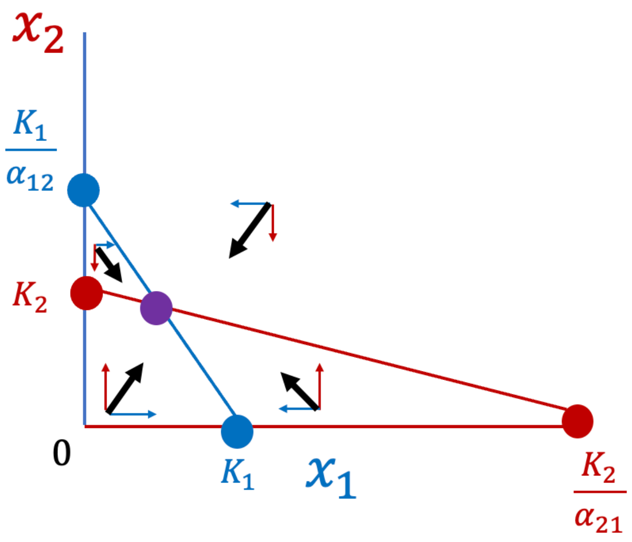
$$(\alpha_{12} * \alpha_{21} > 1)$$



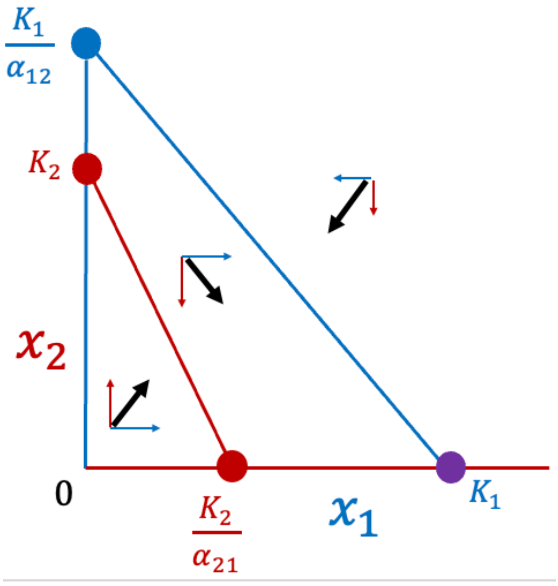
In an **unstable equilibrium**, perturbations ***always*** drive the system away from equilibrium.

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

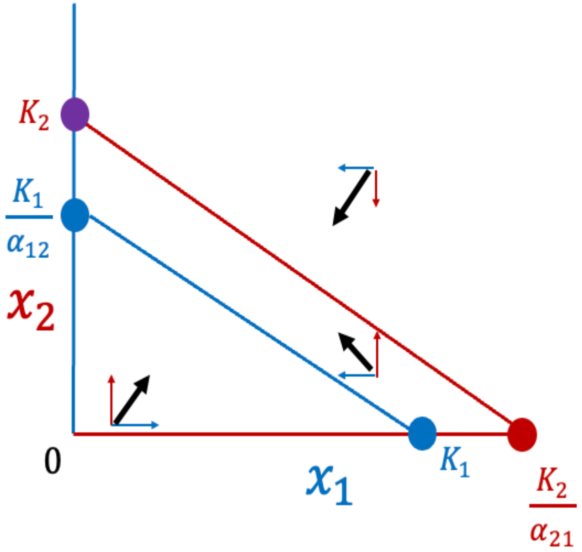
Case 1: Stable coexistence



Case 2: Spp. 1 wins



Case 3: Spp. 2 wins



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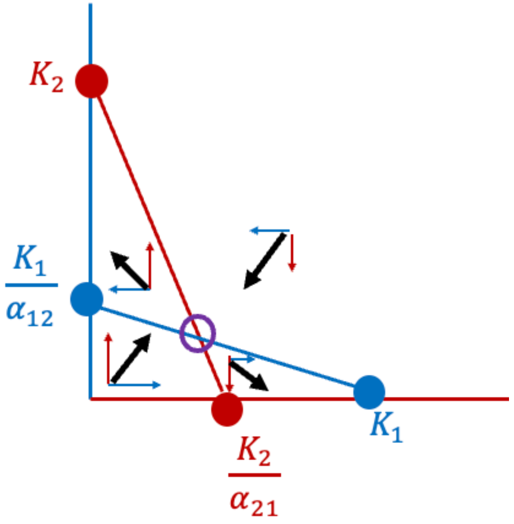
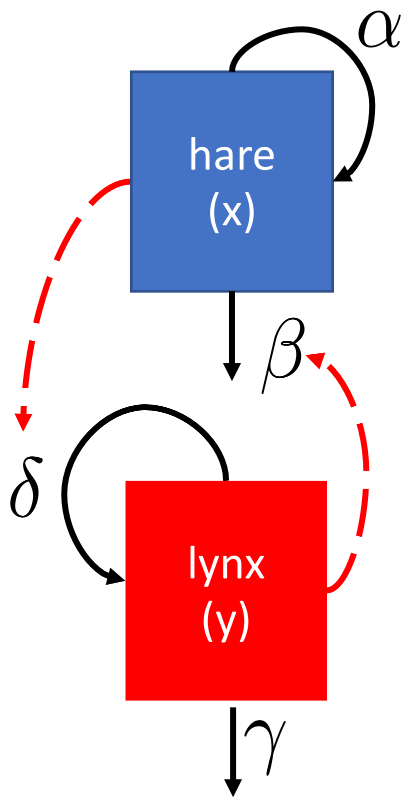


Note the difference with a predator-prey model!

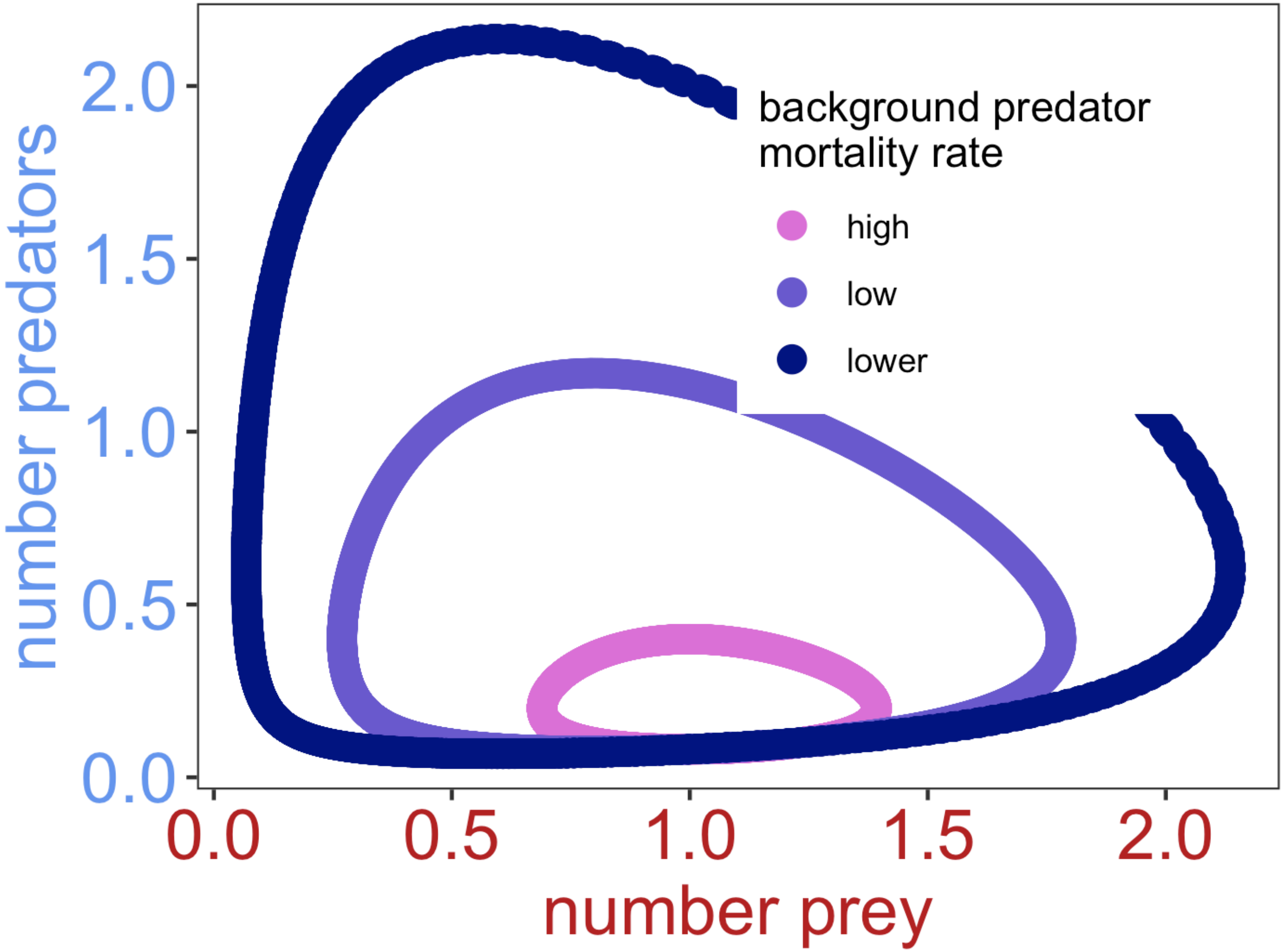


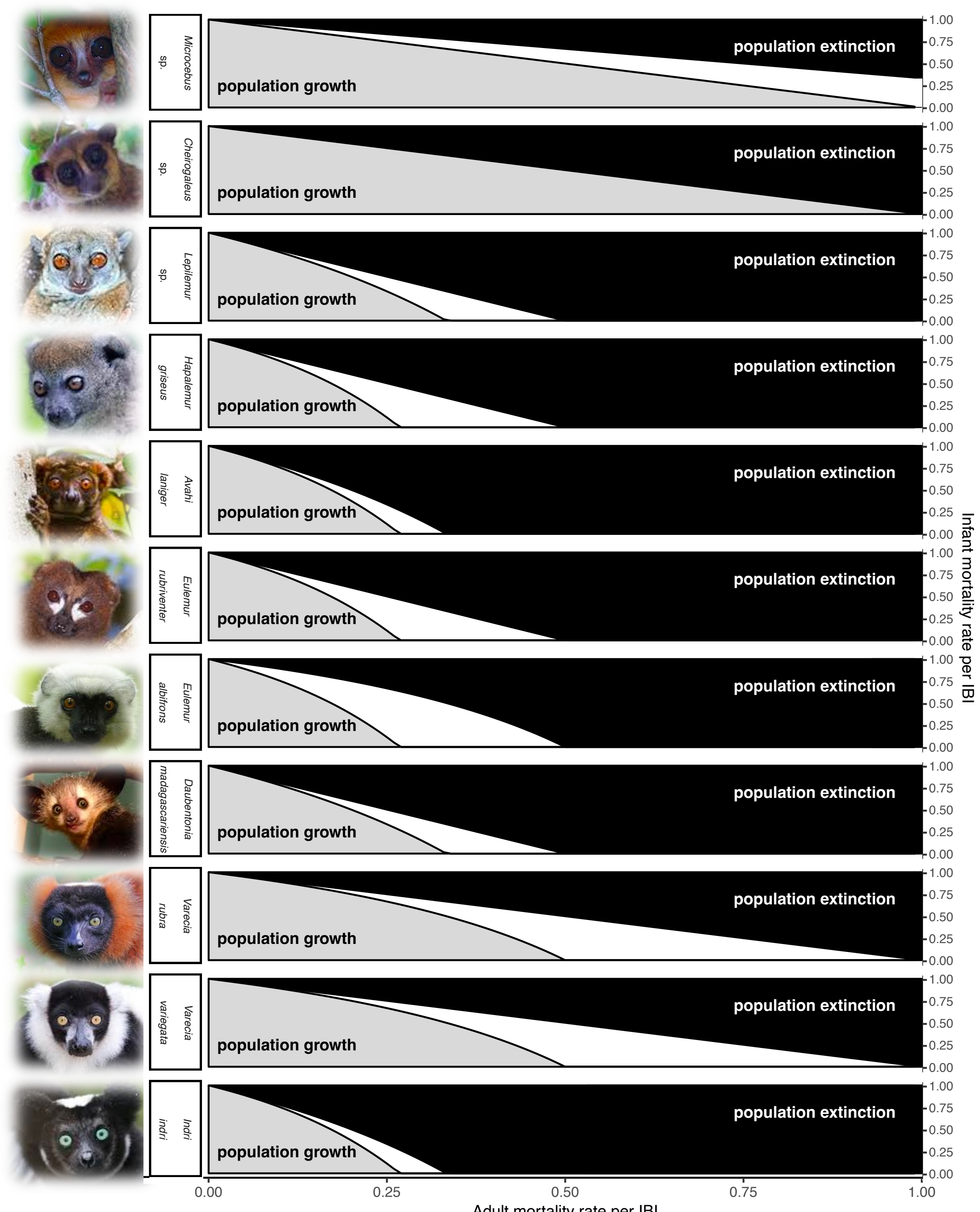
$$\frac{dx}{dt} = \alpha x - \beta xy$$

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

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

Predator-prey cycles can be visualized as oscillations.





