Which flavor of ice cream best represents you?

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Fundamentals of Ecology

Week 7, Ecology Lecture 4

Cara Brook

February 15, 2024

Let’s recap a bit!

Metapopulations

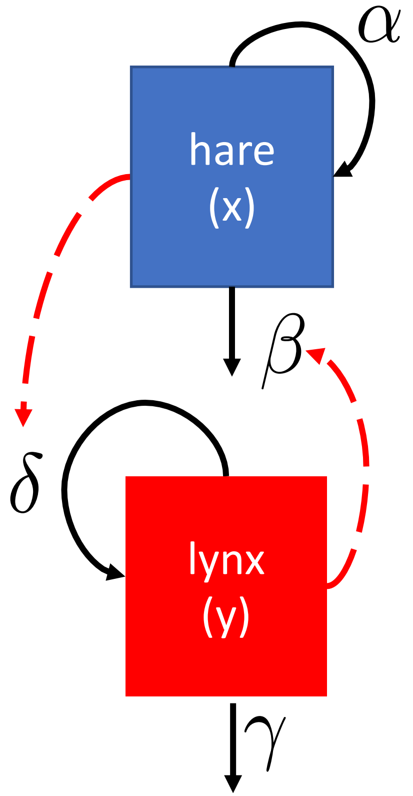
- The term ‘metapopulation’ refers to a ‘population of populations’ that can be modeled using Levins’ patch model that describes rates of colonization and extinction for patches of habitat.
- The ‘rescue effect’ described by Ilkka Hanski highlights how the probability of extinction for a subpopulation is diminished when it can be recolonized by the larger metapopulation.
- Source-sink theory 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 ‘ecological trap’ 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.

Let's recap a bit!

Interspecies interactions

- A community is the level of ecological organization in which multiple species interact: mutualism, commensalism, predation, competition (direct & indirect), and parasitism
- Trophic levels are hierarchical levels of organization in an ecosystem, based on nutritional relationships to the source of energy (primary producer, primary consumer)
- Food chains and food webs demonstrate interactions across trophic levels
- Bottom-up processes describe circumstances when a higher trophic level is limited by the availability of resources provided from a trophic level below it.
- Top-down processes describe circumstances in which a higher trophic level regulates a lower trophic level, usually through consumption. First described in HSS.
- The Lotka-Volterra predator-prey model describes the simplest interactions across just two trophic levels. It has been used to describe dynamics in several famous examples (lynx-hare, wolf-moose) though it often oversimplifies interspecies interactions

Lotka-Volterra predator-prey models with data

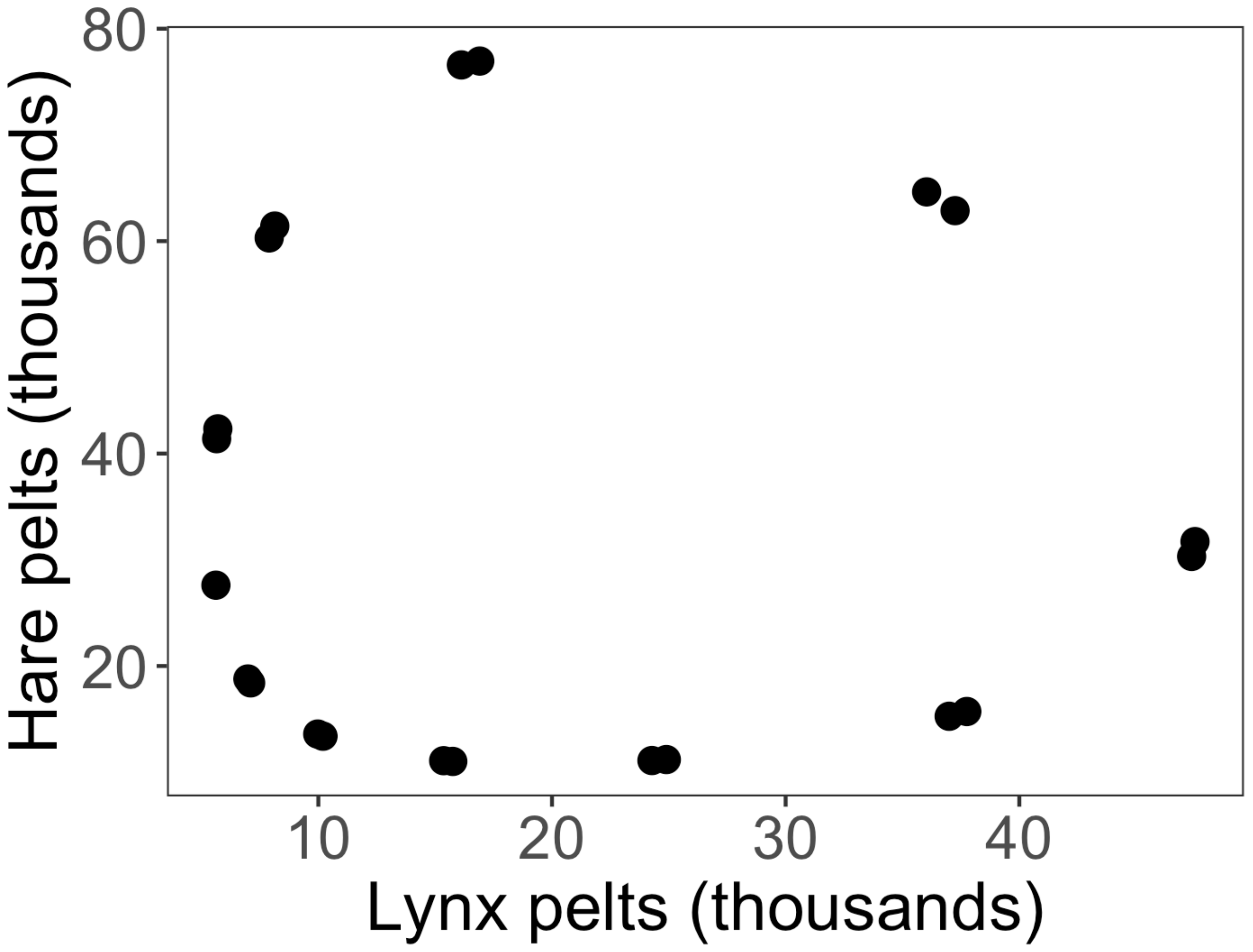


$$\frac{dx}{dt} = \alpha x - \beta xy$$

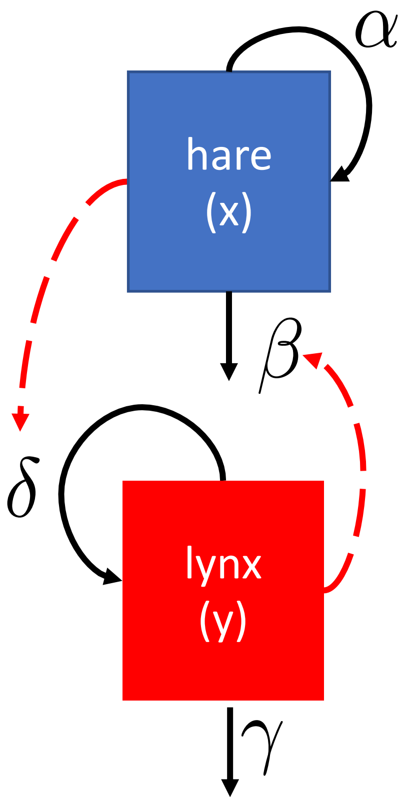
$$\frac{dy}{dt} = \delta xy - \gamma y$$

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

Predator-prey cycles can be visualized as oscillations.



Lotka-Volterra predator-prey models with data



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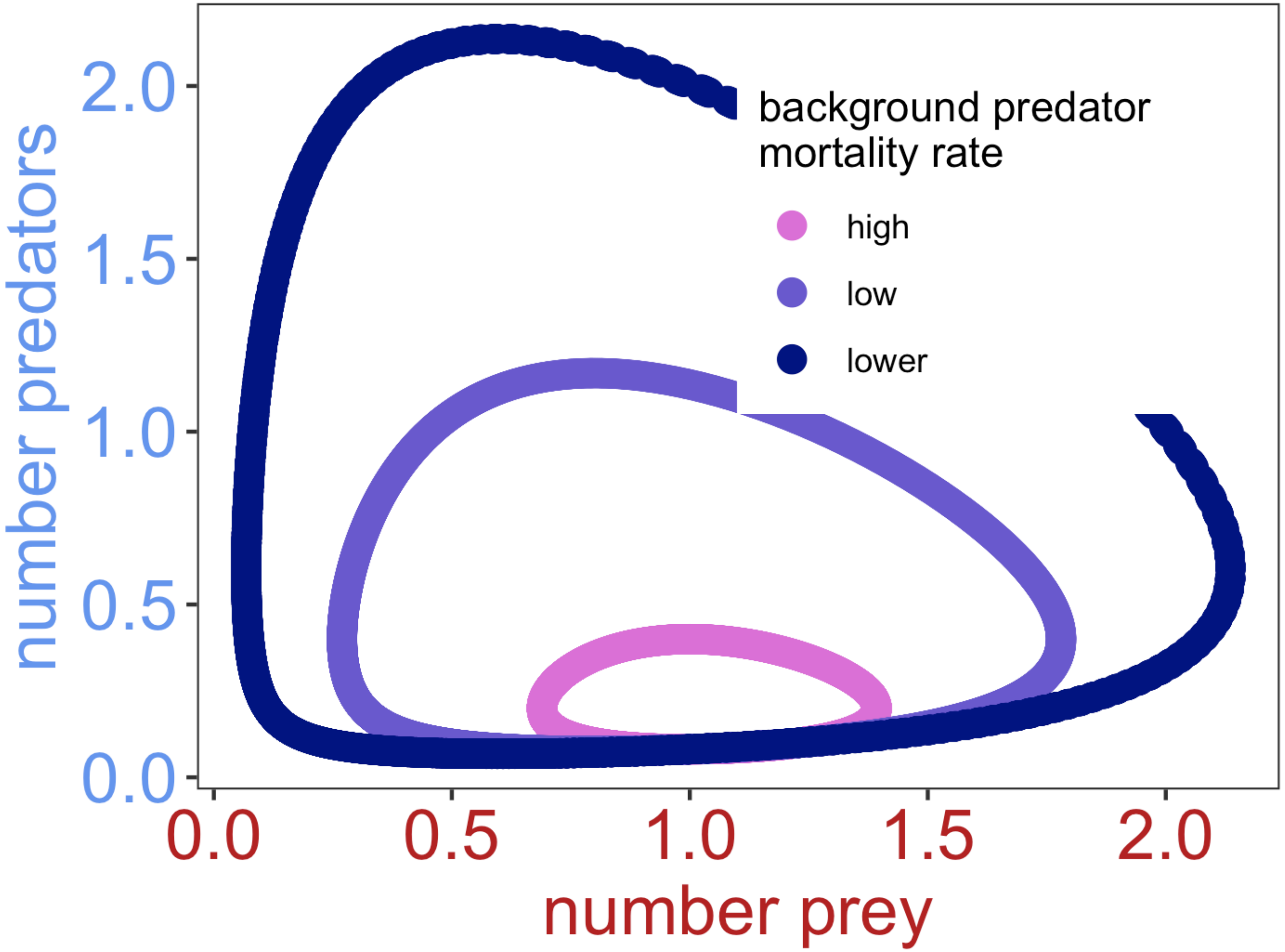
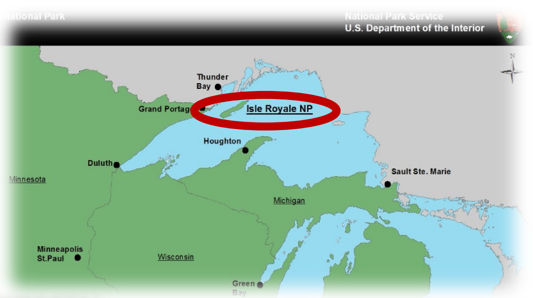
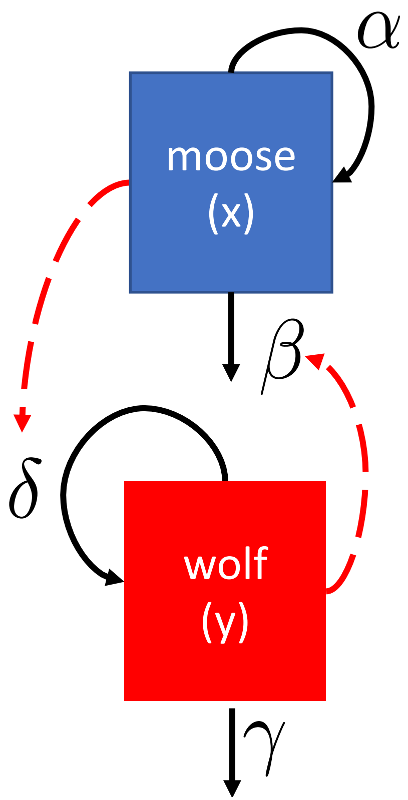


Another famous example: Wolf-Moose on Isle Royale



isleroyalewolf.org



How does ***moose*** *abundance* ***vary*** *with* ***changes*** *in* ***wolf*** *abundance?*

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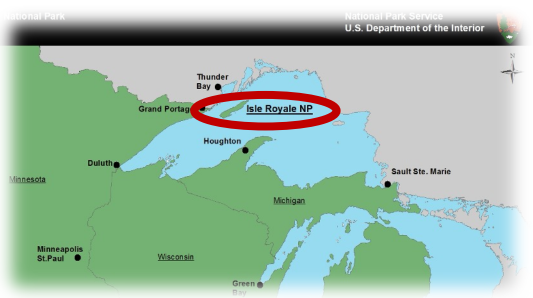

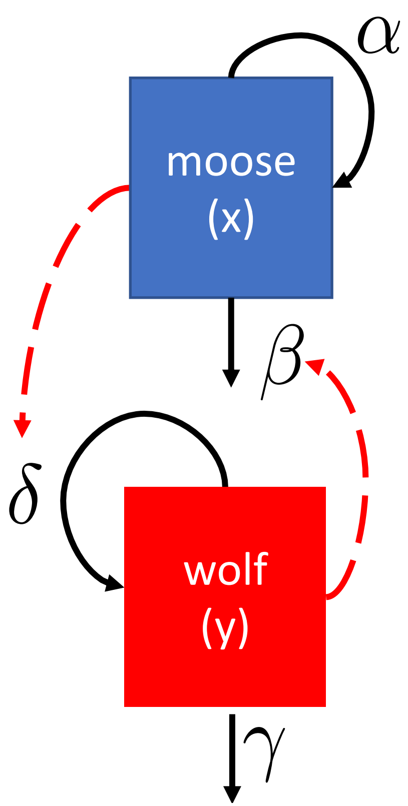

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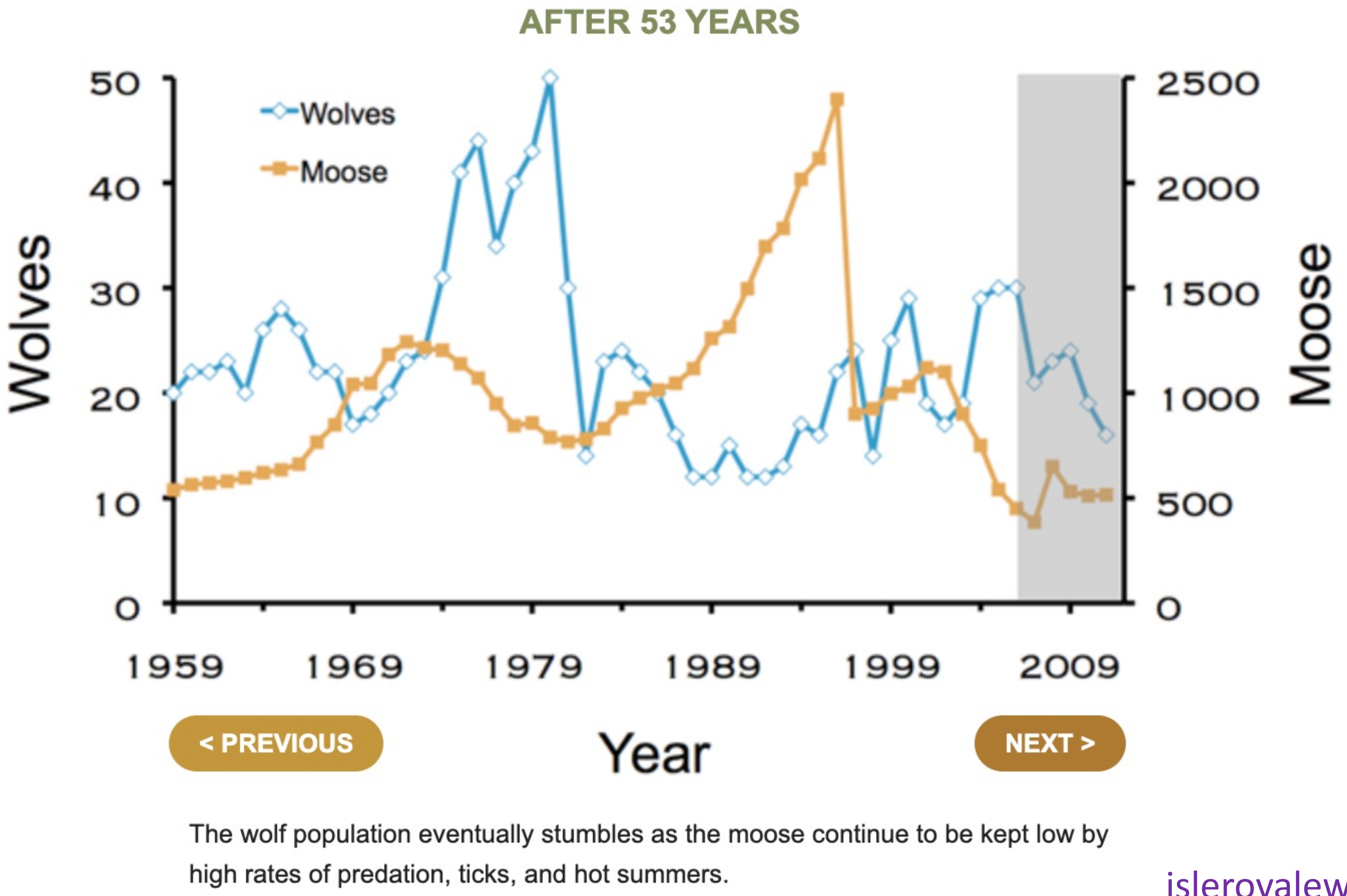