We've seen **zero-growth isoclines** before:

$$N_{t+1} = AN_t$$

$$\begin{array}{ccc} \mathbf{N_{t+1}} & \mathbf{A} & \mathbf{N_t} \\ \begin{bmatrix} J \\ A \end{bmatrix}_{t+1} = & \begin{bmatrix} 0 & s_A F_A \\ s_J & s_A \end{bmatrix} & \begin{bmatrix} J \\ A \end{bmatrix}_t \end{array}$$

We can explore the
zero-growth isocline of λ = 1
for differing values of s_J, s_A, and F_A.

N *= population vector*
A *= transition matrix*

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

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"Neither can live while the other survives."

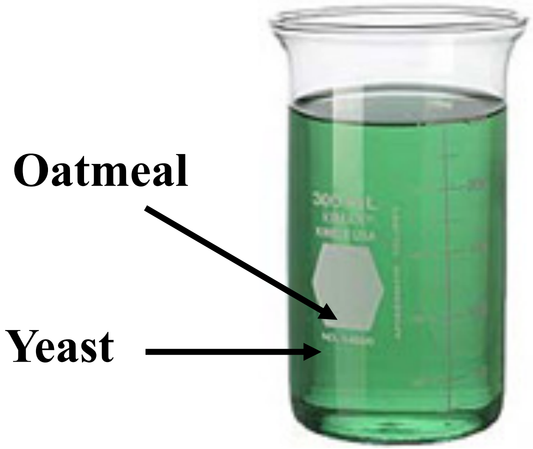
\- J.K. Rowling, 2003

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

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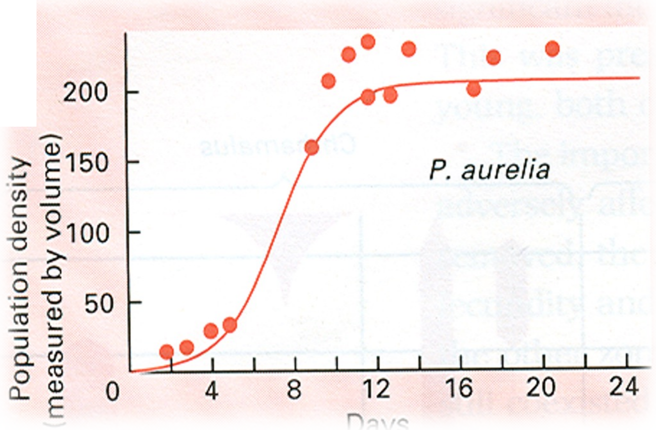
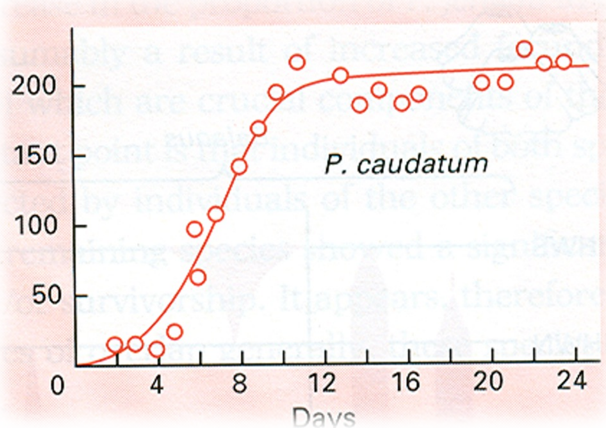
In isolation, each species grew logistically.

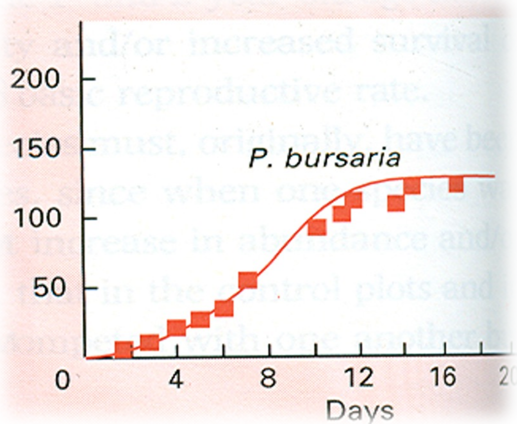
Paramecium aurelia

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

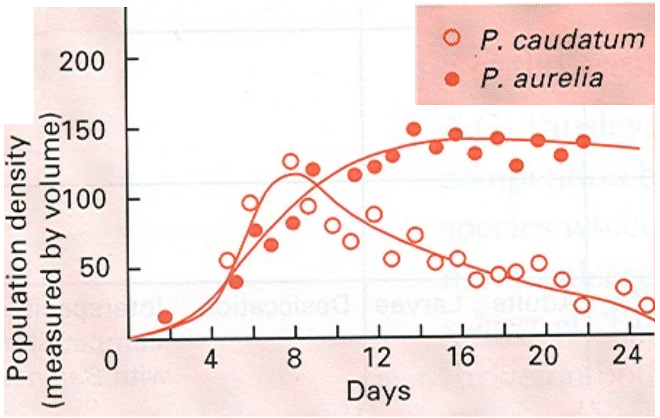
Paramecium bursaria

Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

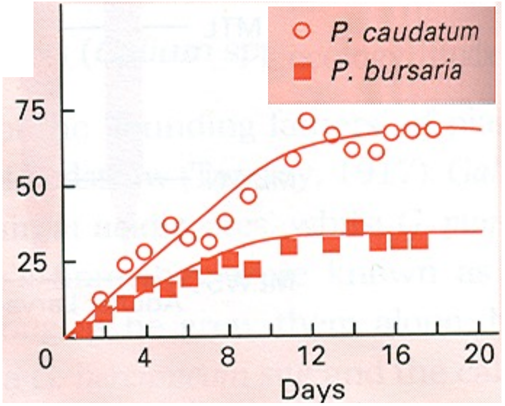
Competitive exclusion was observed:

Paramecium aurelia ***Paramecium caudatum***



Coexistence was observed:

Paramecium caudatum ***Paramecium bursaria***



Gause 1934. *J Experimental Biology.*
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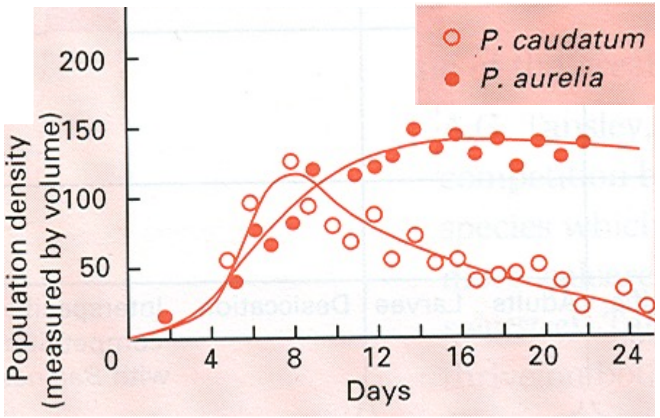
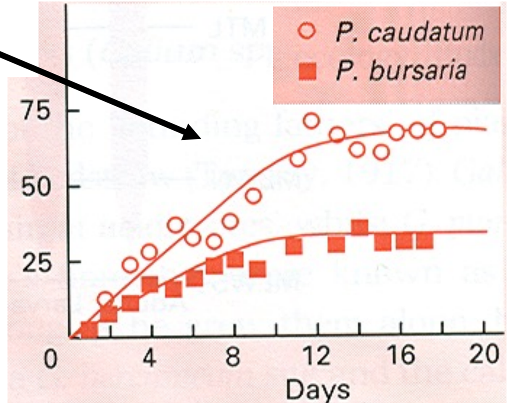


Species coexisted below each species' respective individual carrying capacity.



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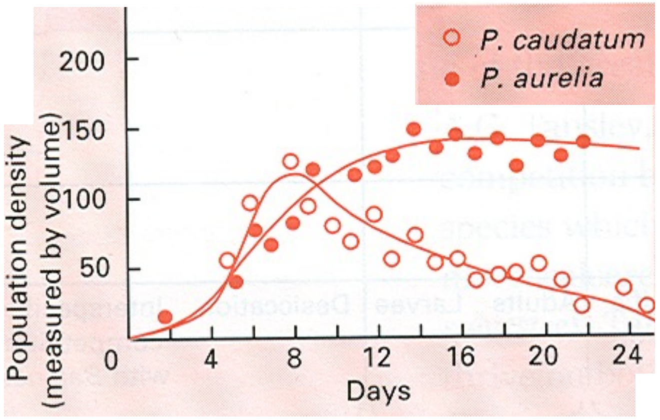
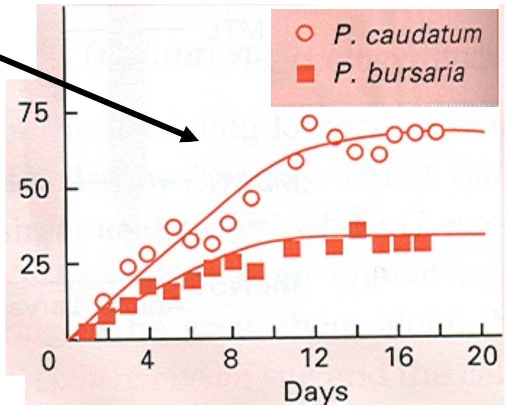


Species coexisted below each species' respective individual carrying capacity.

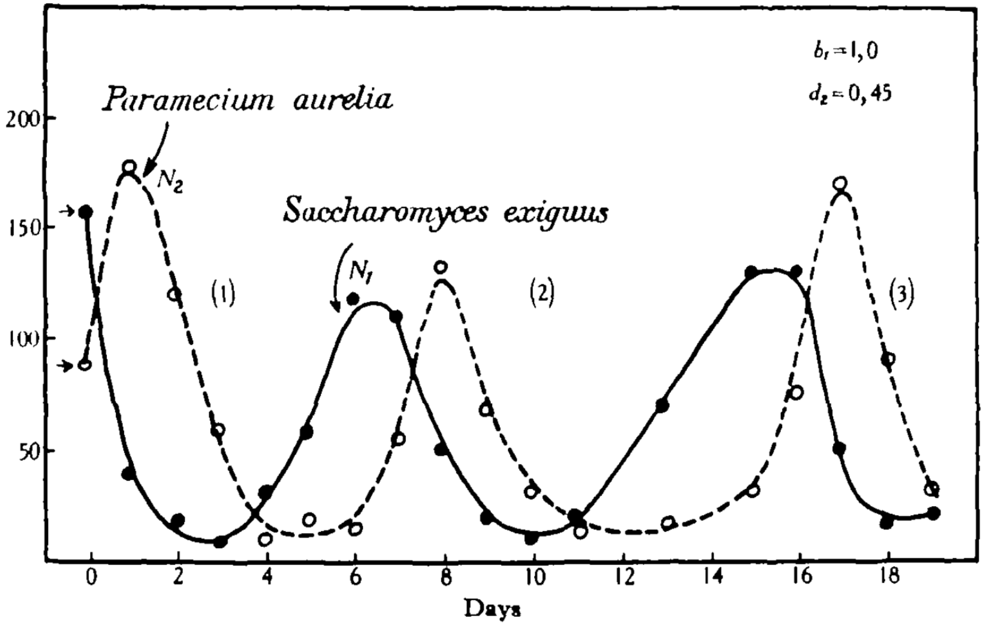
The two coexisting species were largely partitioned in space. *P. bursaria* ate yeast at the bottom and *P. caudatum* consumed bacteria suspended in the medium.

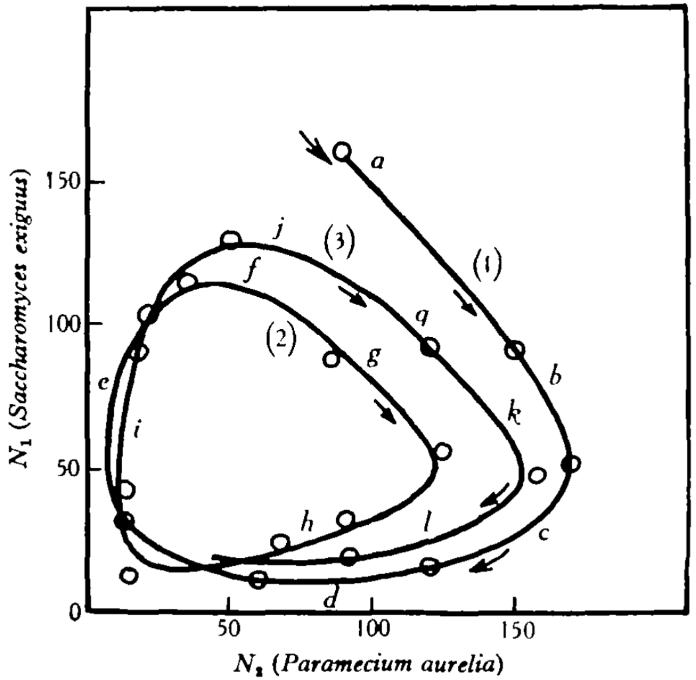


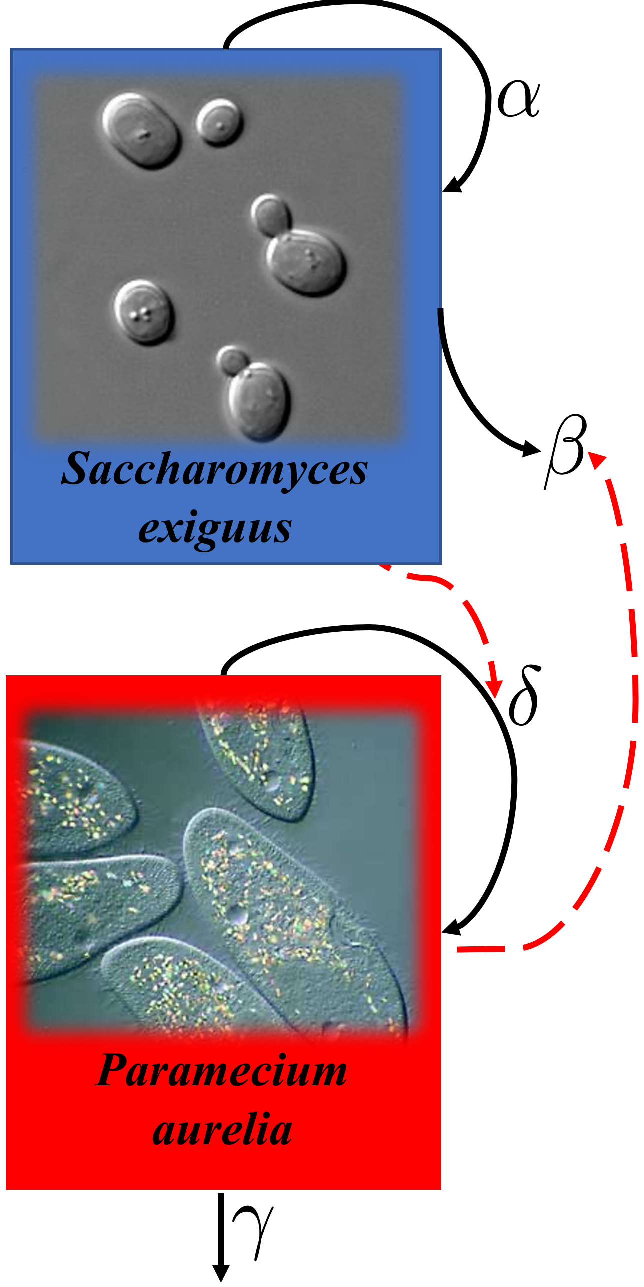
Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

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

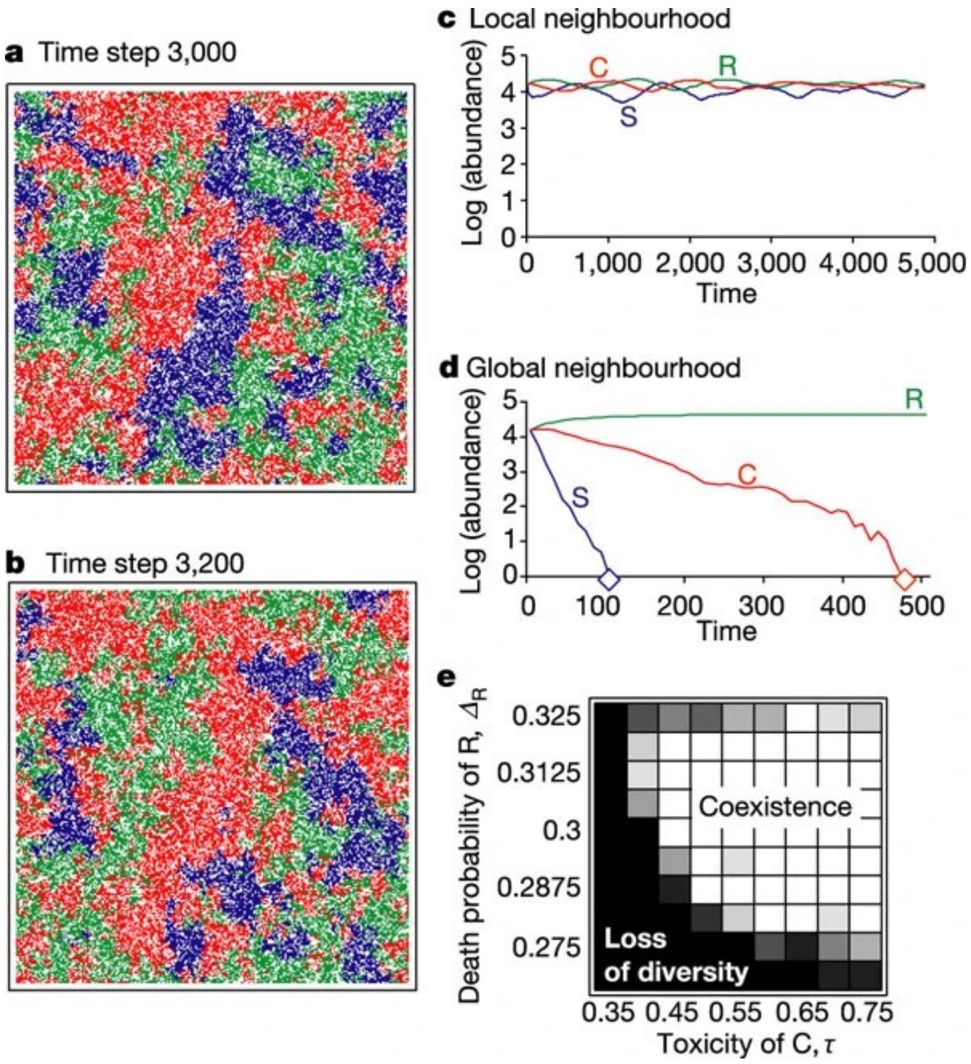






Gause 1935. *Science.*

Sometimes **stochasticity** and **space** are all you need to ensure **coexistence** in a competitive environment



Kerr et al. 2002. *Nature.*

- Kerr et al. modeled a community of 3 strains of *E. coli* with **overlapping resource requirements** (C,R, and S), occupying distinct spatial patches in a metapopulation.

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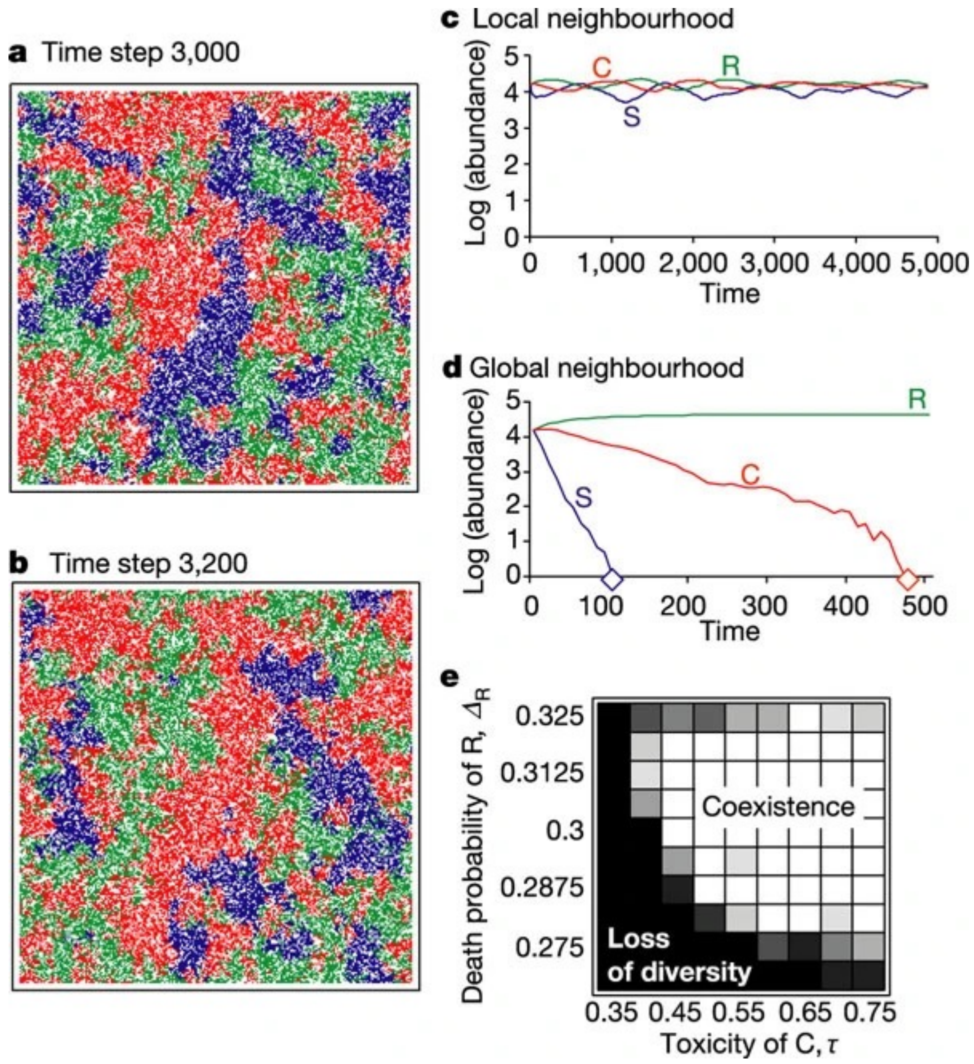

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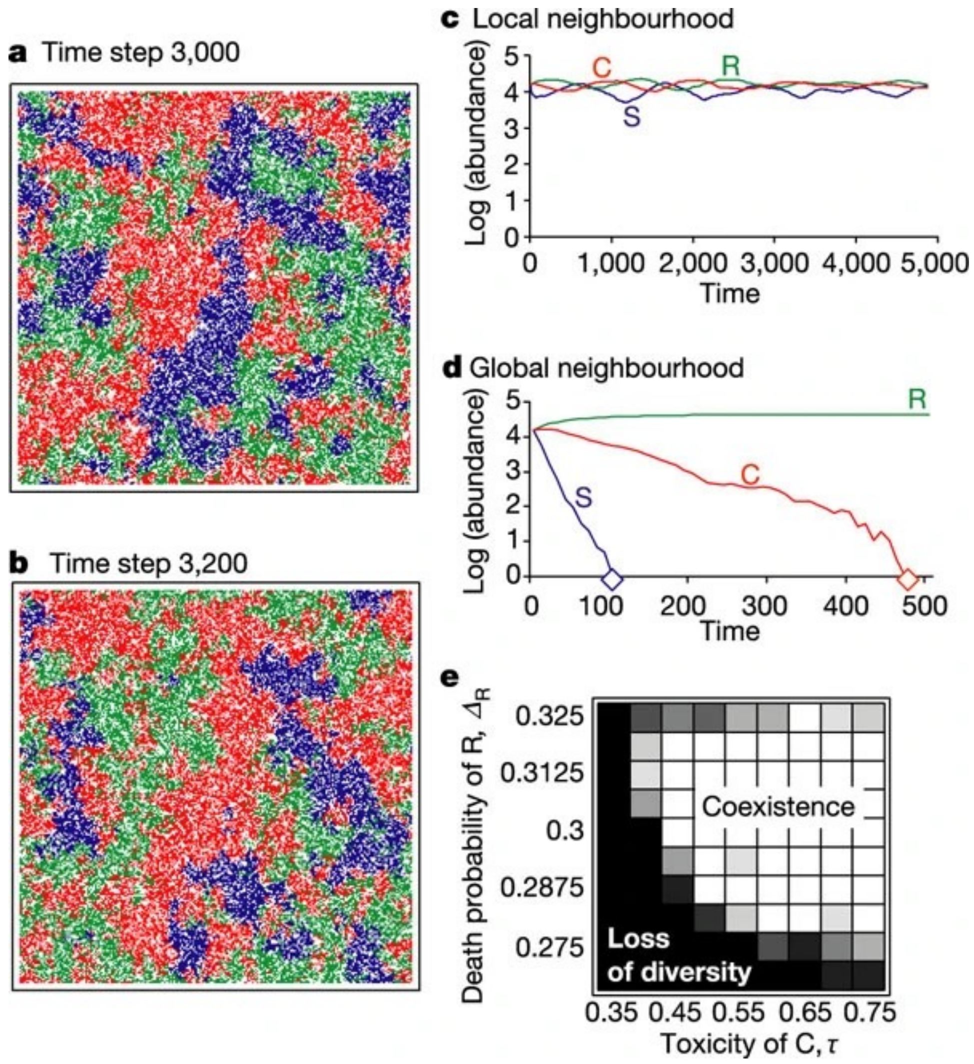