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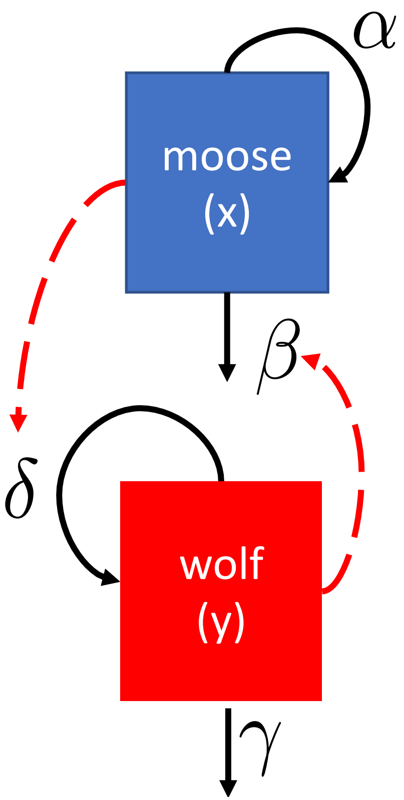
Another famous example: Wolf-Moose on Isle Royale

This could be you!



*How does **moose** abundance **vary** with **changes** in **wolf** abundance?*

Field Work Opportunity for College Students

FIELD WORK OPPORTUNITY FOR COLLEGE STUDENTS FOR MAY/JUNE 2023

We are seeking volunteers to assist with data collection for the 2023 summer field season. This is a great opportunity to gain valuable field experience while working in the remote and beautiful Isle Royale National Park.

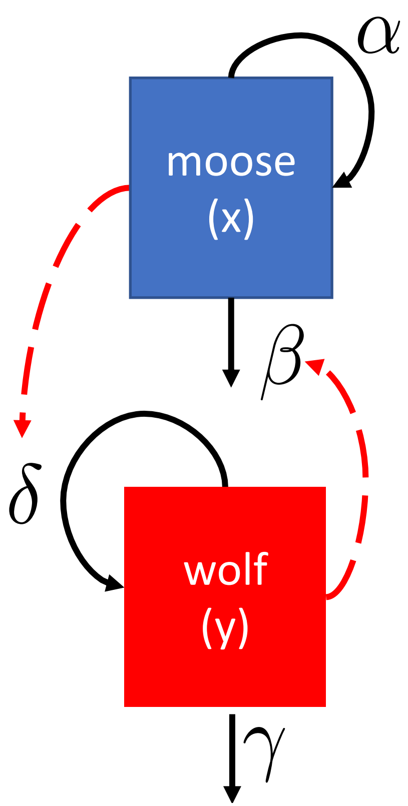
Duration: Approximately 4-5 weeks between early-May and mid-June.

Work Environment: Work is conducted on-trail and off-trail throughout Isle Royale. This is a physically demanding position; the climate, insects (mosquitoes and black flies), and terrain are often difficult. Volunteers may be required to carry up to 60 lbs. for varying distances (up to 10 miles per day) over trail and cross-country conditions. The primary mode of living is backpacking. Most travel is by foot.

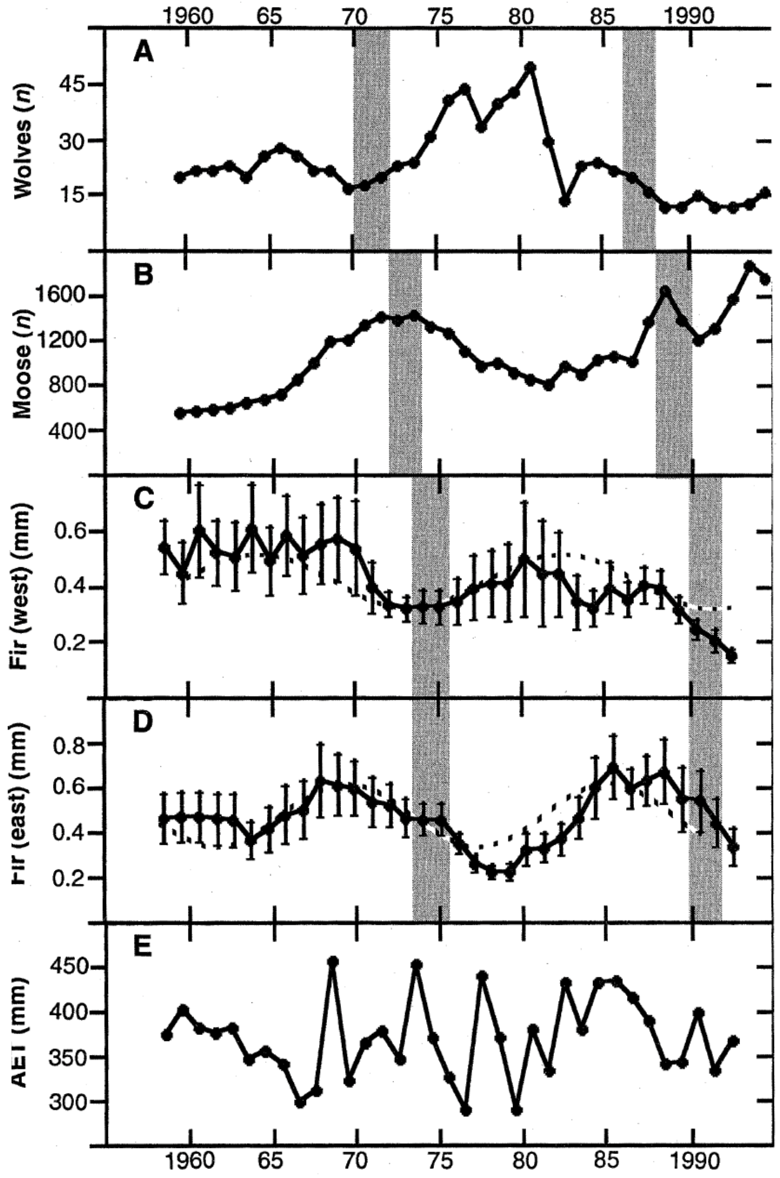
Work Schedule: Typically spend 6-8 days in the field followed by 1-2 days at base camp. Work schedule varies depending upon conditions, project needs and logistics.

isleroyalewolf.org

Another famous example: Wolf-Moose on Isle Royale



*How does **moose** abundance **vary** with **changes** in **wolf** abundance?*



Wolf-moose dynamics on Isle Royale are **more complex than simple predator-prey**.

This 3-way interaction is an example of a **trophic cascade**.

By, definition, **trophic cascades span at least 3 trophic levels**, highlighting the process of **top-down** ecosystem control.

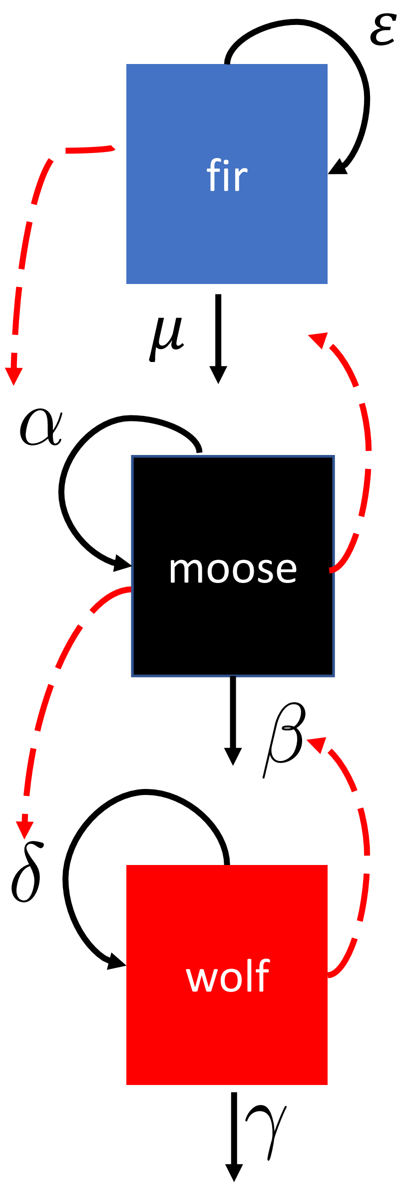
Wolves, Moose, and Tree Rings on Isle Royale

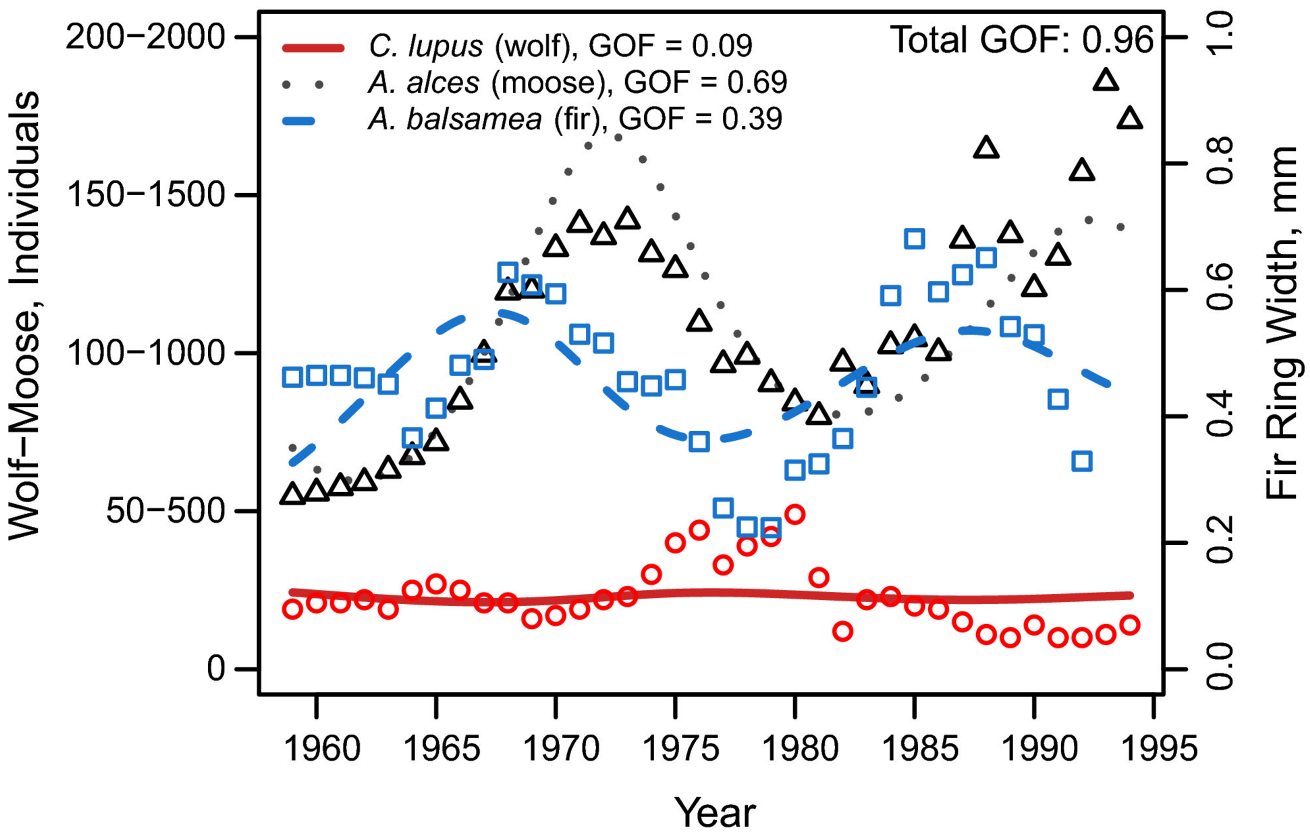
B. E. McLaren* and R. O. Peterson

Investigation of tree growth in Isle Royale National Park in Michigan revealed the influence of herbivores and carnivores on plants in an intimately linked food chain. Plant growth rates were regulated by cycles in animal density and responded to annual changes in primary productivity only when released from herbivory by wolf predation. Isle Royale's dendrochronology complements a rich literature on food chain control in aquatic systems, which often supports a trophic cascade model. This study provides evidence of top-down control in a forested ecosystem.

SCIENCE • VOL. 266 • 2 DECEMBER 1994

Another famous example: Wolf-Moose on Isle Royale





Models incorporating >2 trophic levels can be challenging, but ecologists do sometimes attempt them!

*How does **fir growth** vary with **moose** abundance, which varies with changes in **wolf** abundance?*

Mülhbauer et al. 2020. *Ecology & Evolution.*

HSS: The first theory of **top-down regulation** of trophic levels

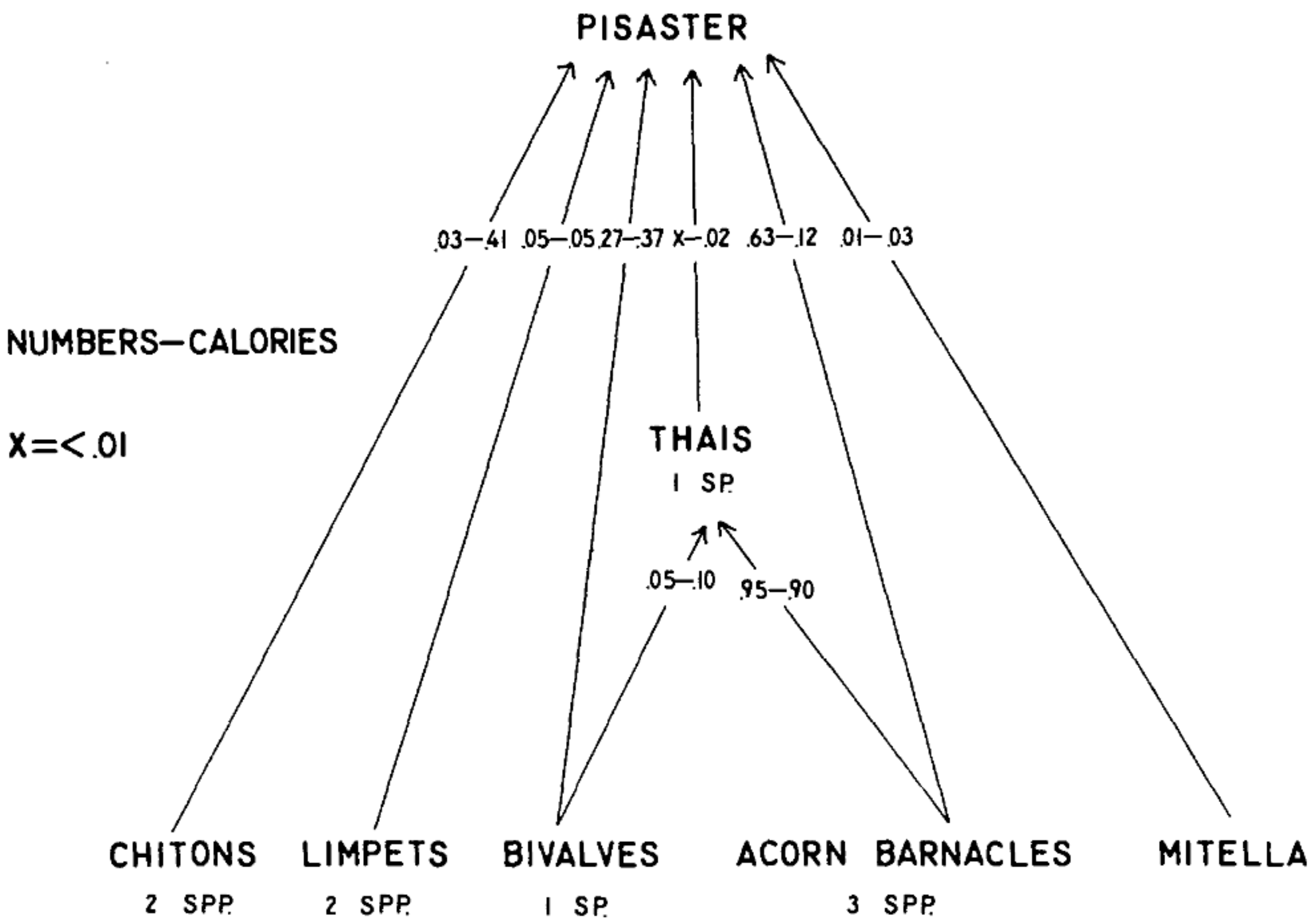
Vol. XCIV, No. 879 The American Naturalist November–December, 1960

COMMUNITY STRUCTURE, POPULATION CONTROL, AND COMPETITION

NELSON G. HAIRSTON, FREDERICK E. SMITH, AND LAWRENCE B. SLOBODKIN

1. Producers, decomposers, and carnivores are **bottom-up controlled** in a density-dependent fashion
2. **Interspecific competition** mediates these interactions
3. Herbivores are **top-down controlled** (because the ‘the world is green’)

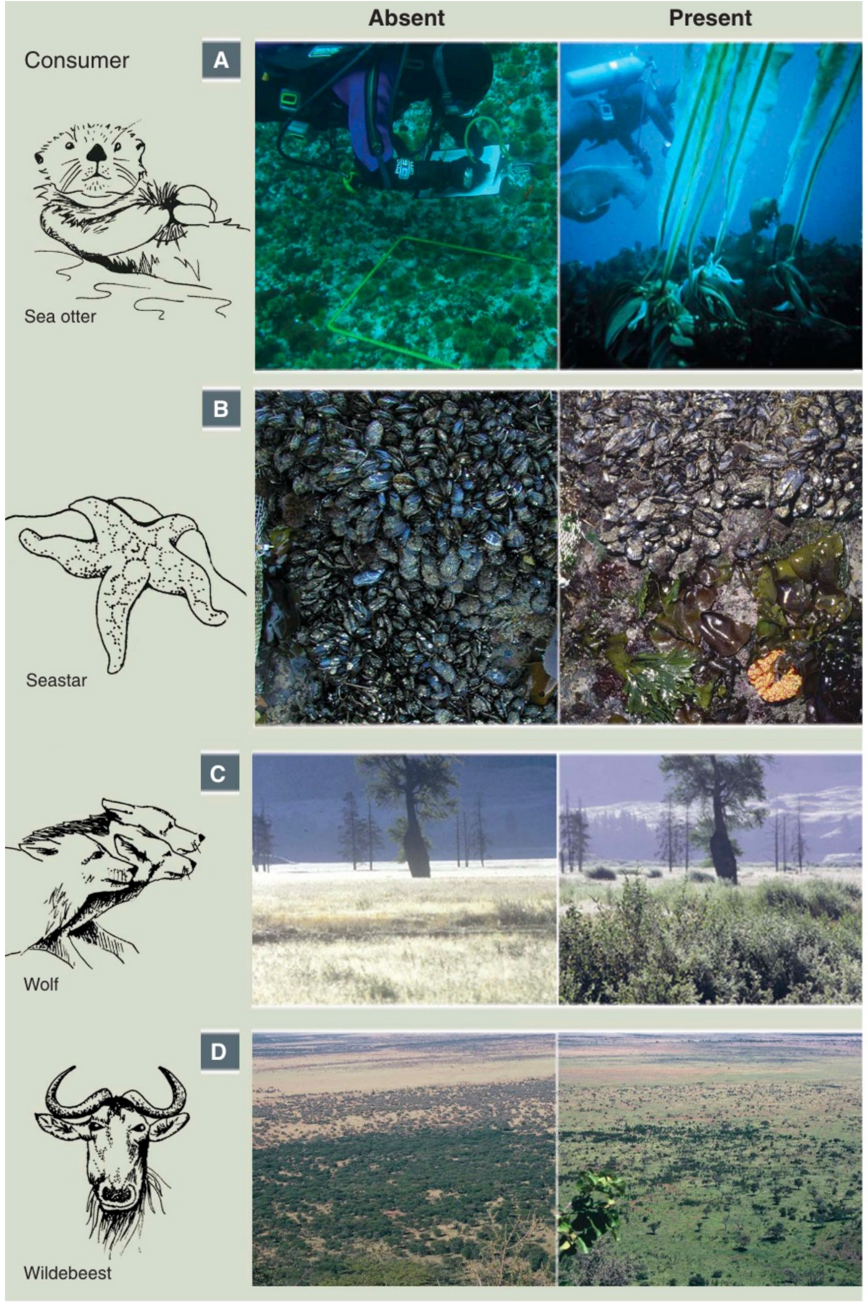
This work inspired empirical studies on **trophic cascades**: *Pisaster* removal on Tatoosh Island



Paine 1966. *The American Naturalist.*

Other famous **trophic cascades:**

Estes et al. 2011. *Science.*

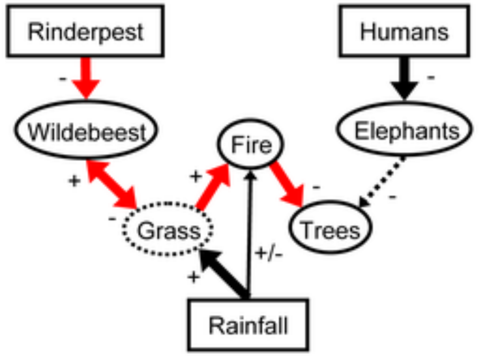


CA sea otters maintain kelp forest diversity by consuming herbivorous sea urchins. (Estes & Duggins 1995. *Ecological Monographs*)

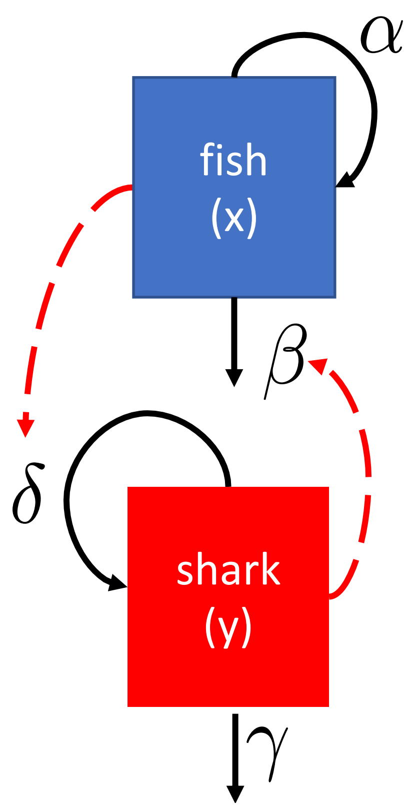
Starfish maintain diversity in Pacific intertidal by consuming space-dominating mussels. (Paine 1966 *The American* Naturalist)

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

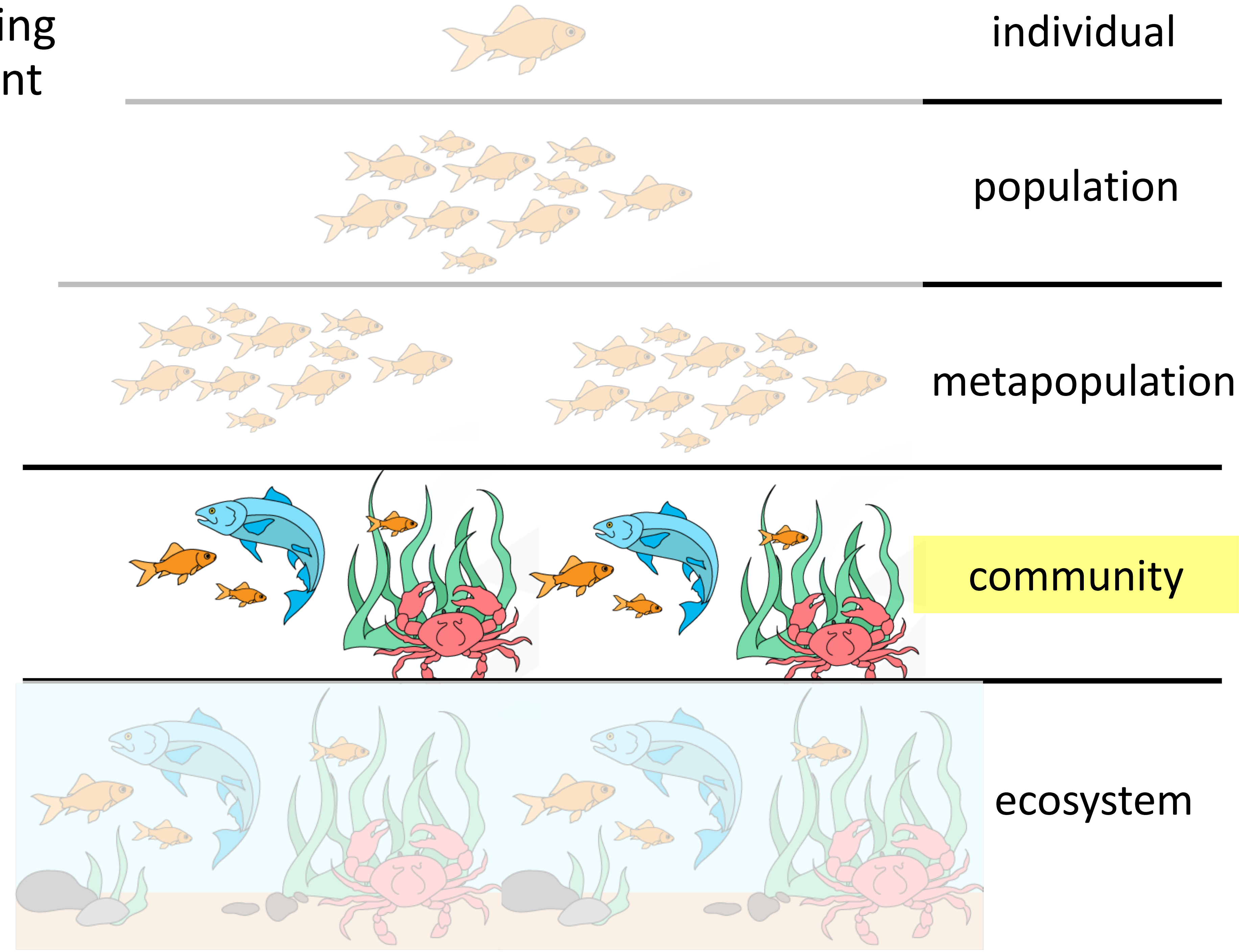
Rinderpest eradication releases wildebeest populations that control savanna, limit fire, and promote tree regrowth (Holdo et al. 2009. *PLoS Biology*)



Community = interacting populations of different species



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



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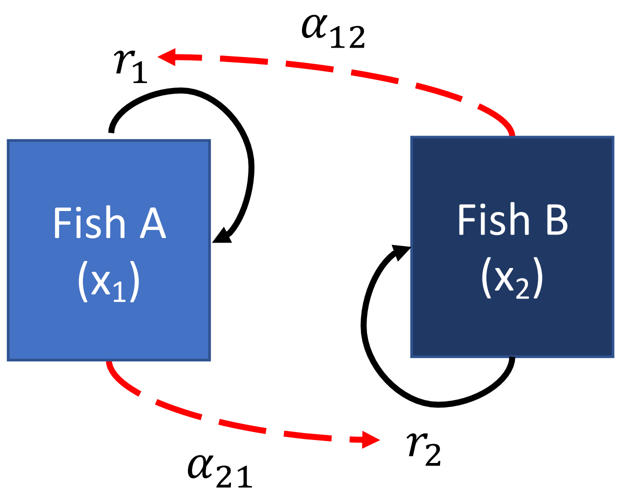
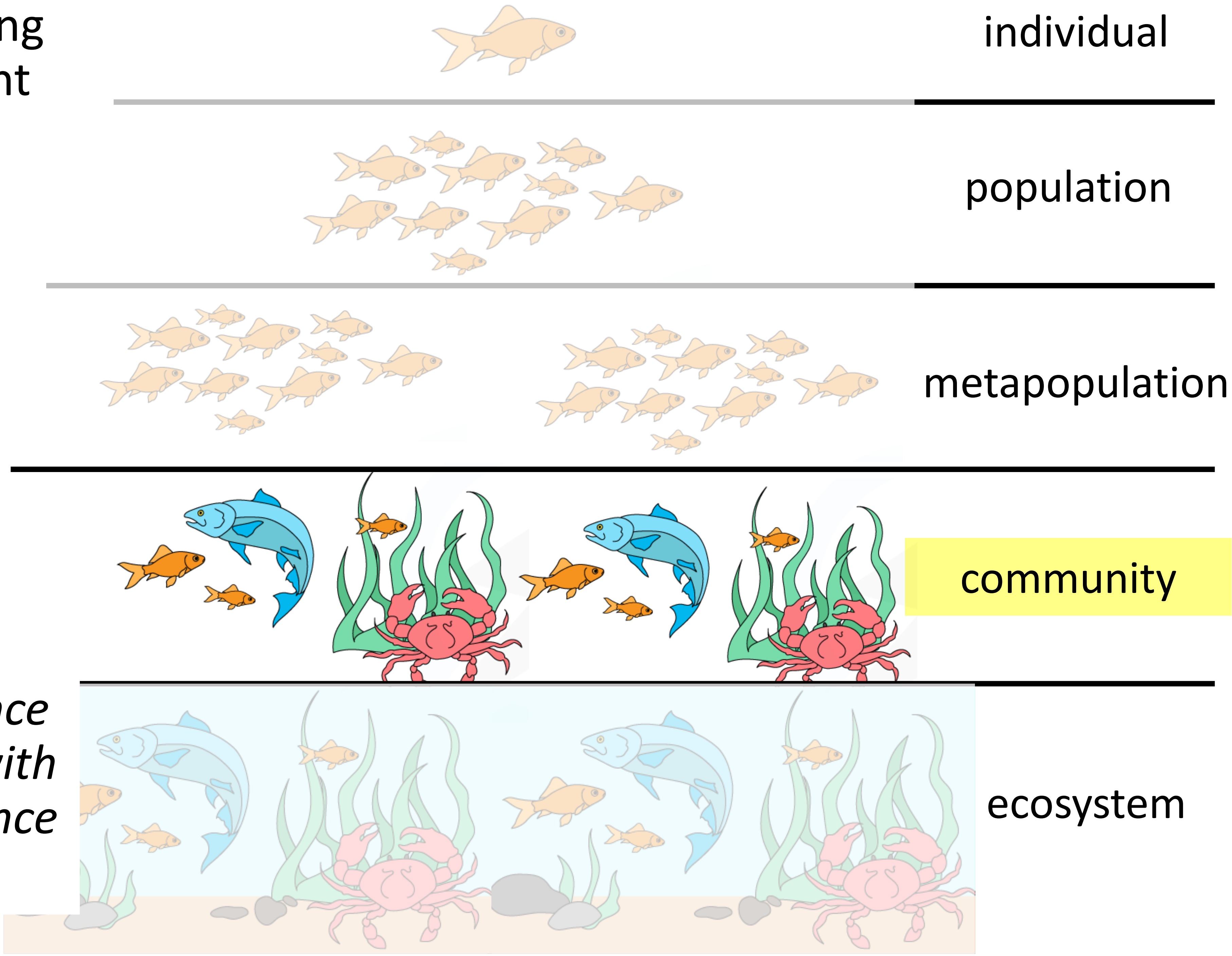


*How does the abundance of **fish species A** vary with changes in the abundance of **fish species B**?*



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.**

$$\frac{dx_1}{dt} = r_1 x_1 - \overbrace{\frac{r_1 (x_1)^2}{K_1}}^{\text{intraspecies competition of species 1 (akin to logistic growth)}} - \overbrace{\frac{r_1 x_1 x_2 \alpha_{12}}{K_1}}^{\text{interspecies competition with species 2}}$$

$$\frac{dx_2}{dt} = r_2 x_2 - \underbrace{\frac{r_2 (x_2)^2}{K_2}}_{\text{intraspecies competition of species 2}} - \underbrace{\frac{r_2 x_2 x_1 \alpha_{21}}{K_2}}_{\text{interspecies competition with species 1}}$$

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:

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

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

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

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

Coexistence.