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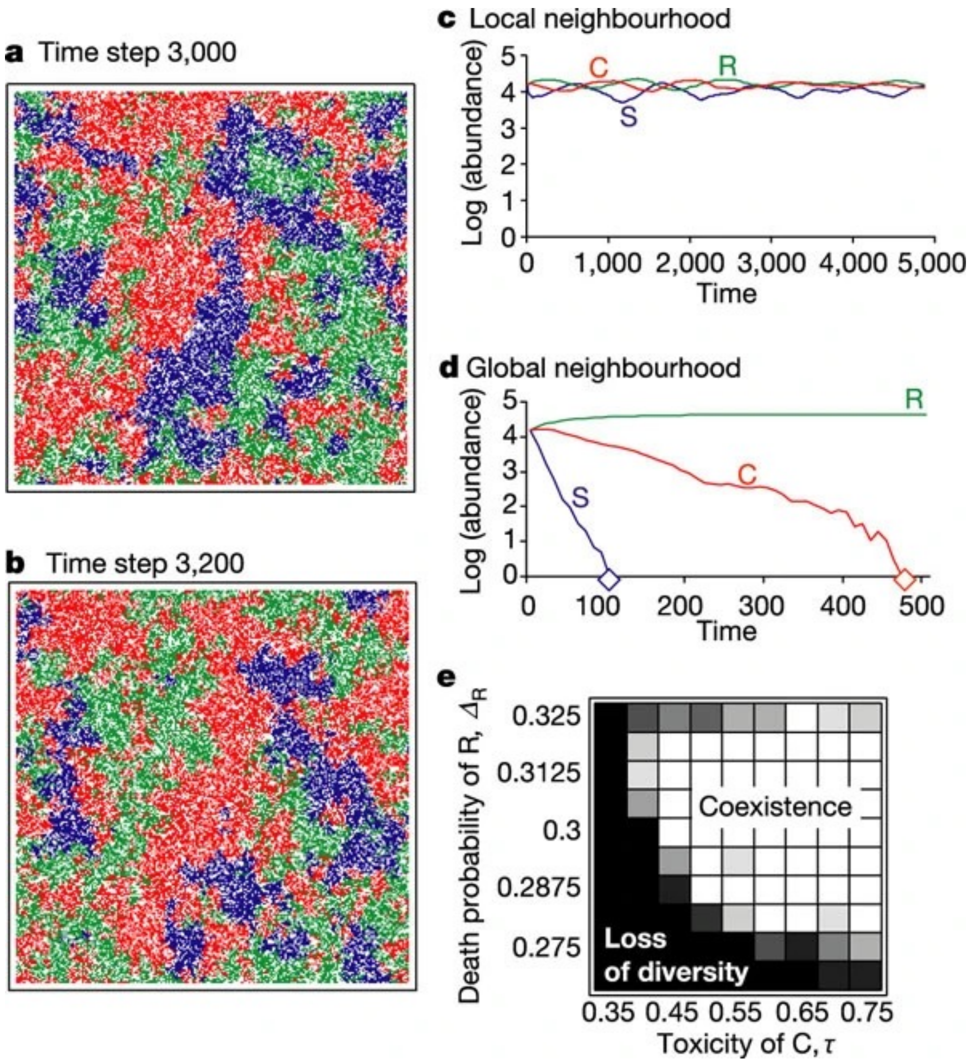
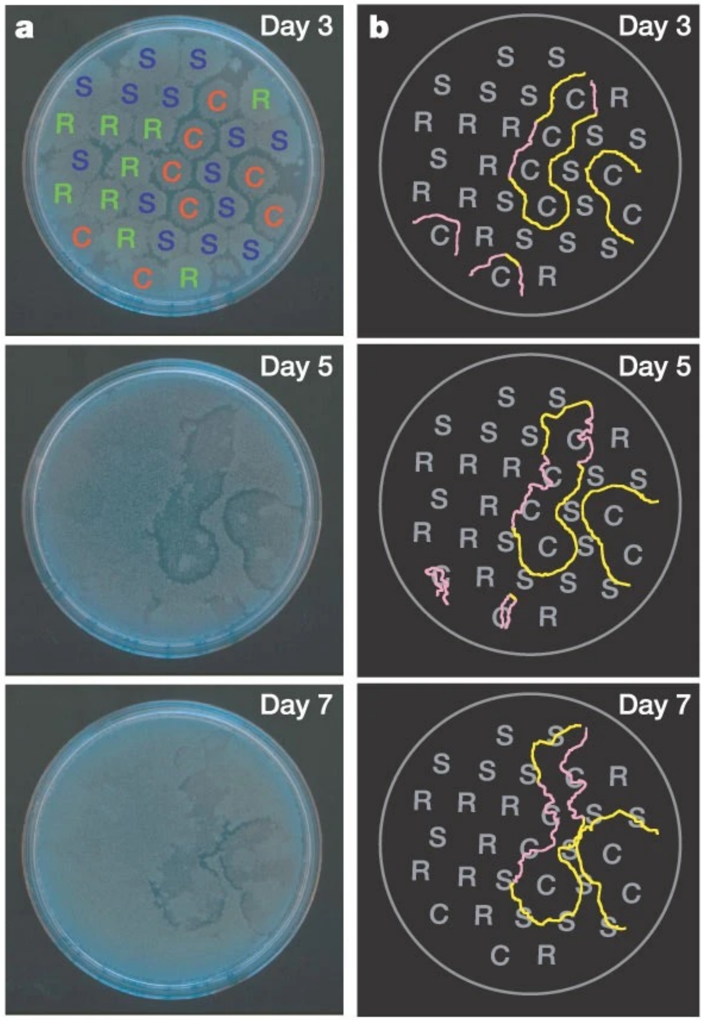
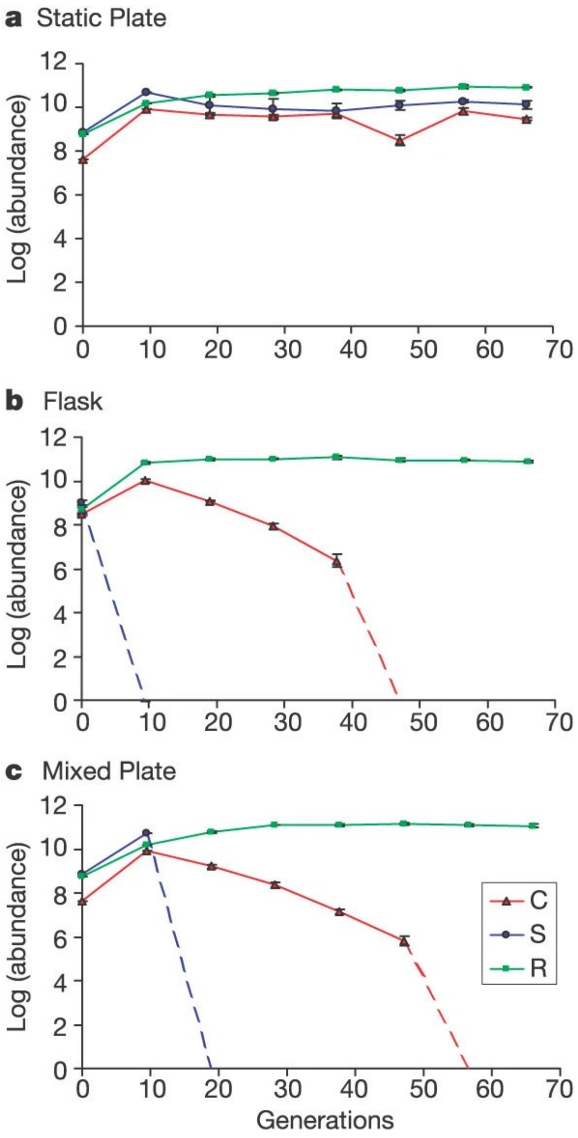
- They produced simulations allowing for a perfectly mixed population (global neighborhood), or a population in which dispersal (mixing) happened only locally.

- **Local interactions allowed for the coexistence of all three strains** (in theory). What about experimentally?

Sometimes adding **stochasticity** and **space** (remember metapopulations!) is all you need to ensure **coexistence**!



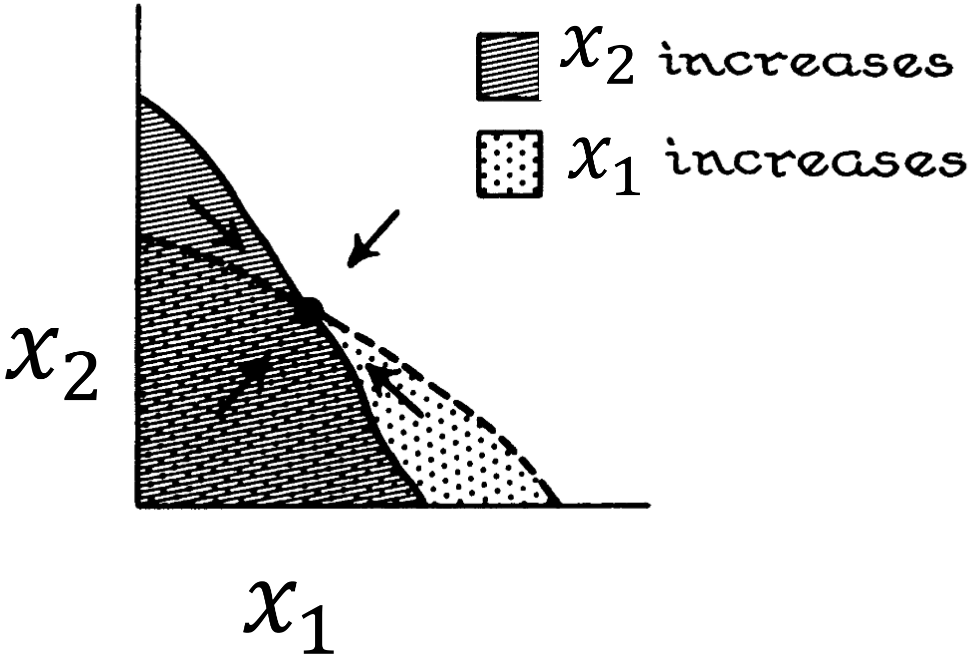




Kerr et al. 2002. *Nature.*

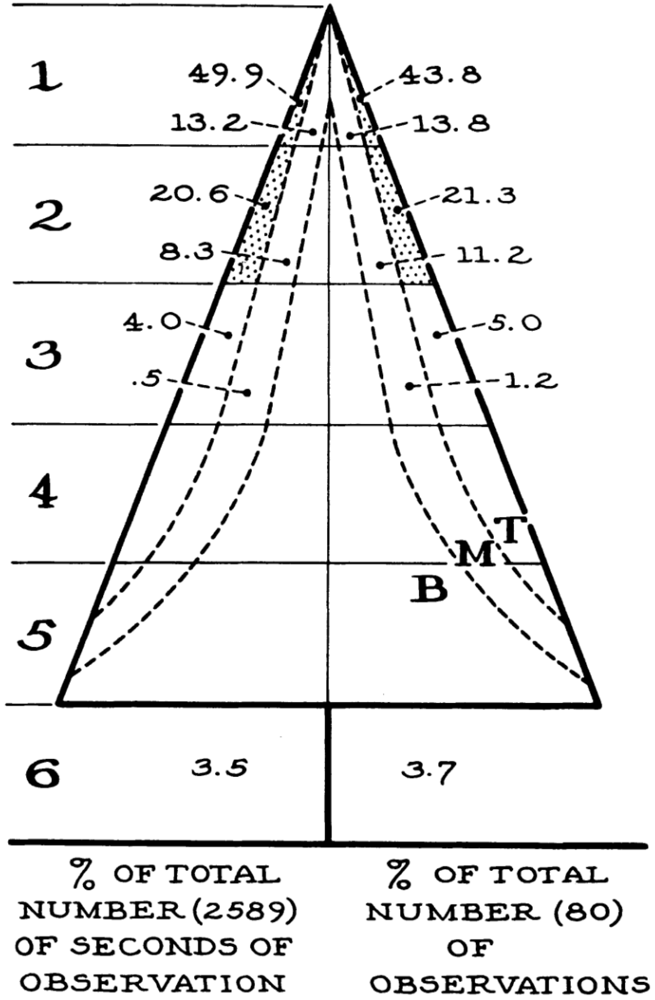
Niche partitioning enables organisms to avoid competitive exclusion

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

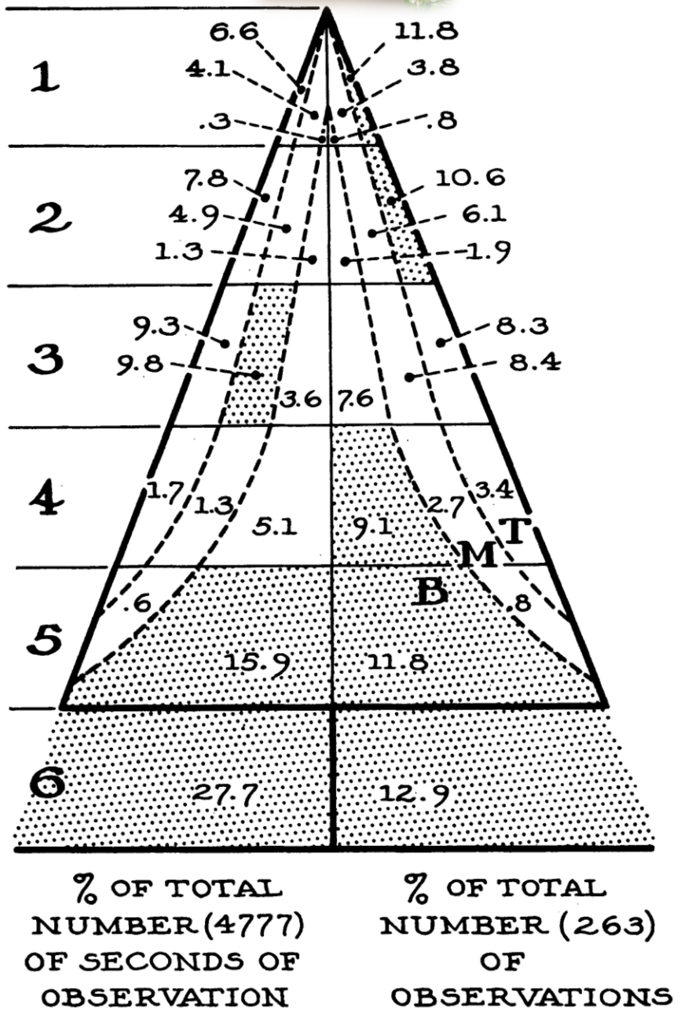


MacArthur 1968. *Ecology.*

Cape May Warbler

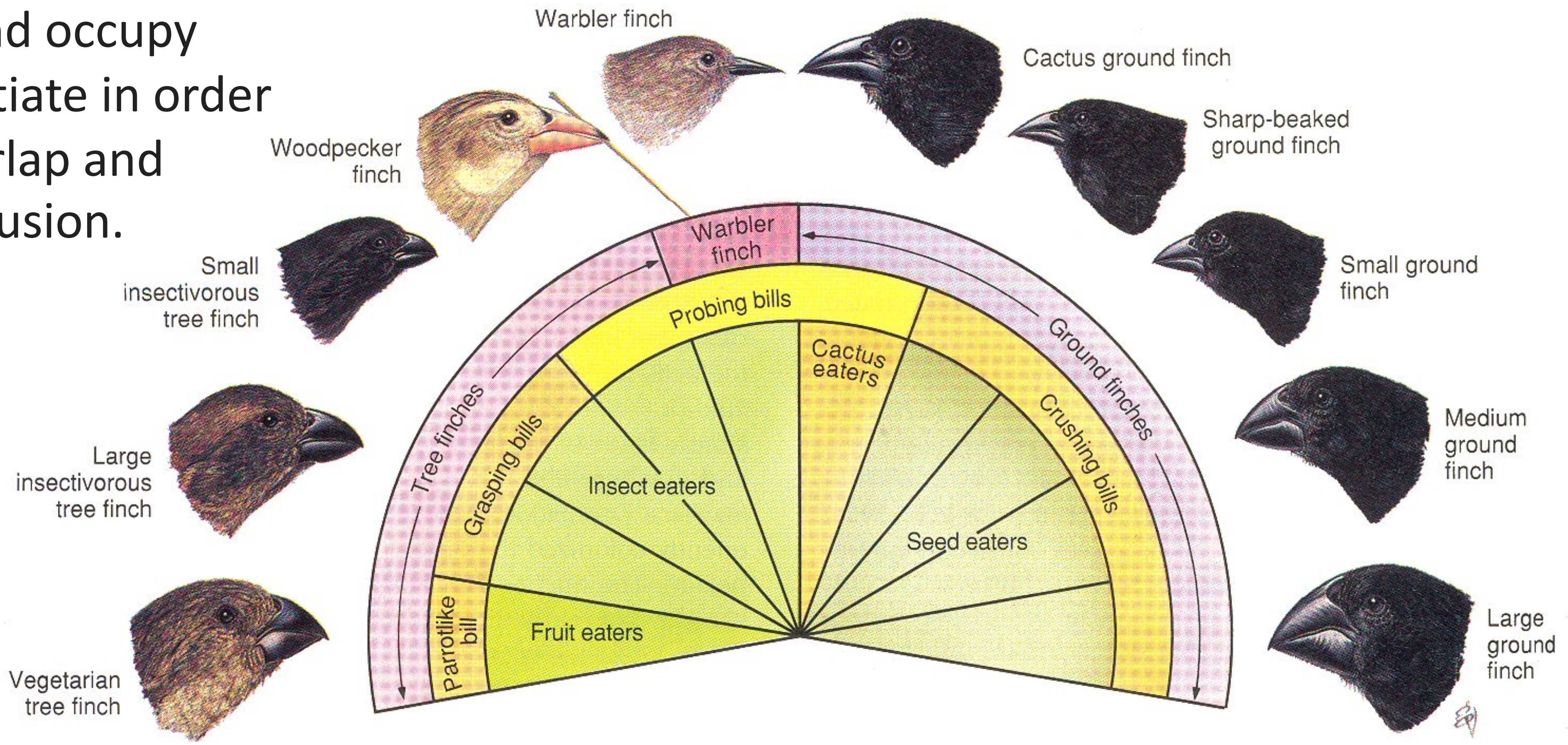


Myrtle Warbler



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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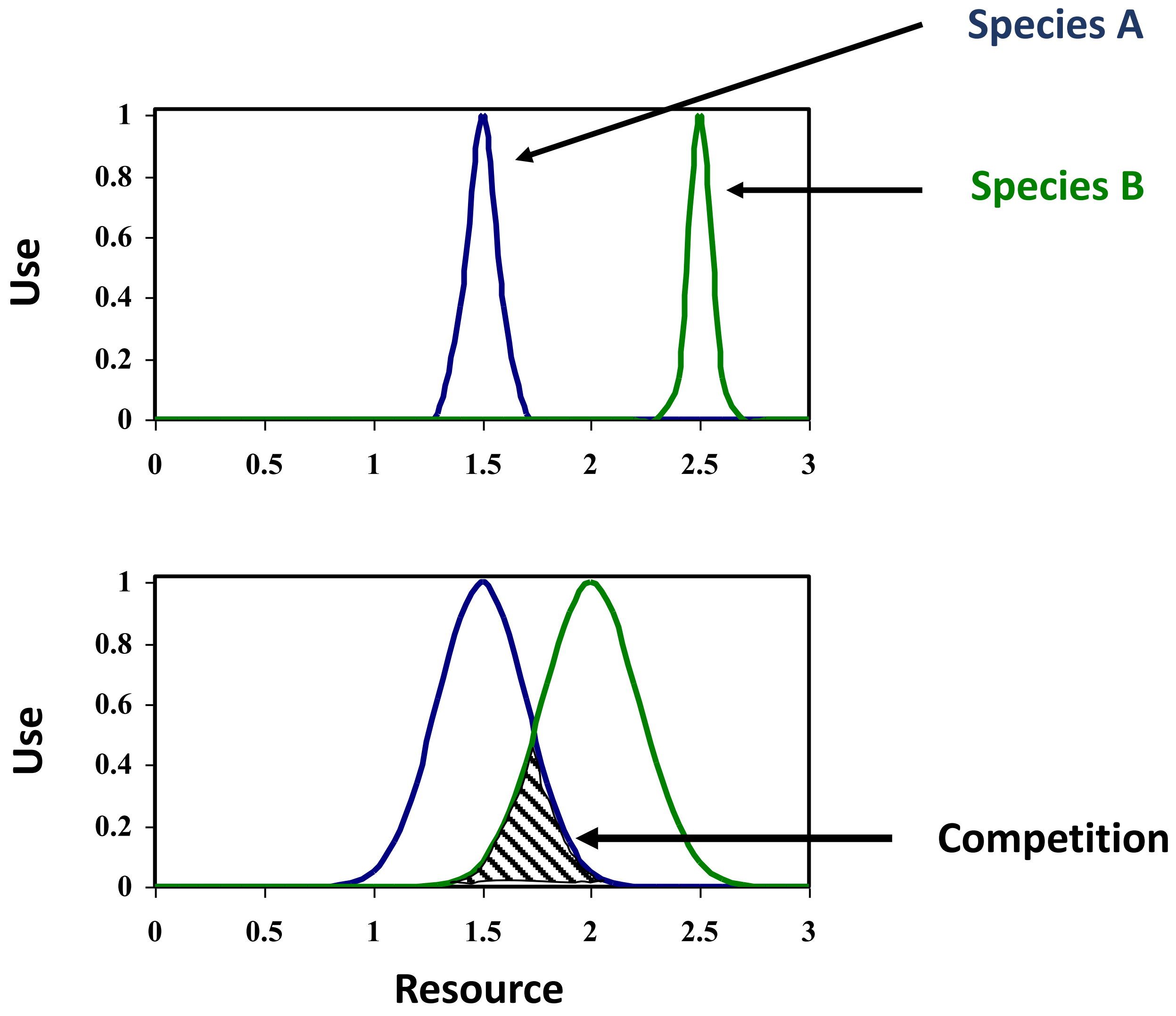
Grant & Grant 2006. *Science.*