Que 1. In the competition equations below, what is α_{12}? The effect of:

104

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

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

A) Species 1 on its own growth

B) Species 2 on its own growth

C) Species 1 on the growth of species 2

D) Species 2 on the growth of species 1

Que 1. In the competition equations below, what is α_{12}? The effect of:

104

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

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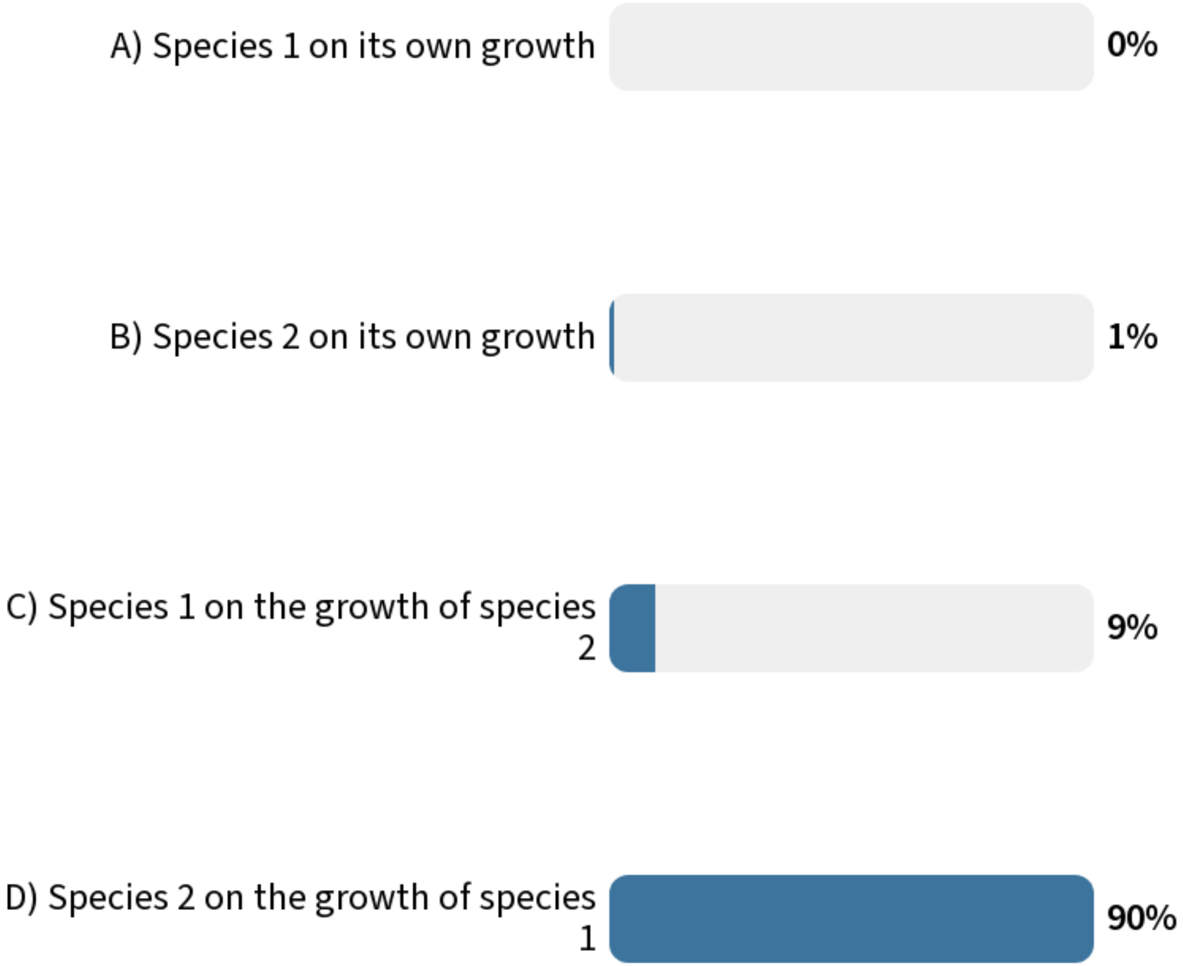

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104

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

A) Species 1 on its own growth 0%

B) Species 2 on its own growth 1%

C) Species 1 on the growth of species 2 9%

D) Species 2 on the growth of species 1 90%

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 $\frac{dx_1}{dt} = 0$

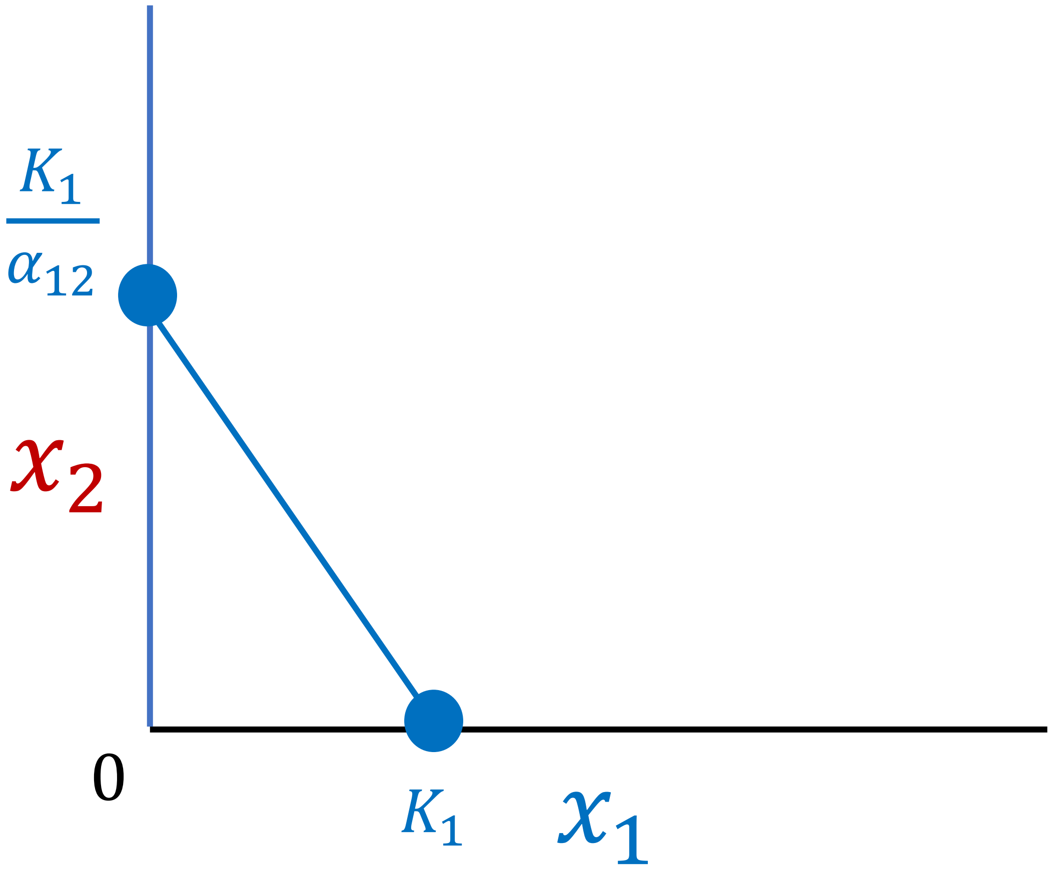
$$0 = \frac{dx_1}{dt} = r_1 x_1 - \frac{r_1 (x_1)^2}{K_1} - \frac{r_1 x_1 x_2 \alpha_{12}}{K_1}$$

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

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

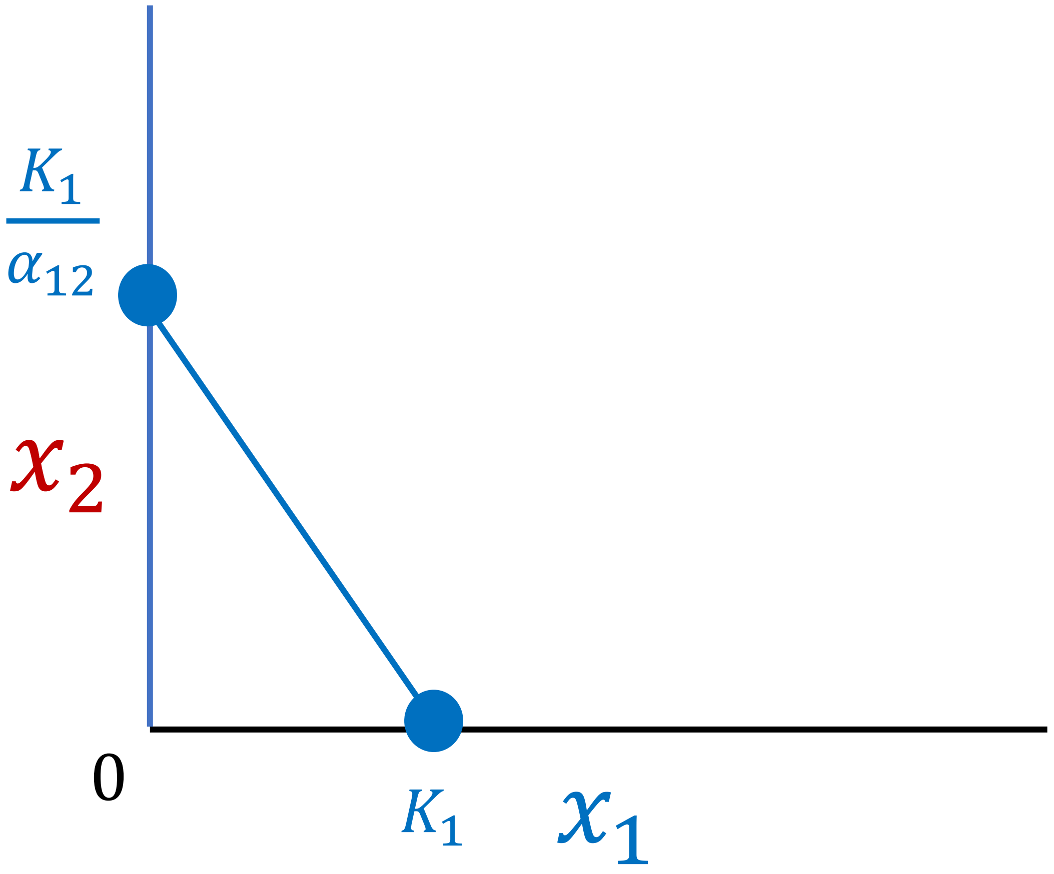
first nullcline at $x_1 = 0$

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



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

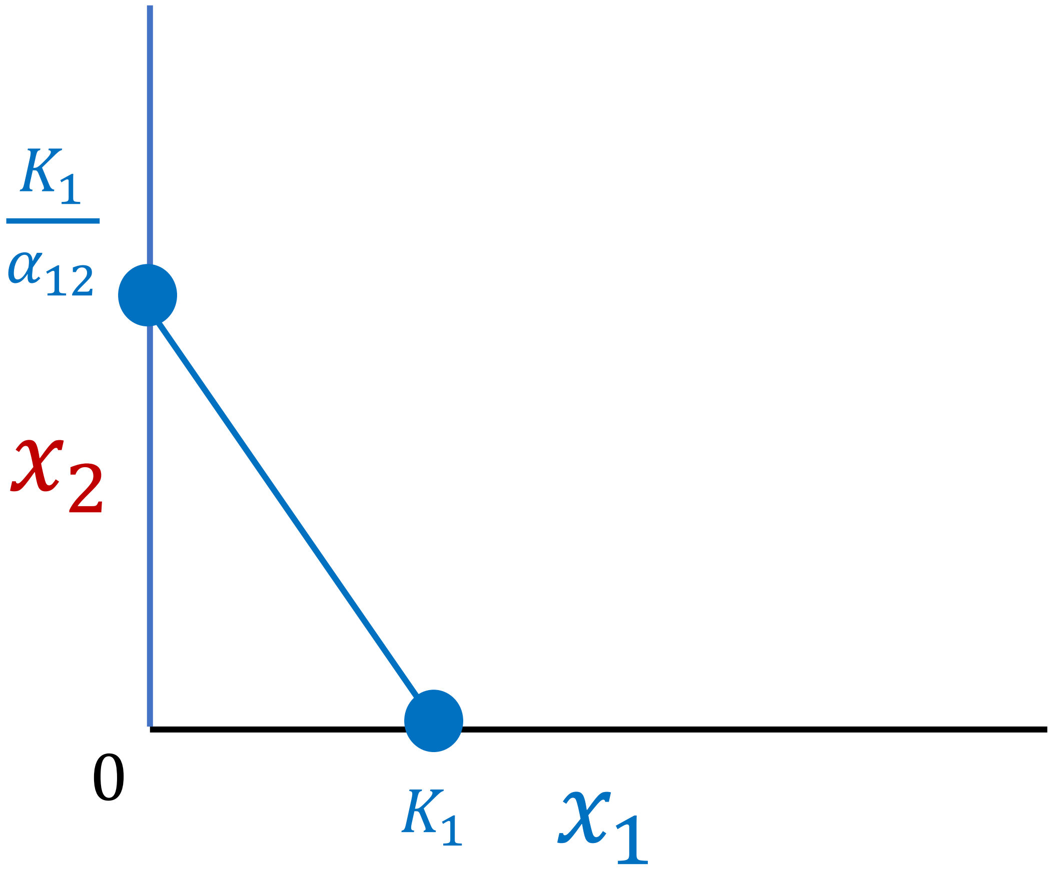
- Following a perturbation, the population should return to equilibrium!
- For x_1, this will always mean moving along the x-axis to the nullcline, then along the nullcline to equilibrium.



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

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

- 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.
- You can also test it by solving $\frac{dx_1}{dt}$ for different values!



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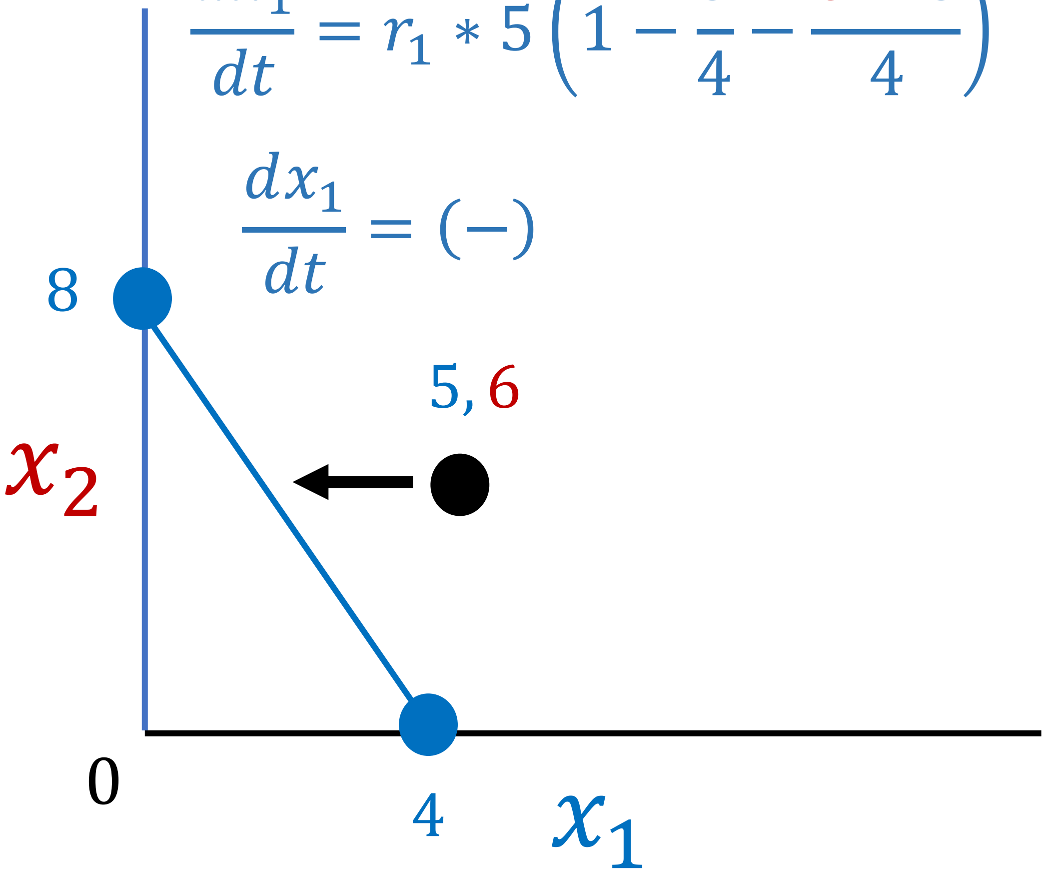
- You can also test it by solving $\frac{dx_1}{dt}$ for different values!
- $K_1 = 4\,;\alpha_{12} = .5$