When niches overlap, competition results

Niche partitioning enables organisms to avoid competitive exclusion

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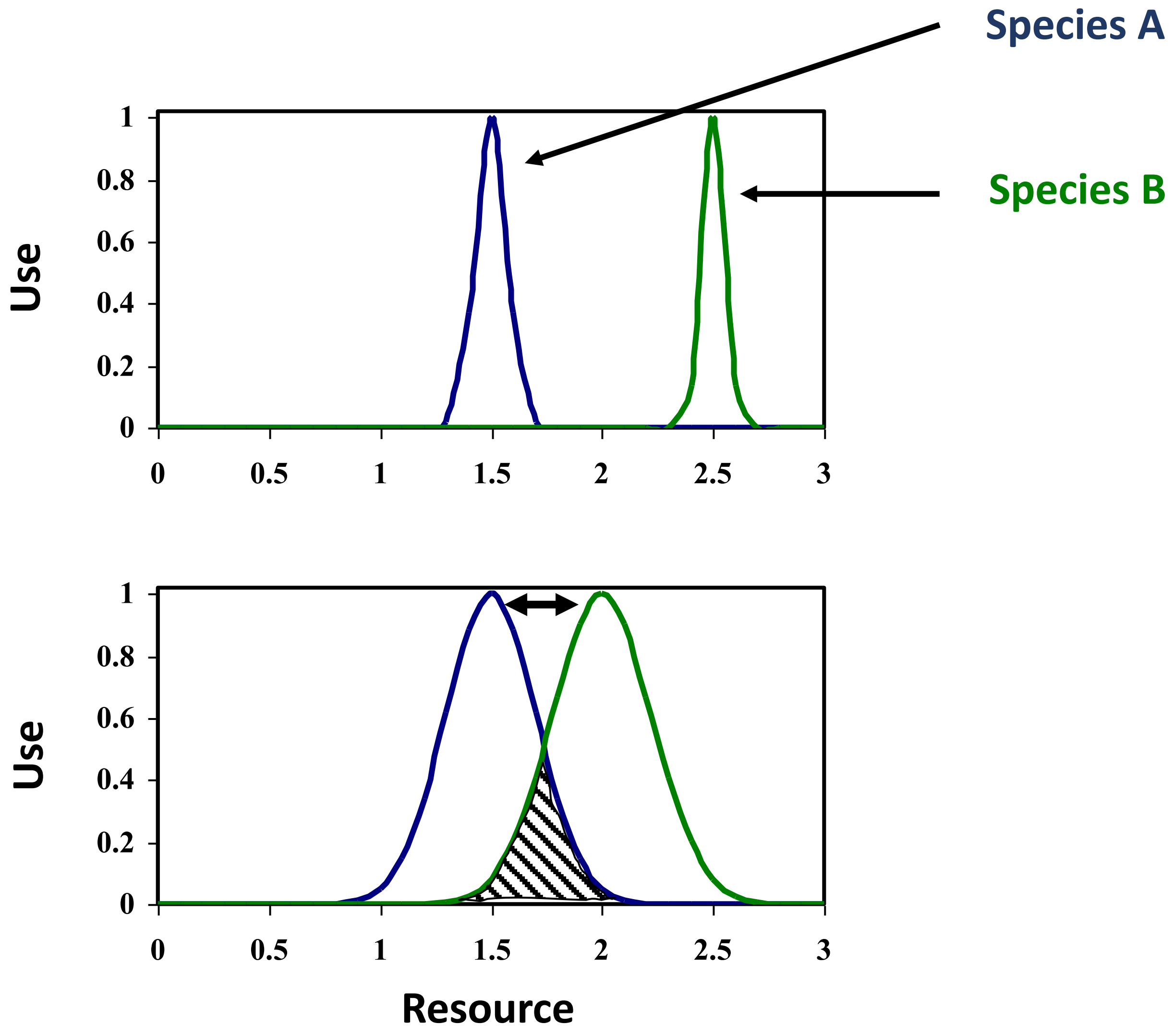
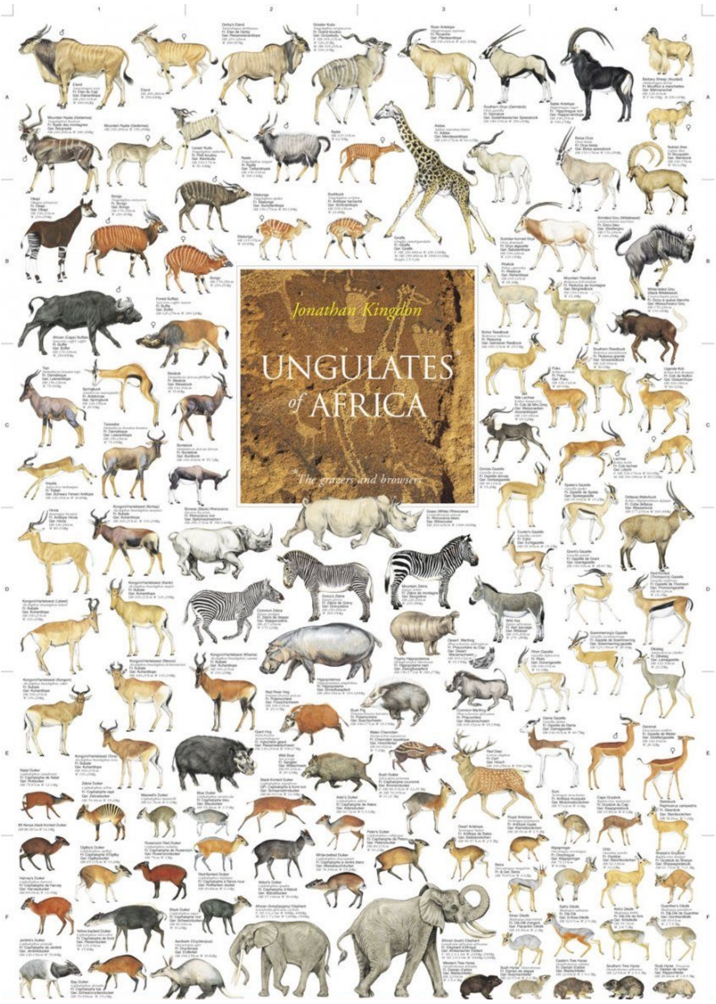
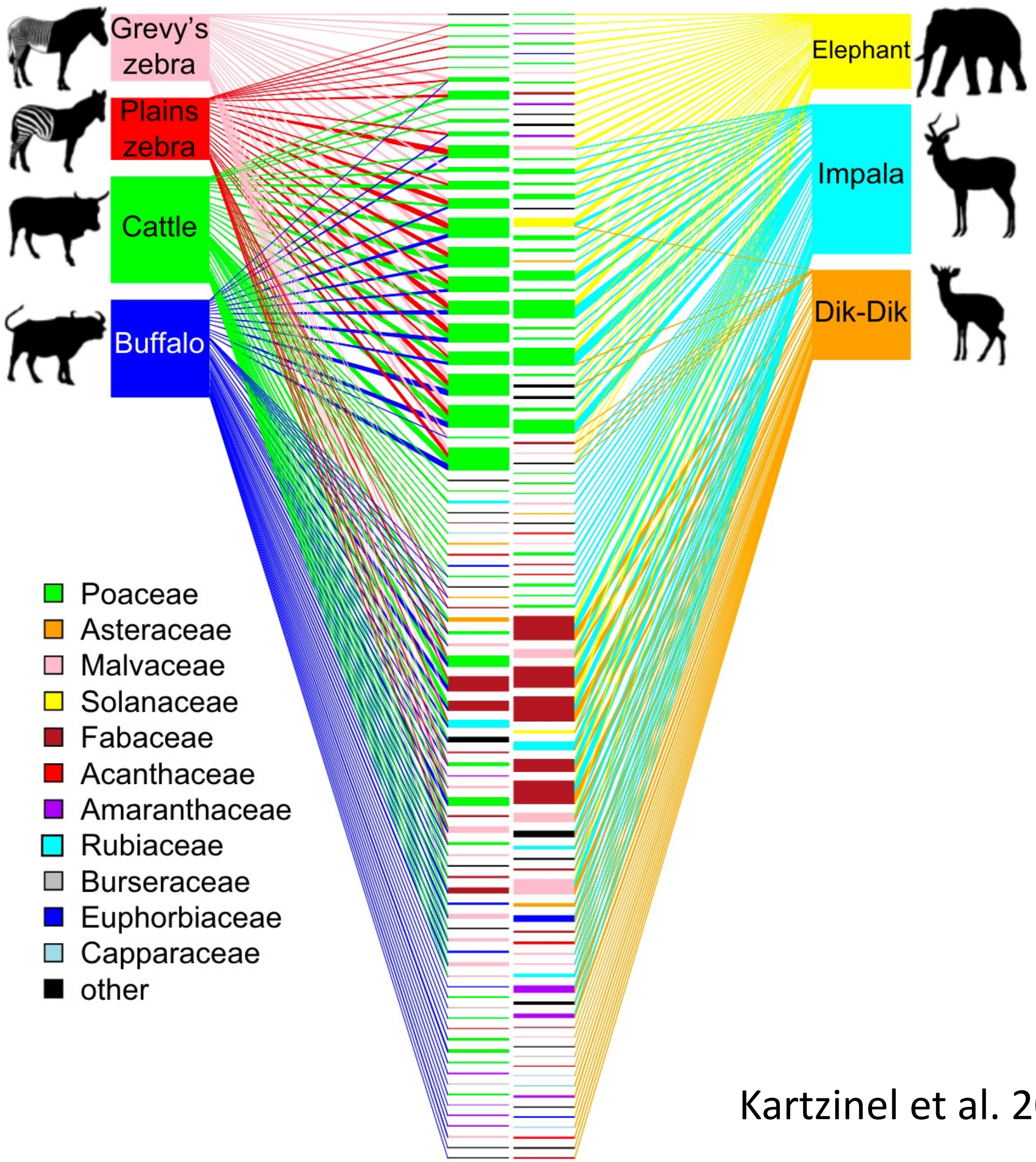


Character displacement forces niches apart.