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

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

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



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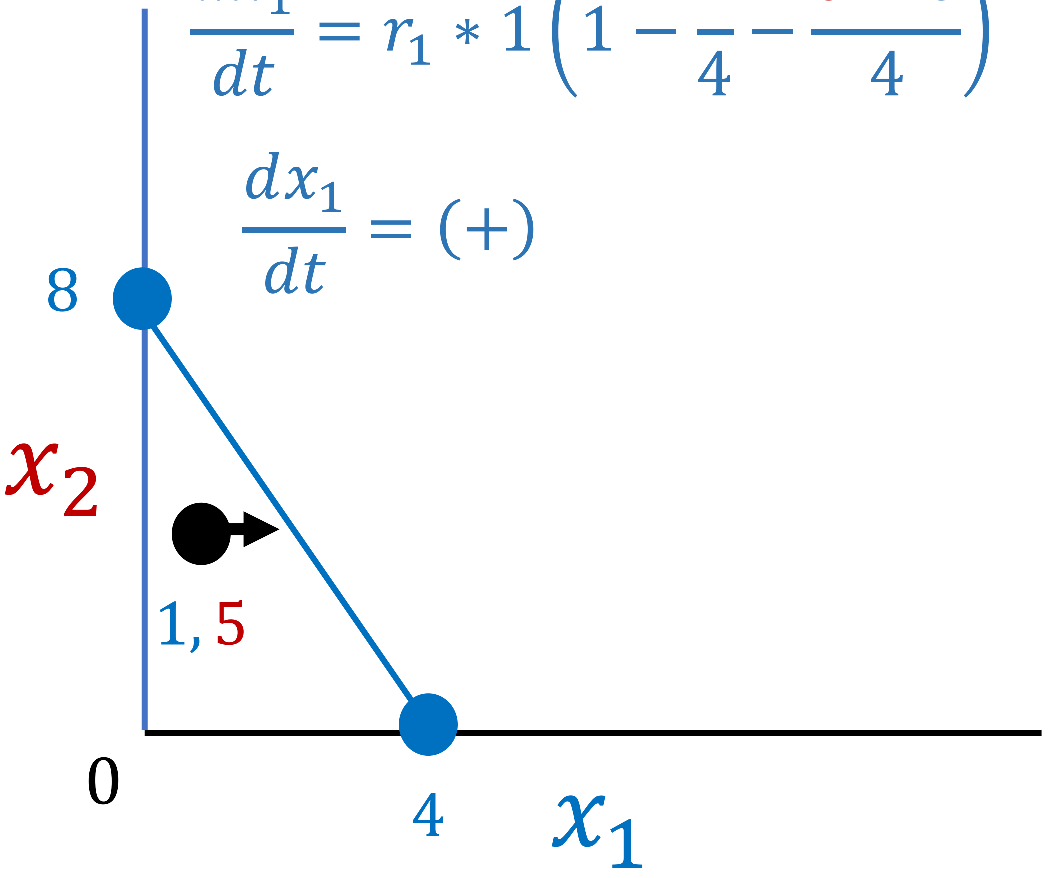
- $K_1 = 4\,; \alpha_{12} = .5$

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

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

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



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 $\frac{dx_2}{dt} = 0$

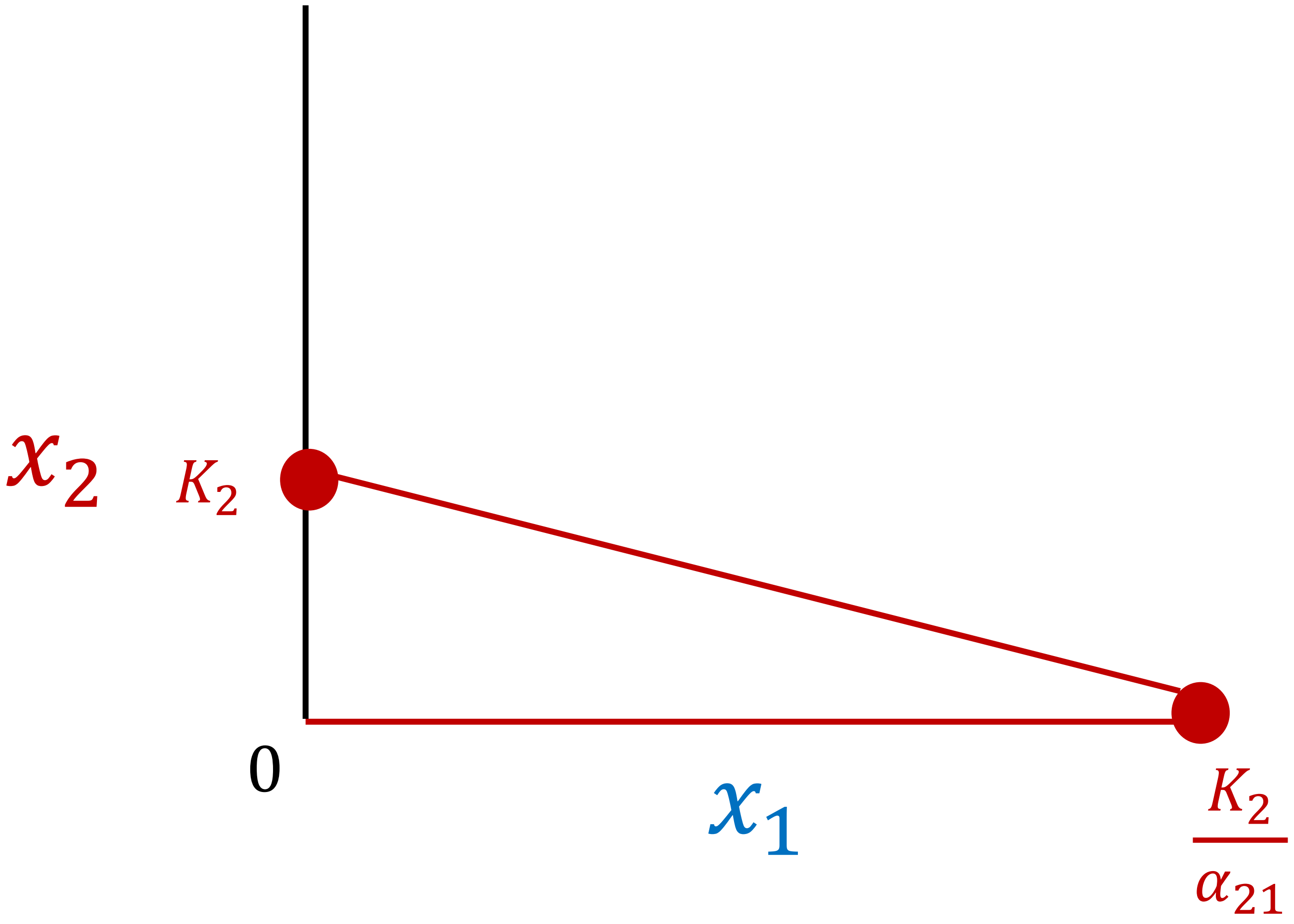
$$0 = \frac{dx_2}{dt} = r_2 x_2 - \frac{r_2 (x_2)^2}{K_2} - \frac{r_2 x_2 x_1 \alpha_{21}}{K_2}$$

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

$$0 = r_2 x_2 \left(1 - \frac{x_2}{K_2} - \frac{x_1 \alpha_{21}}{K_2}\right)$$

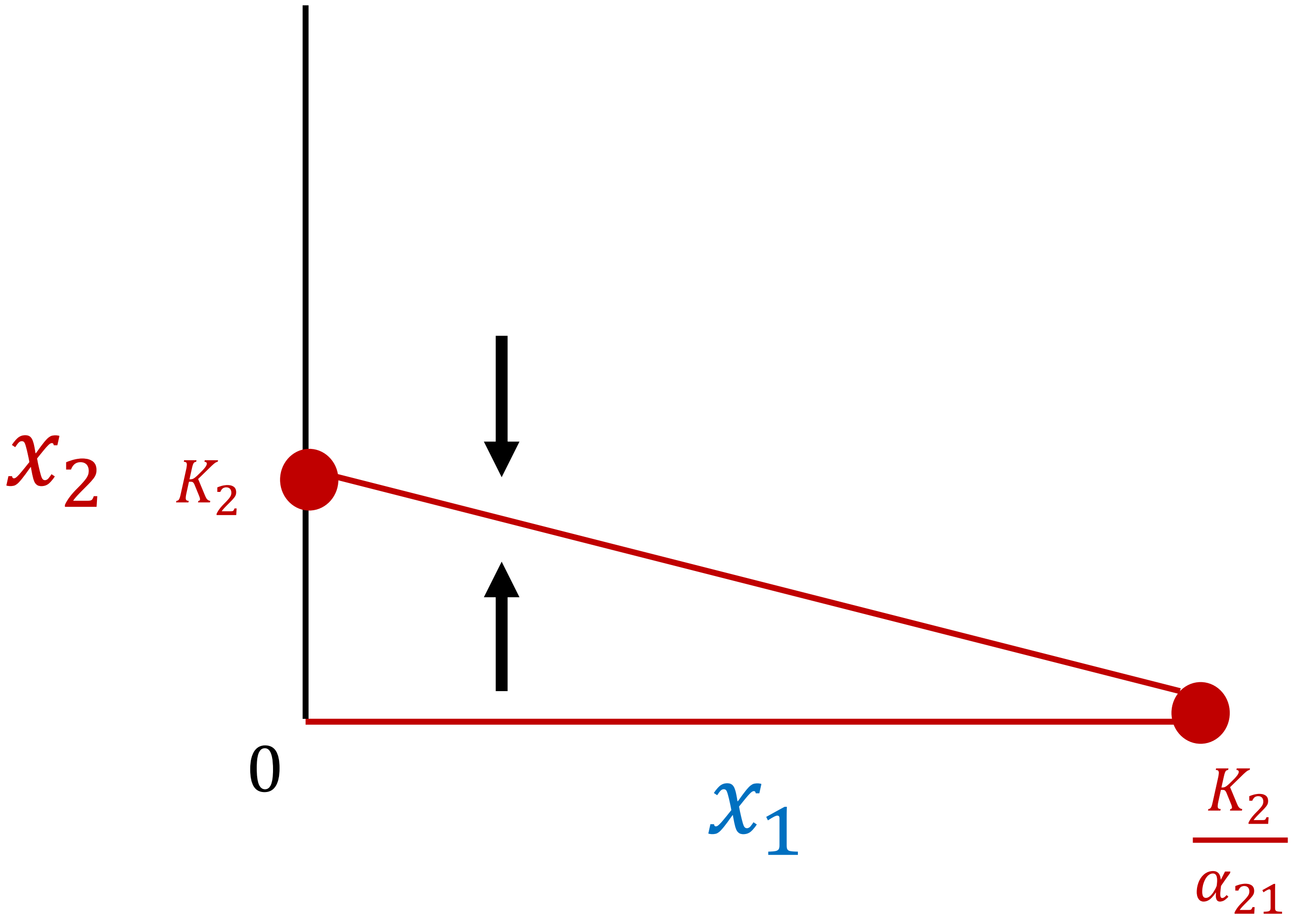
first nullcline at $x_2 = 0$

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



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

- 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.



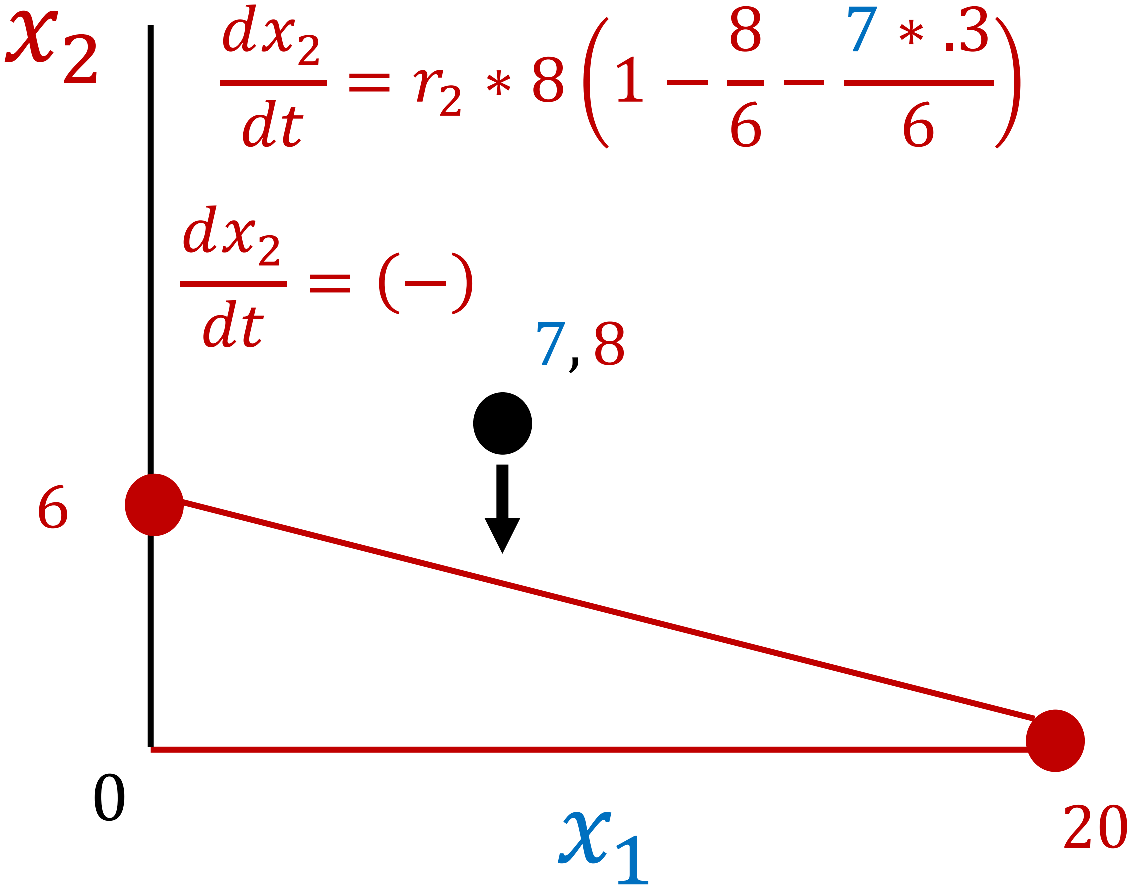
Nullclines (or **isoclines**) of the **Lotka-Volterra competition model**

- 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!
- $K_2 = 6\,; \alpha_{21} = .3$

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

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

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



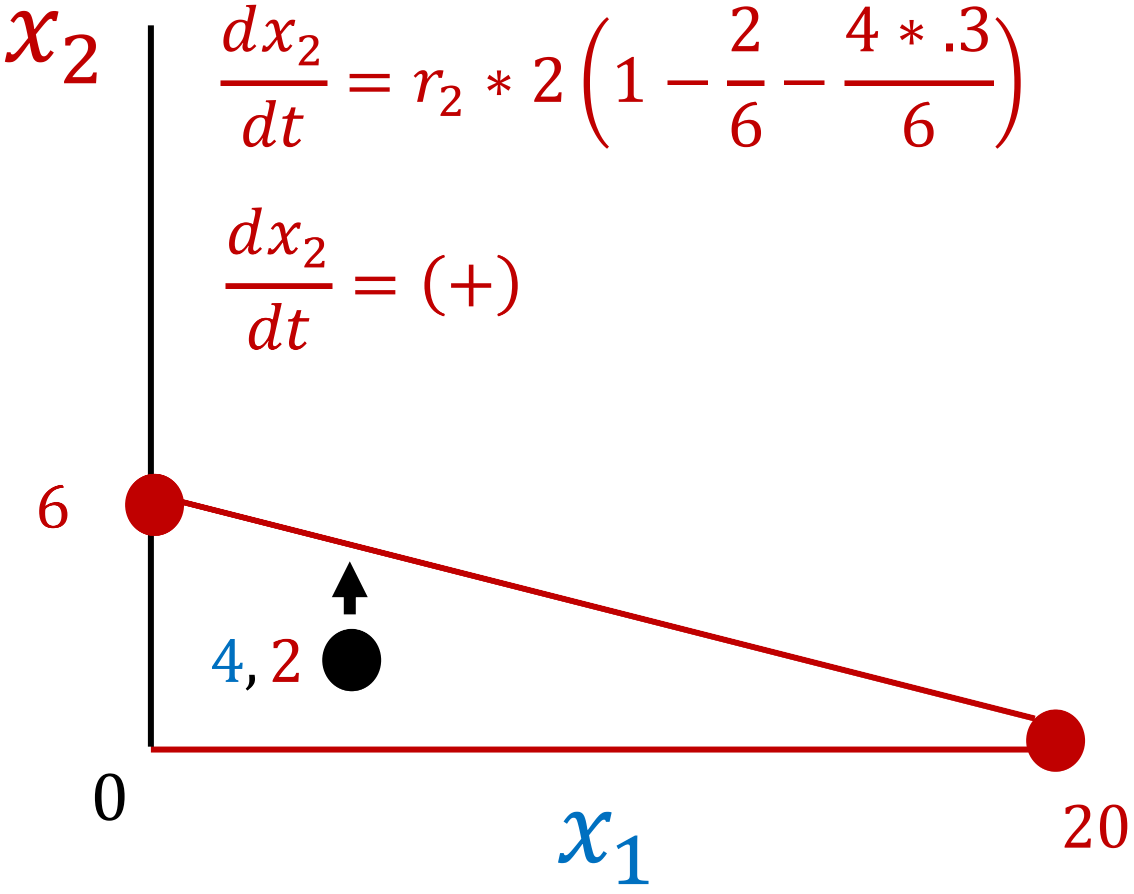
Nullclines (or **isoclines**) of the **Lotka-Volterra competition model**

- 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!
- $K_2 = 6\,; \alpha_{21} = .3$

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

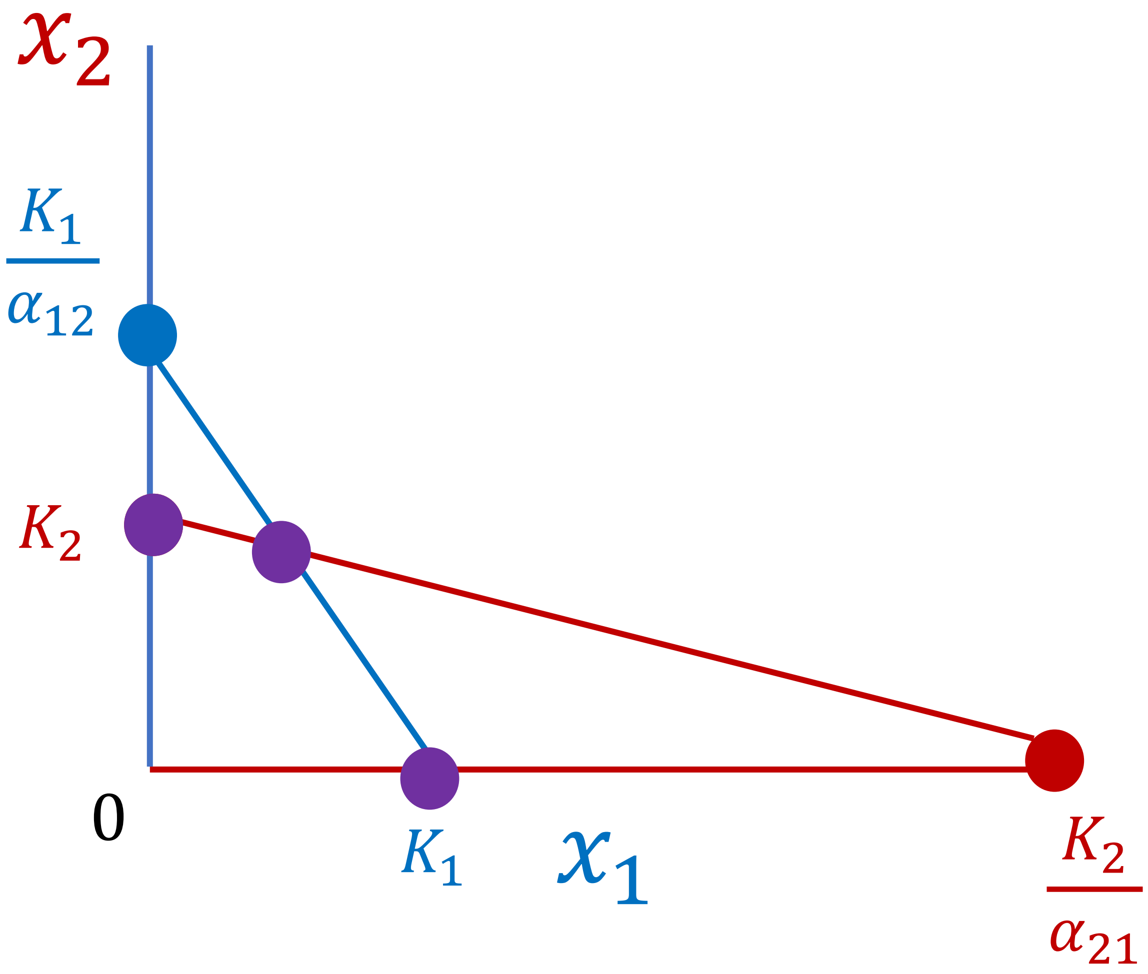
$$\frac{dx_2}{dt} = r_2 * 2 \left(1 - \frac{2}{6} - \frac{4 * .3}{6}\right)$$

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

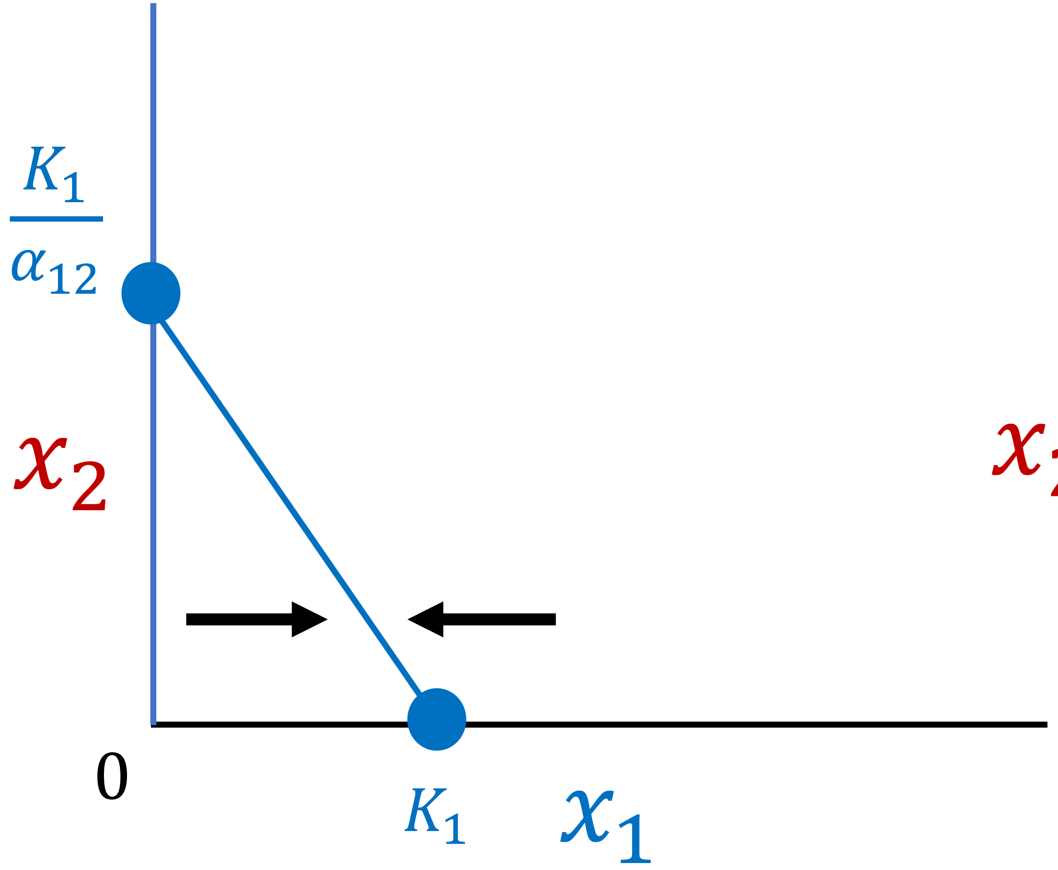


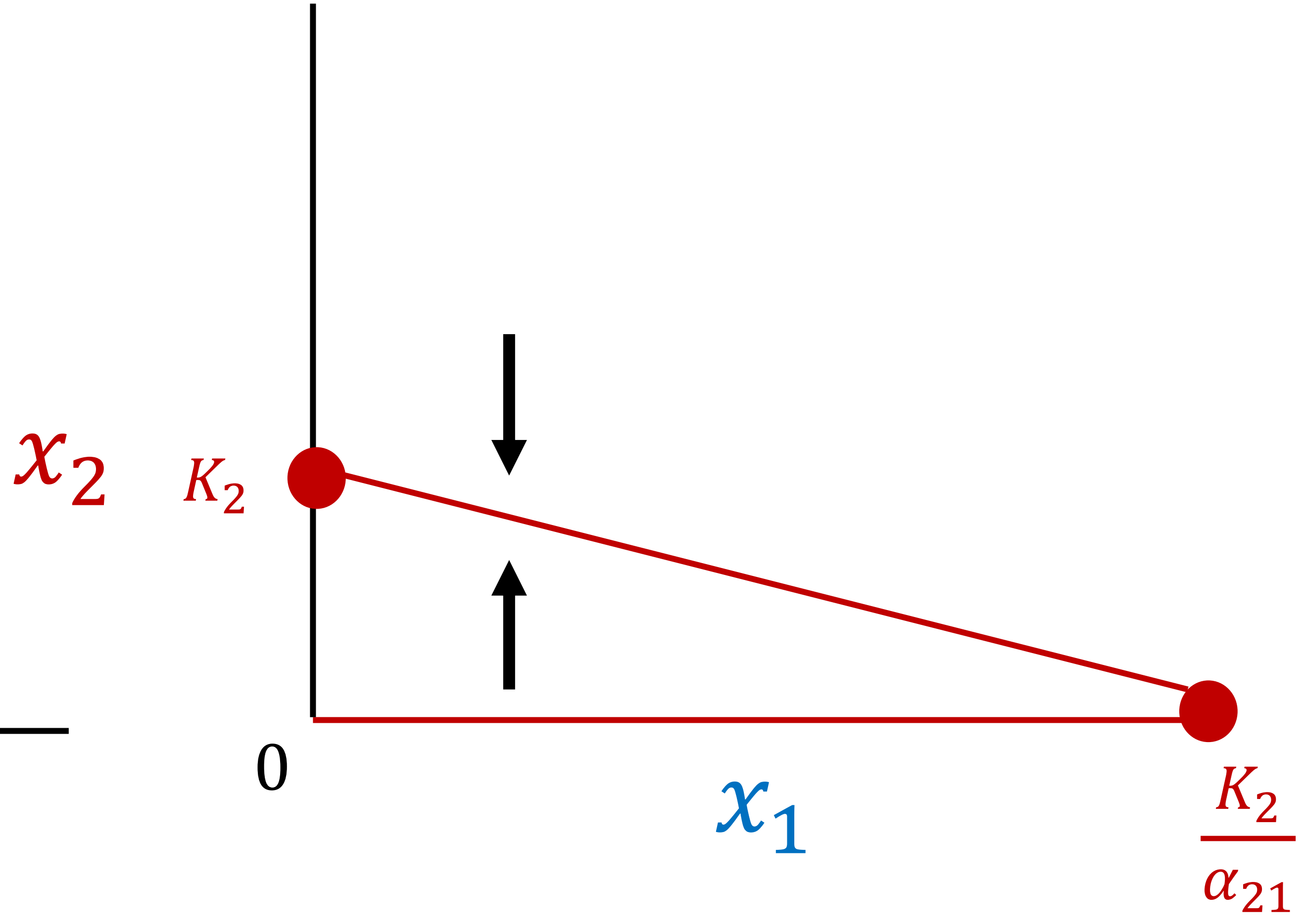
Given different combinations of x_1 and x_2 what is the outcome of competition?

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



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





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

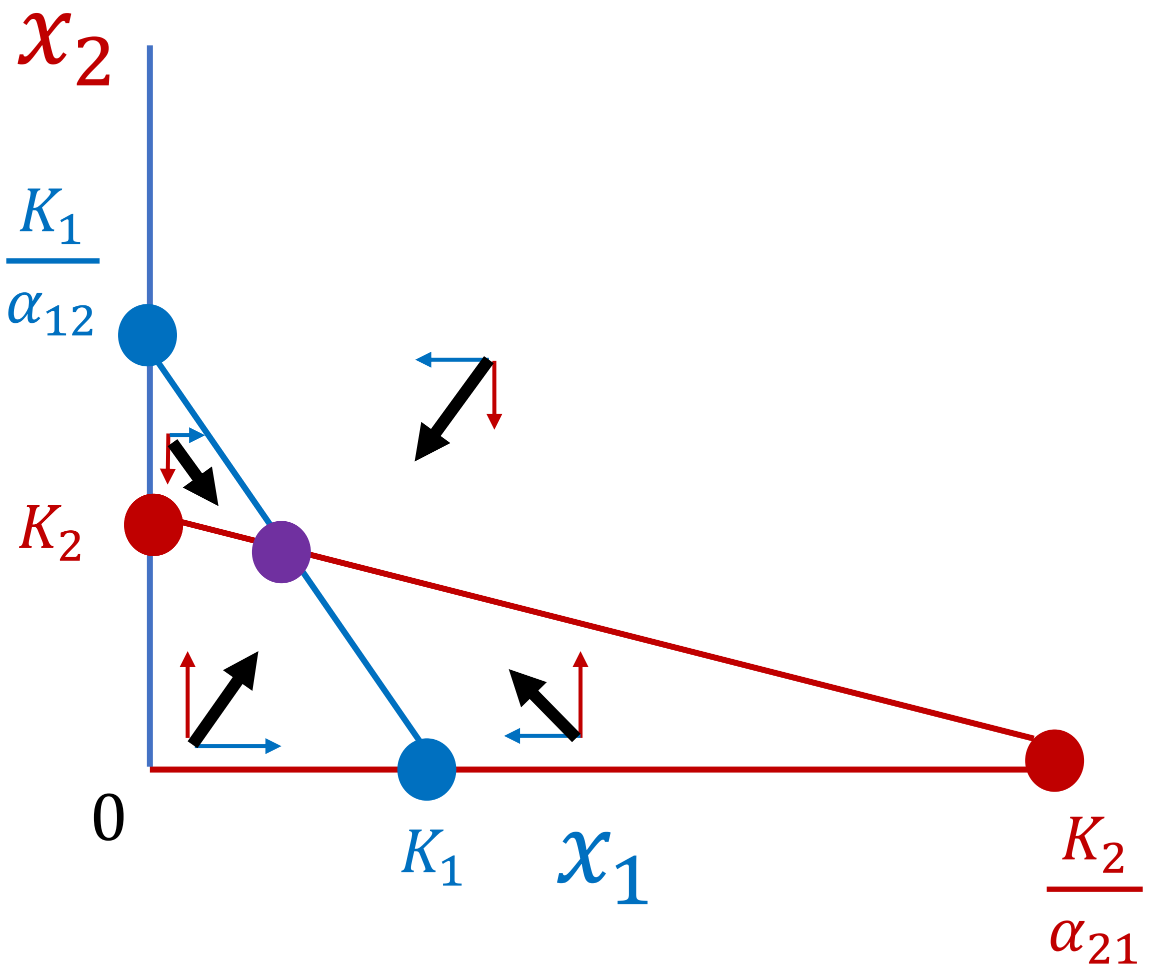
Given different combinations of x_1 and x_2 what is the outcome of competition?

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:

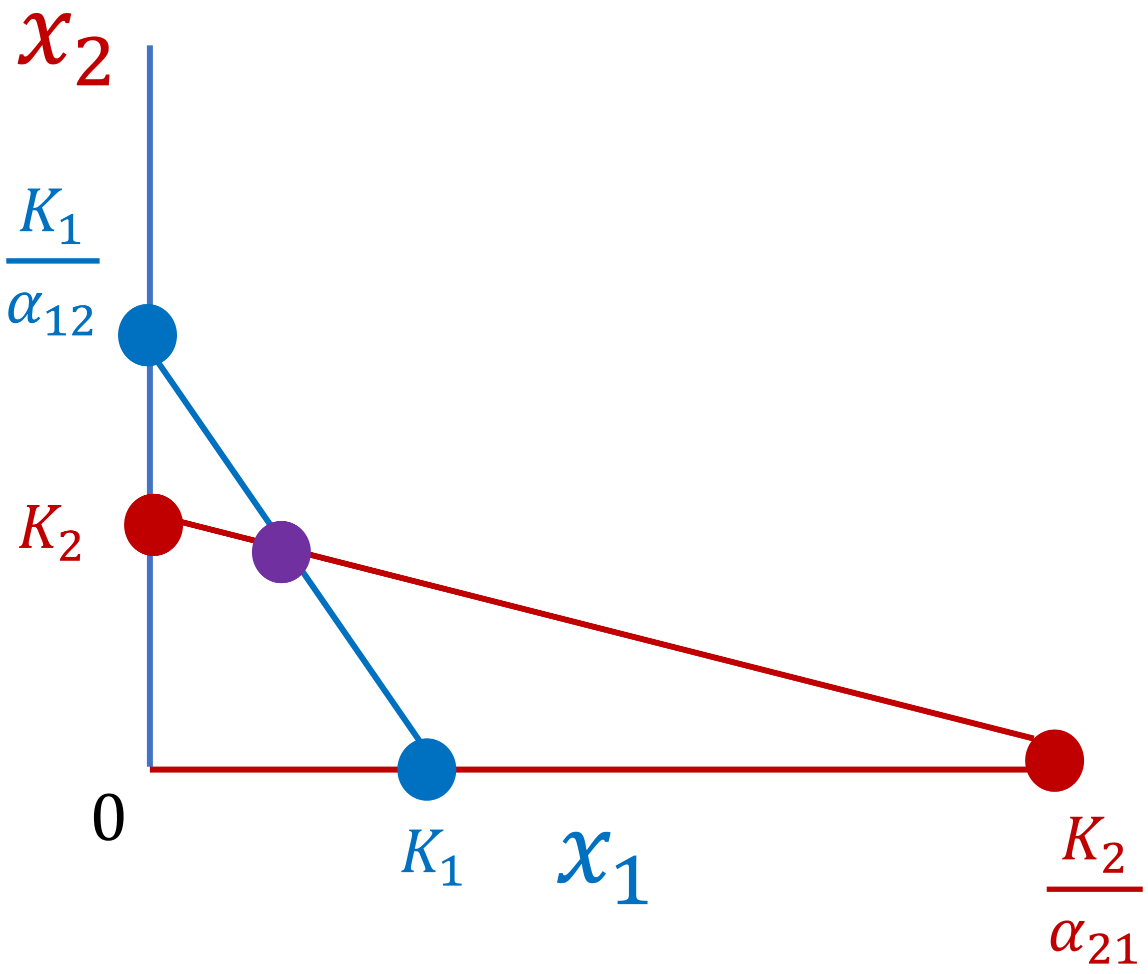
$$x_1^* = \frac{K_1 - K_2\alpha_{12}}{1 - \alpha_{21}\alpha_{12}} \quad x_2^* = \frac{K_2 - K_1\alpha_{21}}{1 - \alpha_{12}\alpha_{21}}$$



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!