Niche partitioning enables organisms to avoid competitive exclusion

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

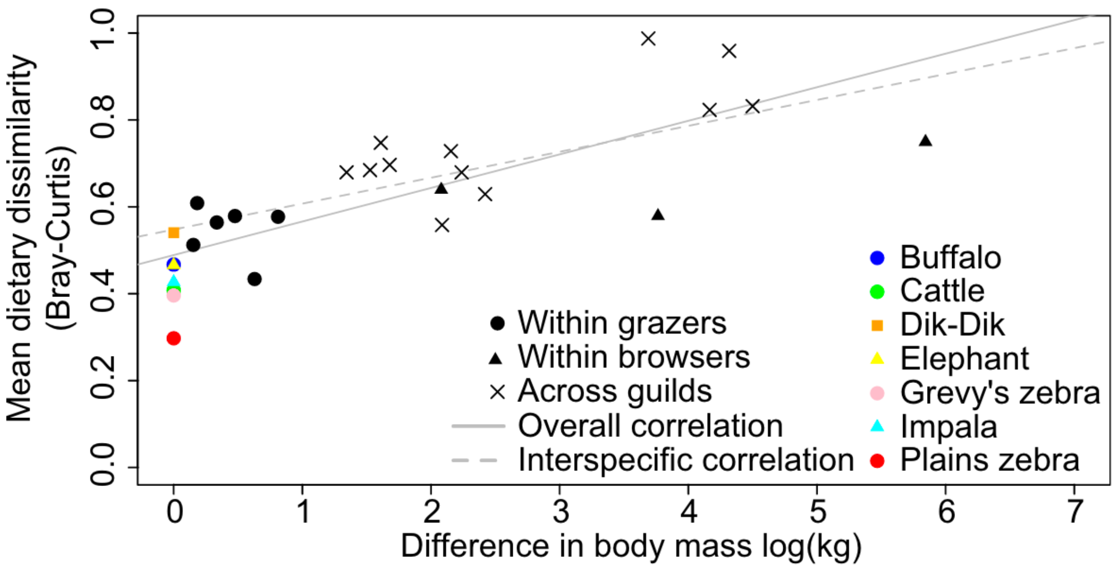


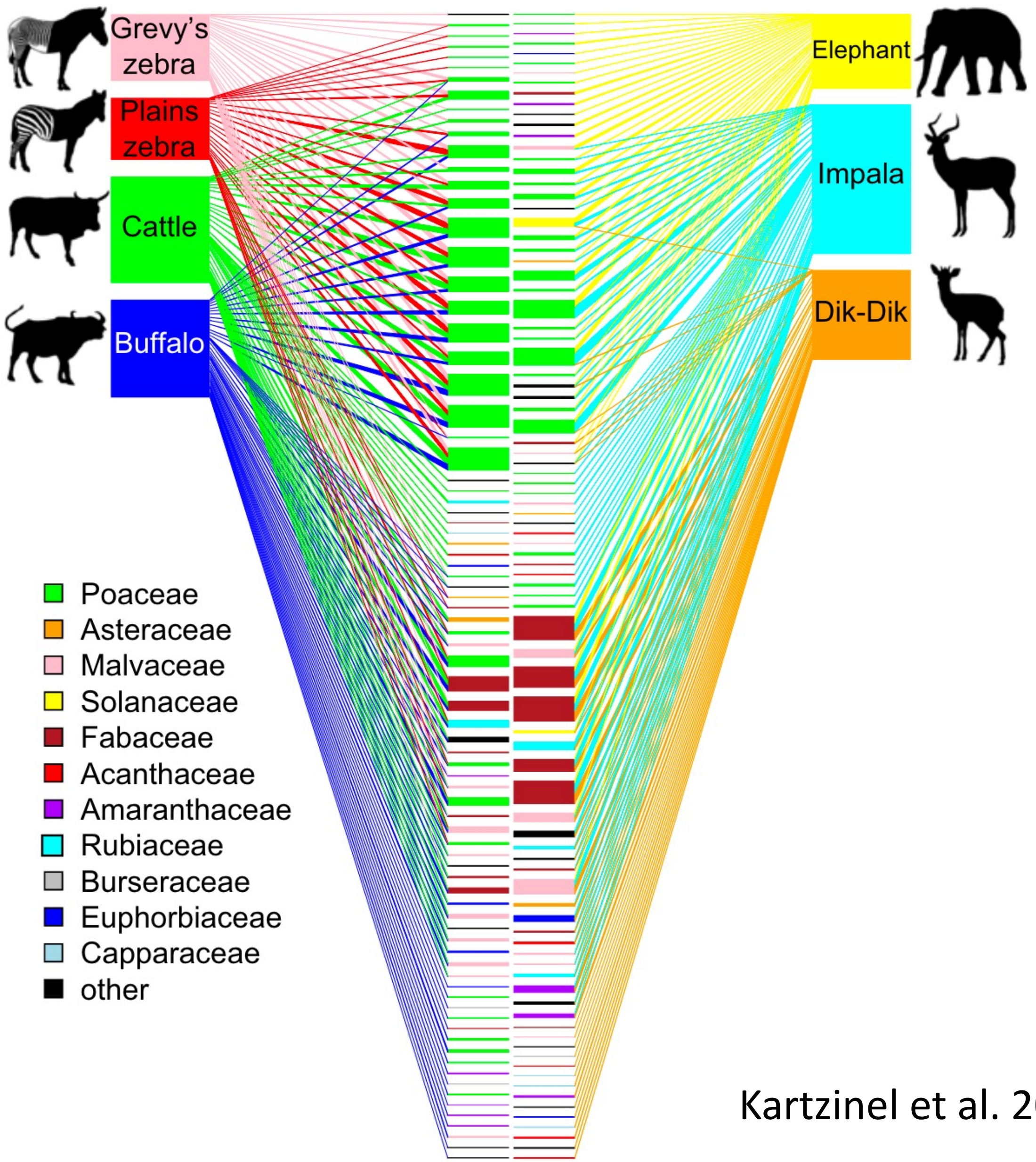


Kartzinel et al. 2015. *PNAS.*

Niche partitioning enables organisms to avoid competitive exclusion

Dietary overlap is higher in similar-sized mammals





Kartzinel et al. 2015. *PNAS.*

Lotka-Volterra equation can be **generalized** to encompass **many interacting species**

i species

$$\frac{dx_i}{dt} = x_i f_i(x)$$

where $f = r + Ax$

vector of intrinsic growth rates for i species

community matrix of interactions between species i and j

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vector of intrinsic growth rates for i species

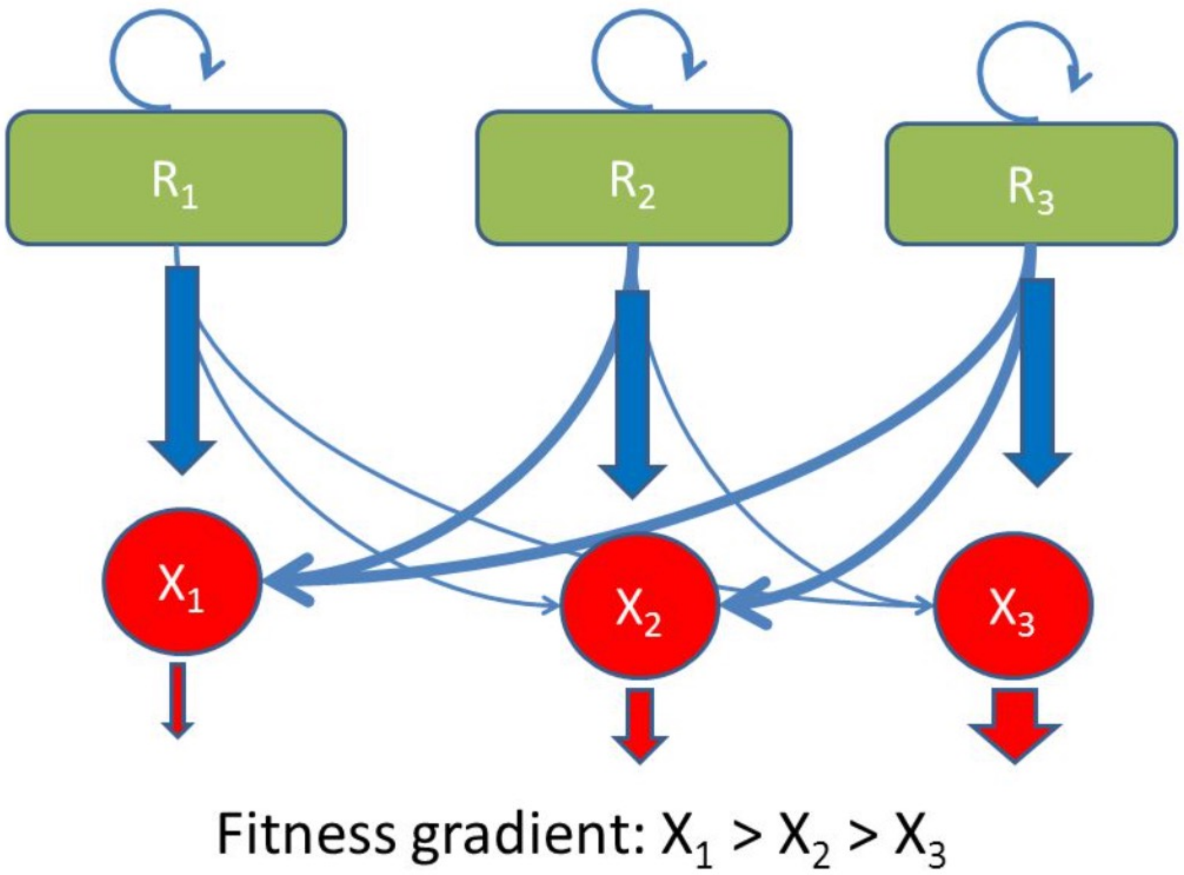
community matrix of interactions between species i and j

The simple condition that "intra-specific competition must exceed inter-specific competition for coexistence" does not hold for more than two competitors!

Stability assessed from the eigenvalues of the community matrix.

Dynamics get much more complex.

In later work, **consumer-resource models** added definition to competitive interactions



Here, ecologists explicitly model individual resources consumed by competing species, **providing mechanism for the interaction terms (α_{21} & α_{12}) of Lotka-Volterra**.

MacArthur 1969. *PNAS.*

MacArthur & Levins 1964. *PNAS.*

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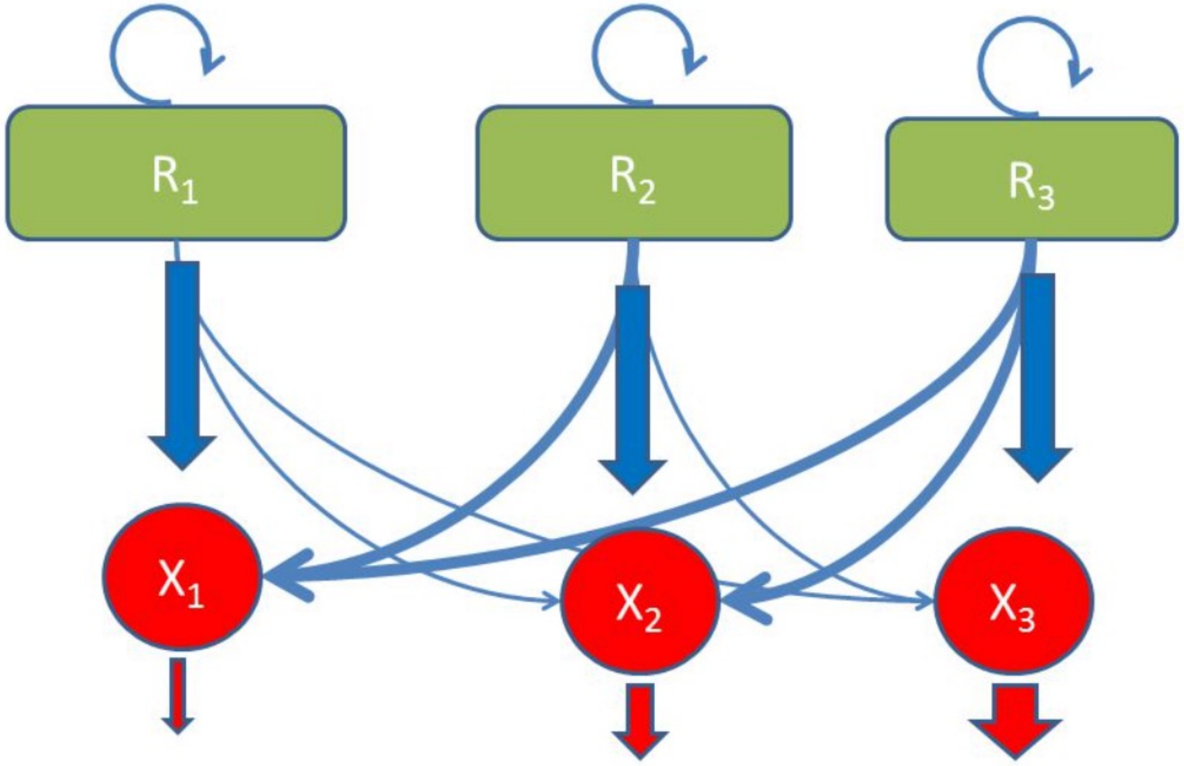

Fitness gradient: $X_1 > X_2 > X_3$

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Competitive exclusion still applies, as, theoretically, **complete competitors require unique resources to coexist.**

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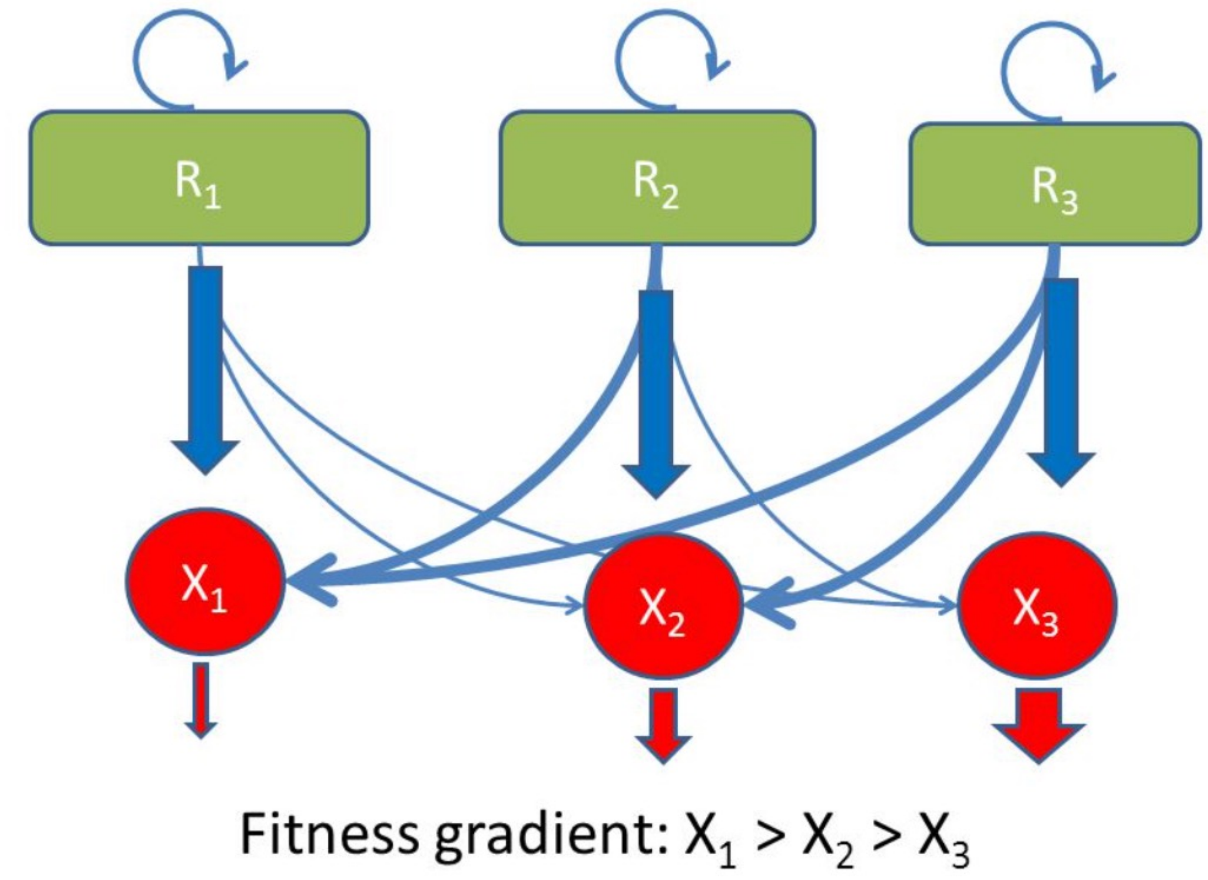


Here, ecologists explicitly model individual resources consumed by competing species, **providing mechanism for the interaction terms (α_{21} & α_{12}) of Lotka-Volterra**.

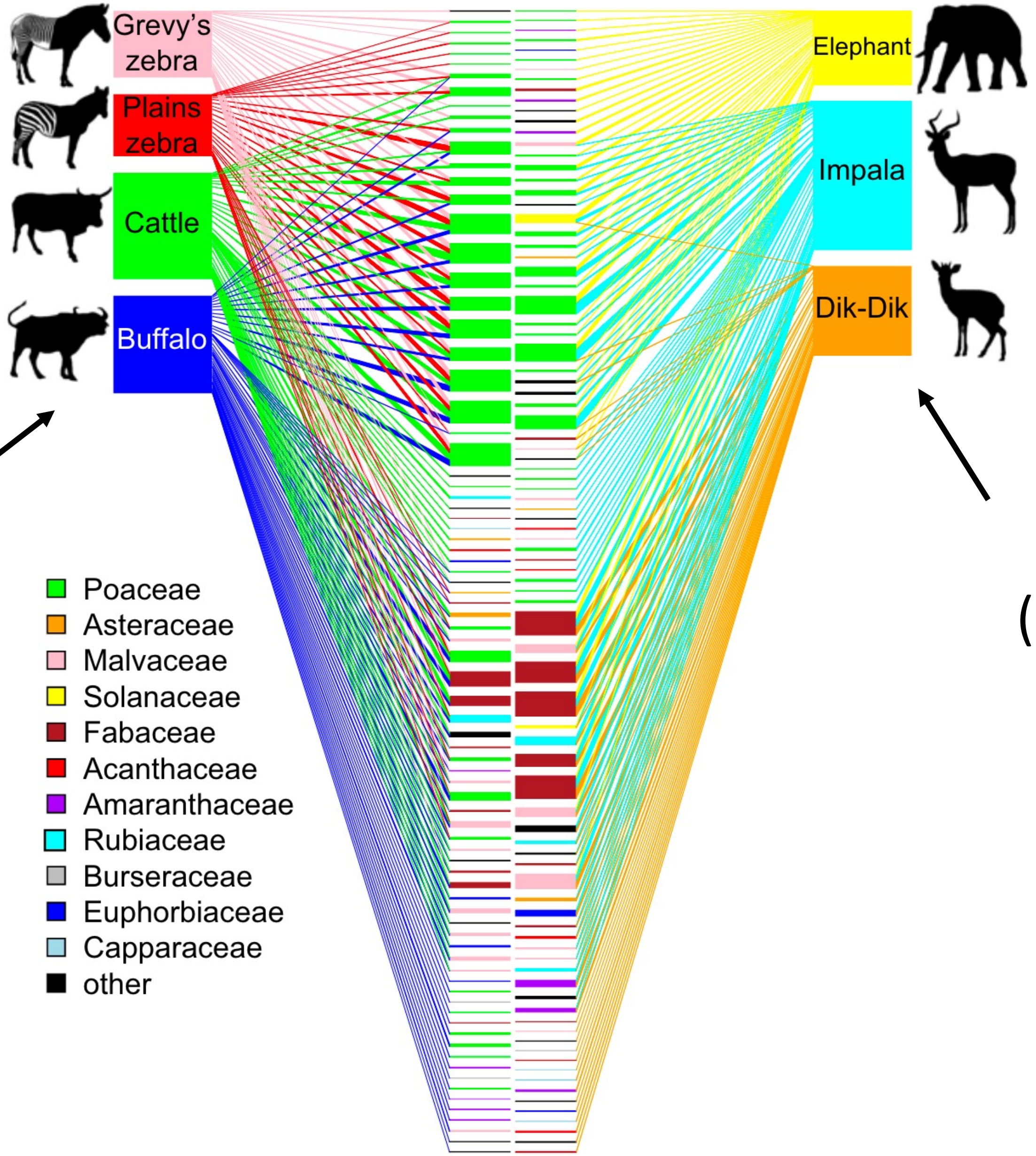
Competitive exclusion still applies, as, theoretically, **complete competitors require unique resources to coexist.**

Generalists are species that exploit a strategy of inefficient consumption of many resources, while **specialists** are species that can outcompete all others on a particular resource.

MacArthur 1969. *PNAS.*

MacArthur & Levins 1964. *PNAS.*

Consumer resource partitioning in the African savanna



Grazer (generalist)

Browser (specialist)

Kartzinel et al. 2015. *PNAS.*

Tilman modeled competition for limited resources, both theoretically and empirically

j species

j species mortality

$$\frac{dN_j}{dt} = N_j\big(\overbrace{a_j R}^{\text{species resource consumption by species } j} - d\big)$$

$$\frac{dR}{dt} = r - R\sum_j a_j N_j$$

Cedar Creek experiment from the University of Minnesota

Tilman 1980. *The American Naturalist.*

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growth of resource in absence of consumption

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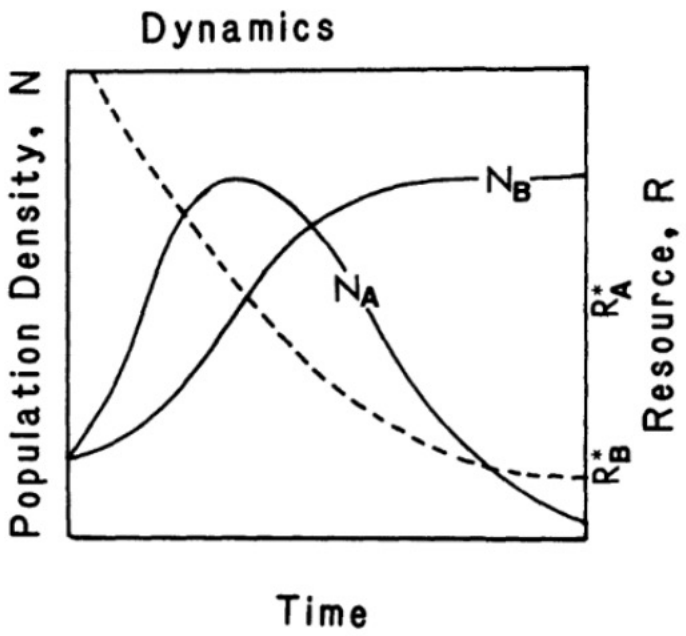
$$\frac{dN_j}{dt} = \overbrace{N_j}^{j\text{ species}}(\overbrace{a_j R}^{\text{species resource consumption by species } j} - \overbrace{d}^{j\text{ species mortality}})$$

$$\frac{dR}{dt} = \underbrace{r}_{\text{growth of resource in absence of consumption}} - \underbrace{R\sum_j a_j N_j}_{\text{consumption of resource by all interacting species}}$$

$$R_j^* = \frac{d}{a_j}$$ **equilibrium resource density**

Each consumer has a distinct R* for each resource



Tilman 1980. *The American Naturalist.*

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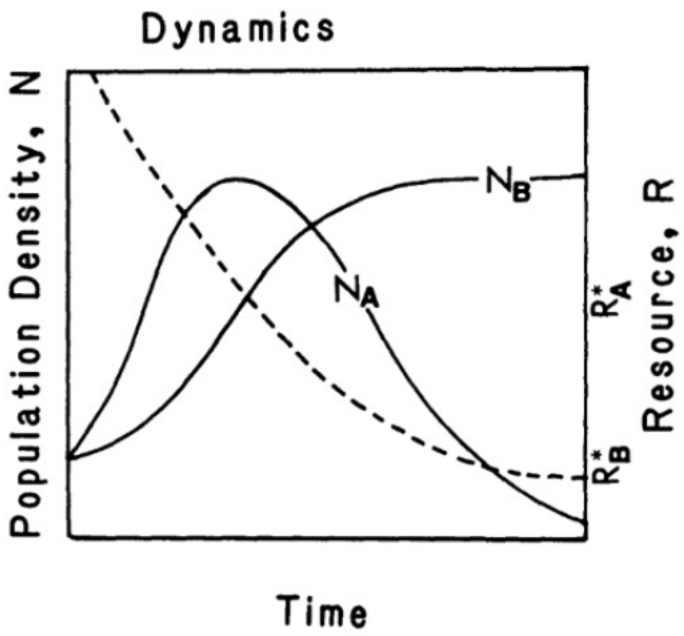
$$\frac{dN_j}{dt} = \underset{j\text{ species}}{N_j}\Big(\underbrace{a_j R}_{\text{species resource consumption by species } j} - \underset{j\text{ species mortality}}{d}\Big)$$

$$\frac{dR}{dt} = \underset{\text{growth of resource in absence of consumption}}{r} - \underbrace{R\sum_j a_j N_j}_{\text{consumption of resource by all interacting species}}$$

$$R_j^* = \frac{d}{a_j}$$ **equilibrium resource density**

If multiple species compete for the same limiting resource, **the species with the lowest equilibrium resource level (R*) will competitively exclude** the others.



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species resource consumption by species *j*

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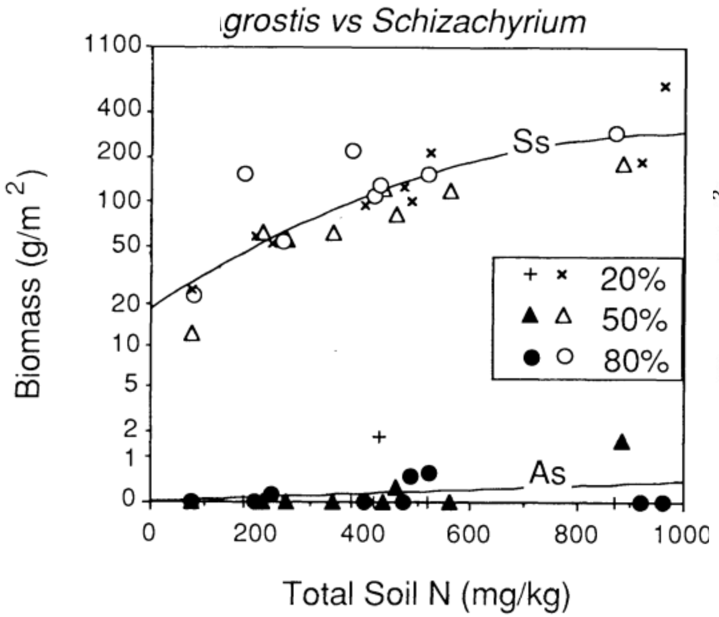
growth of resource in absence of consumption

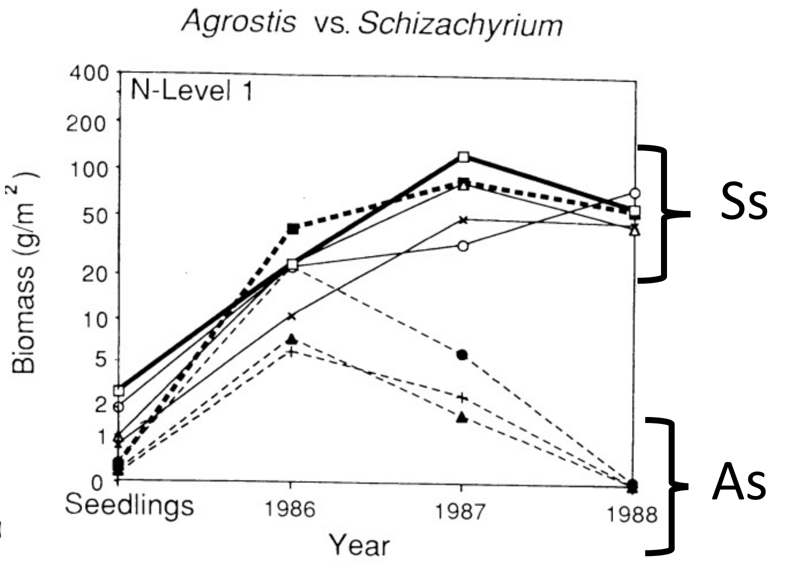
consumption of resource by all interacting species

$$R_j^* = \frac{d}{a_j}$$

equilibrium resource density

Tilman reproduced these theoretical results empirically at Cedar Creek





Tilman and Wedin 1991. *Ecology*