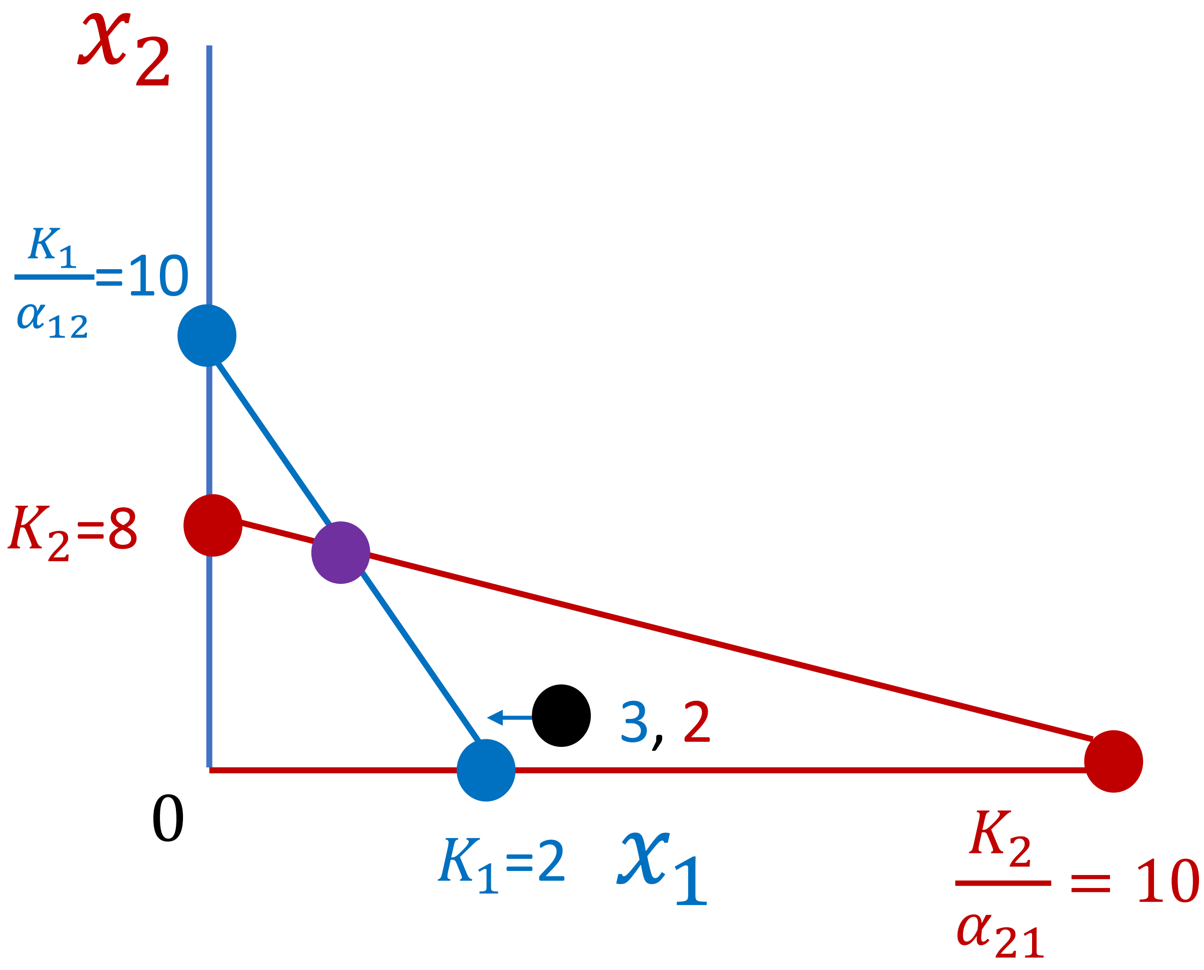
$K_1 = 2\,; \alpha_{12} = .3$
$K_2 = 8\,; \alpha_{21} = .8$

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

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

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

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



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

Let's try it!

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

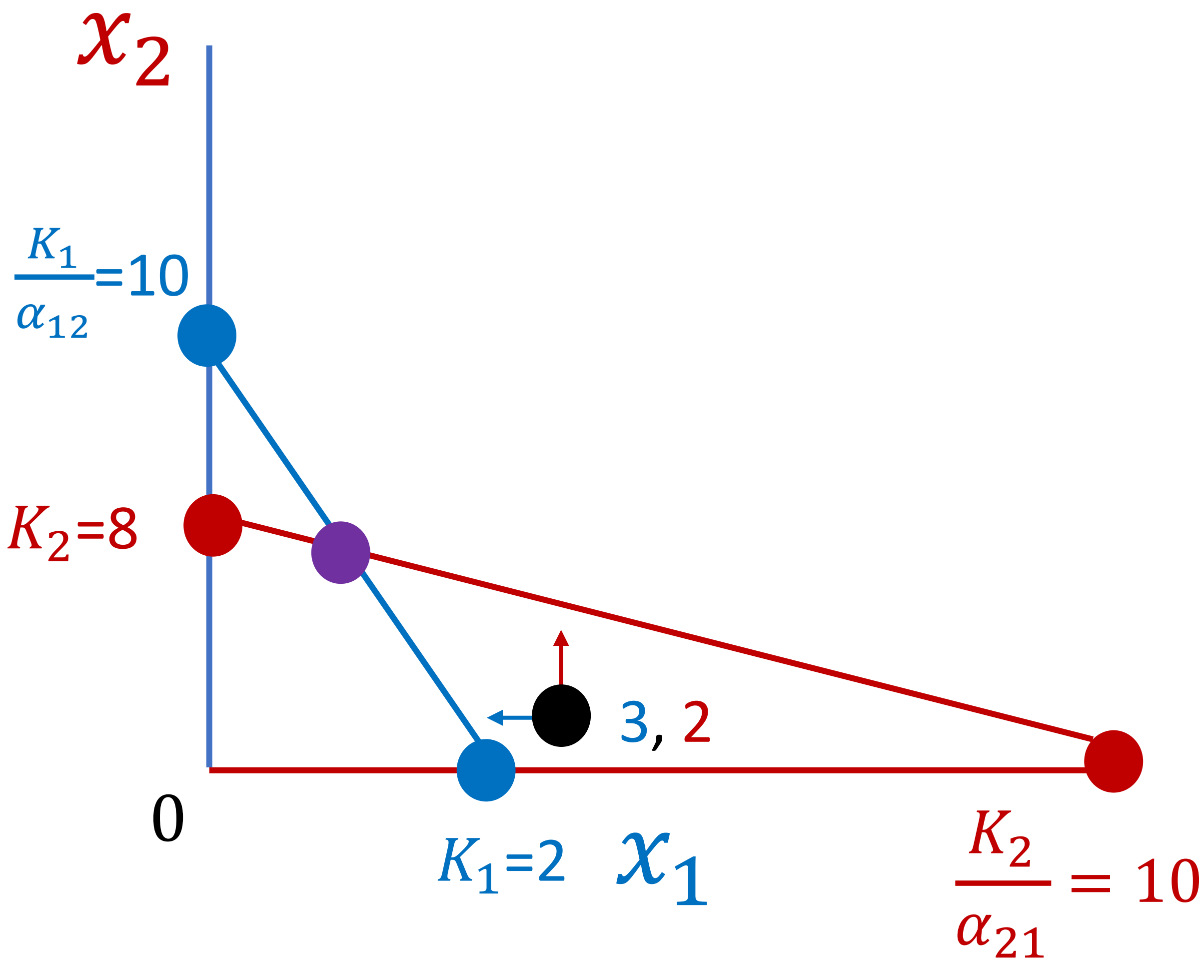
$K_2 = 8\,;\alpha_{21} = .8$

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

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

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

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

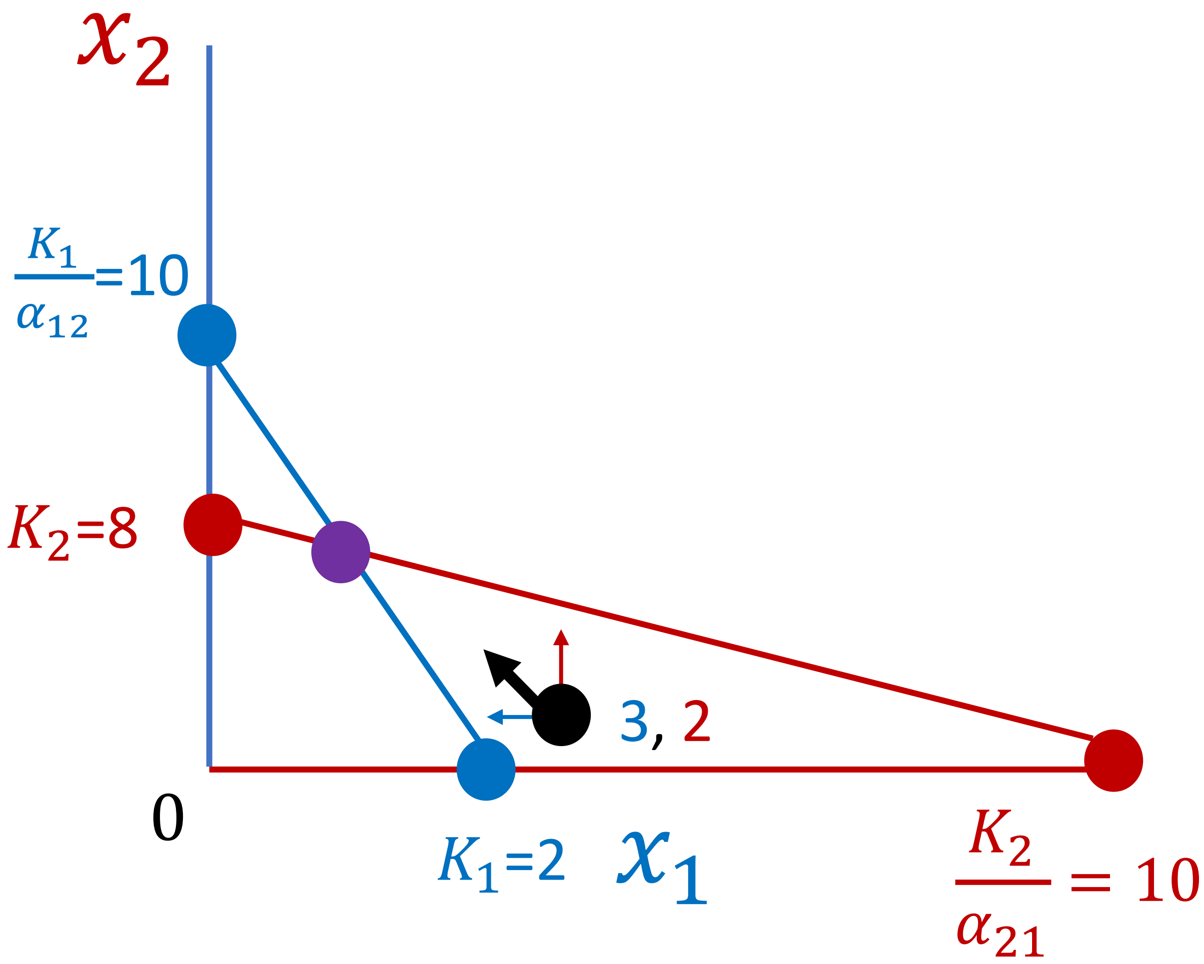


Given different combinations of x_1 and x_2 what is the outcome of competition?

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:

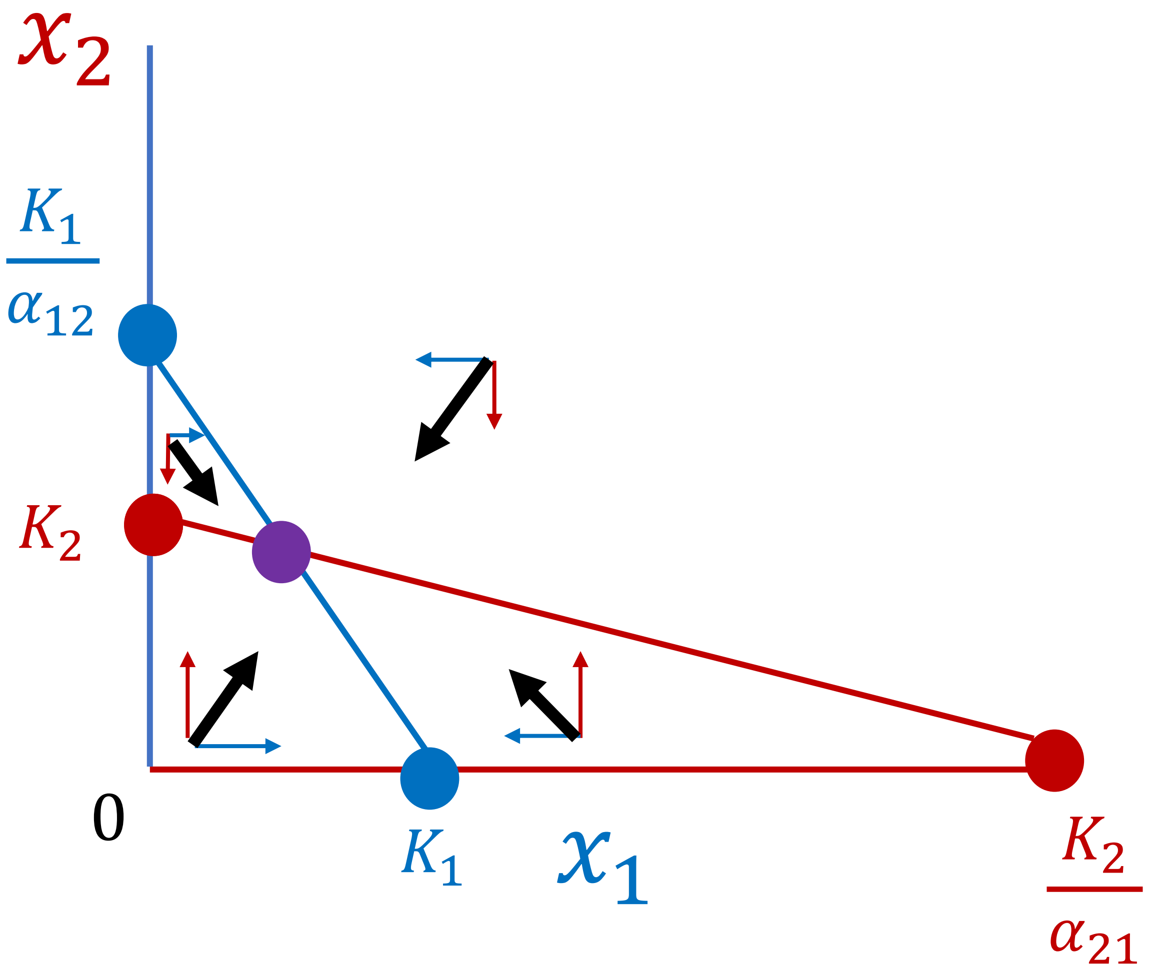
Stable equilibrium, with **coexistence** at:

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

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

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

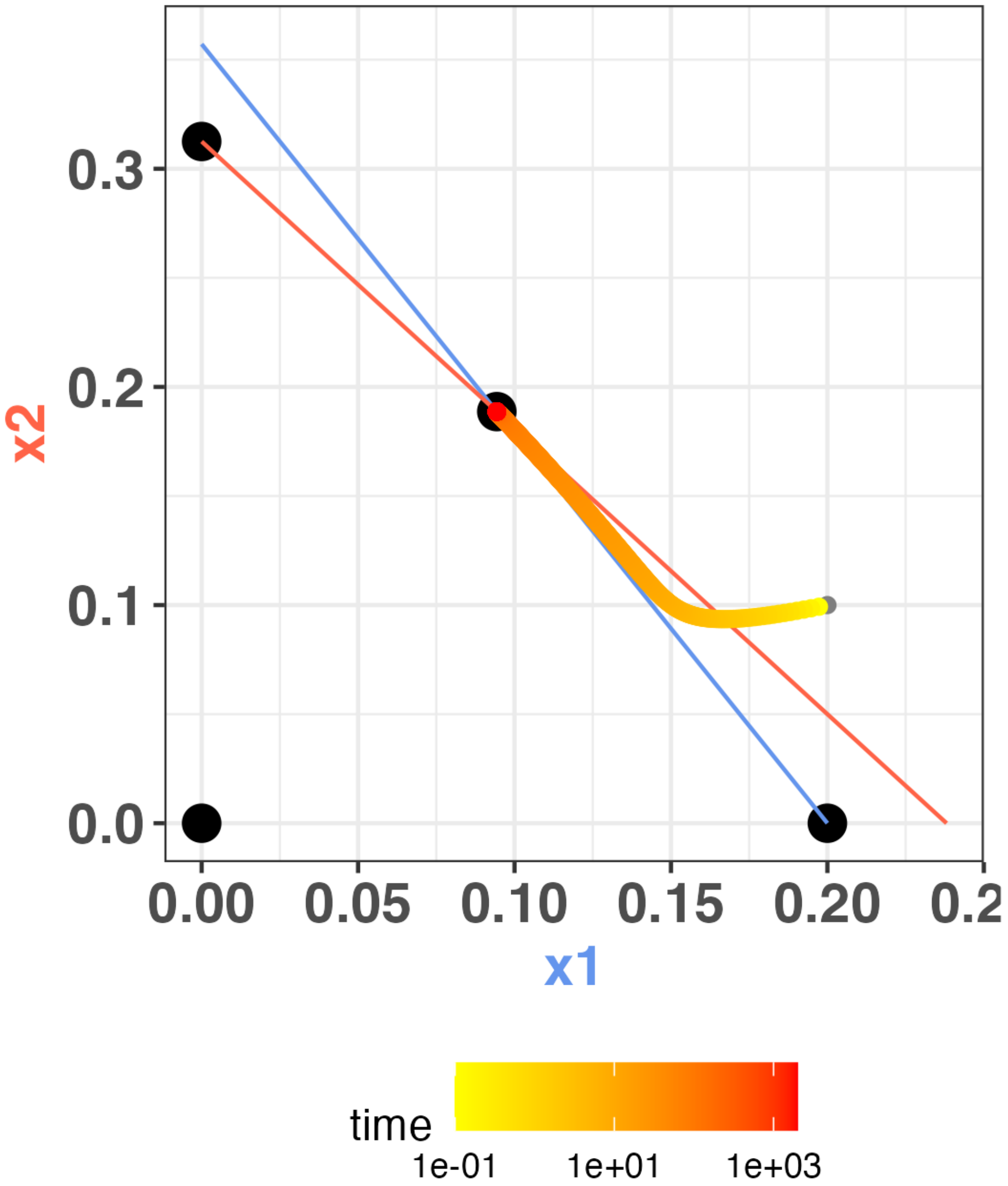
- Species coexist stably but **below carrying capacity** for each individual population.
- **Intraspecific** competition is stronger than **interspecific** competition.

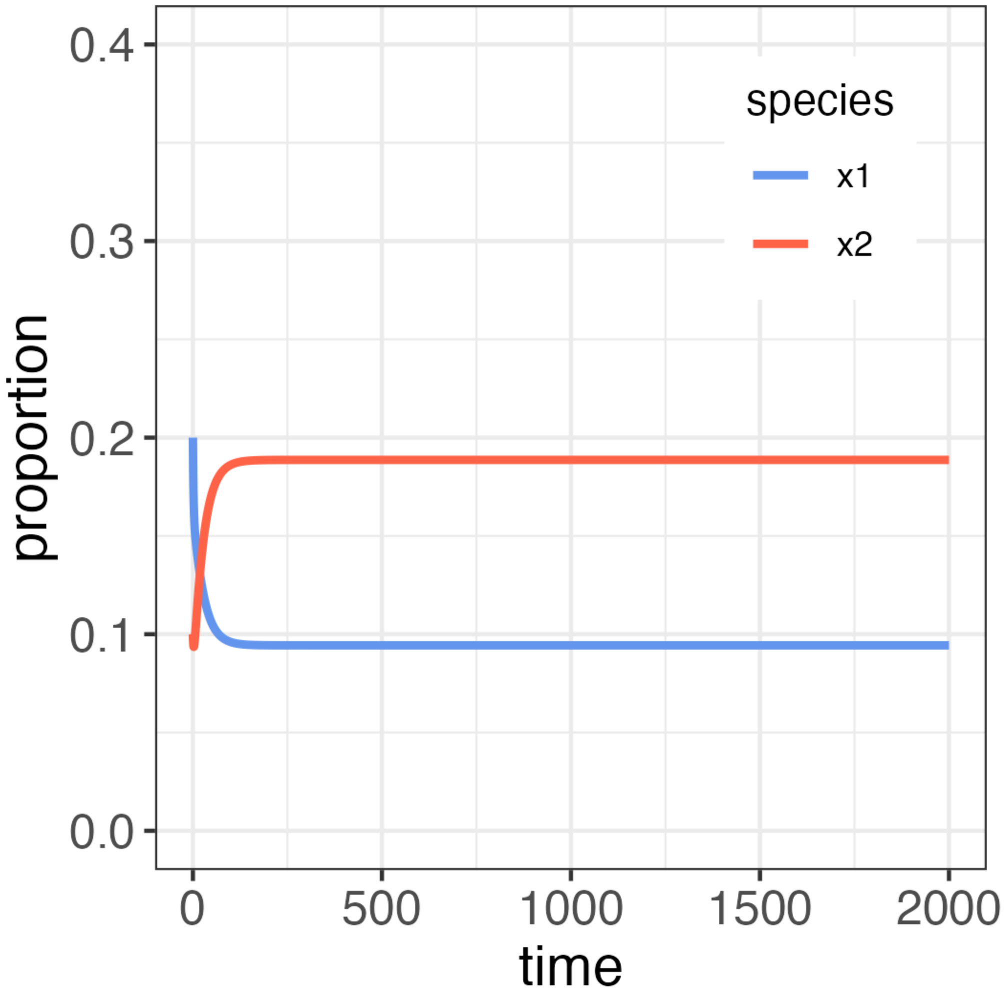


Case 1:

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

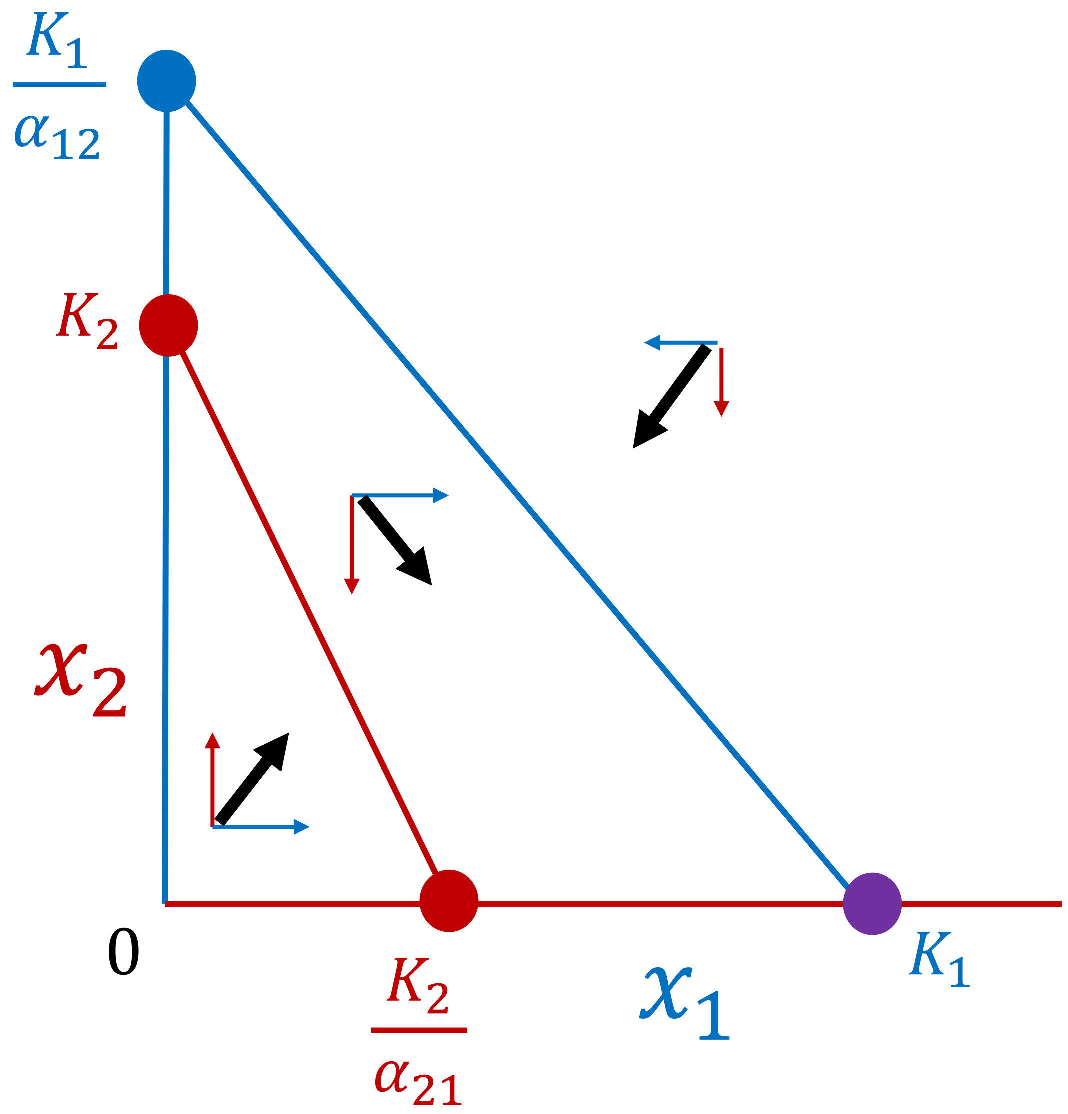
Case 2:

Species 1 outcompetes species 2

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

System collapses to equilibrium:

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



Case 2:

Species 1 outcompetes species 2

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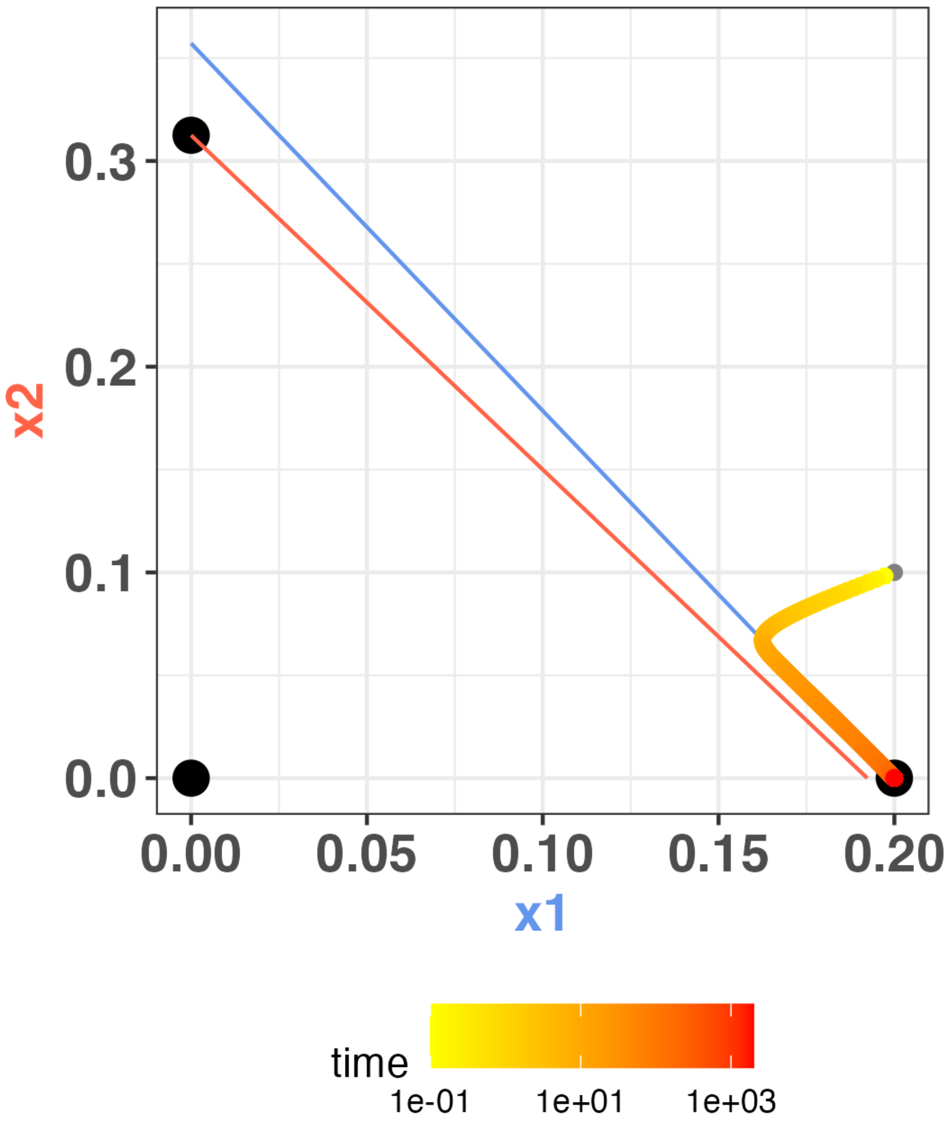
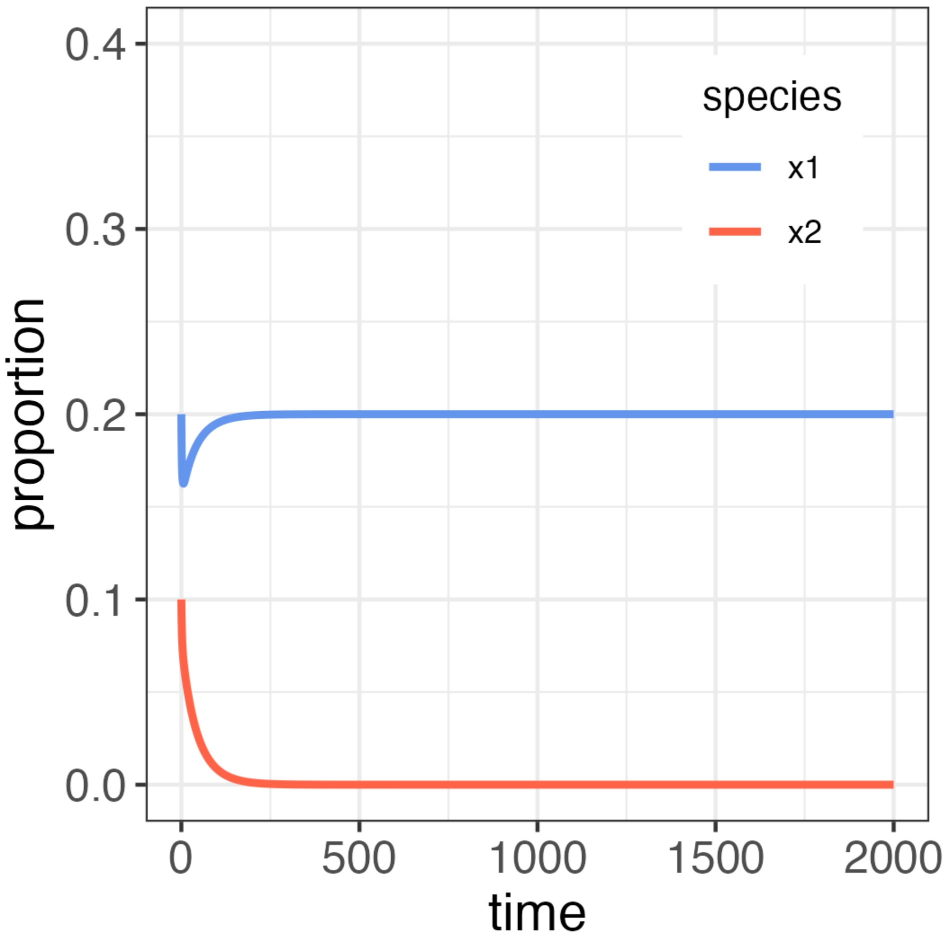




Four possible outcomes for competition

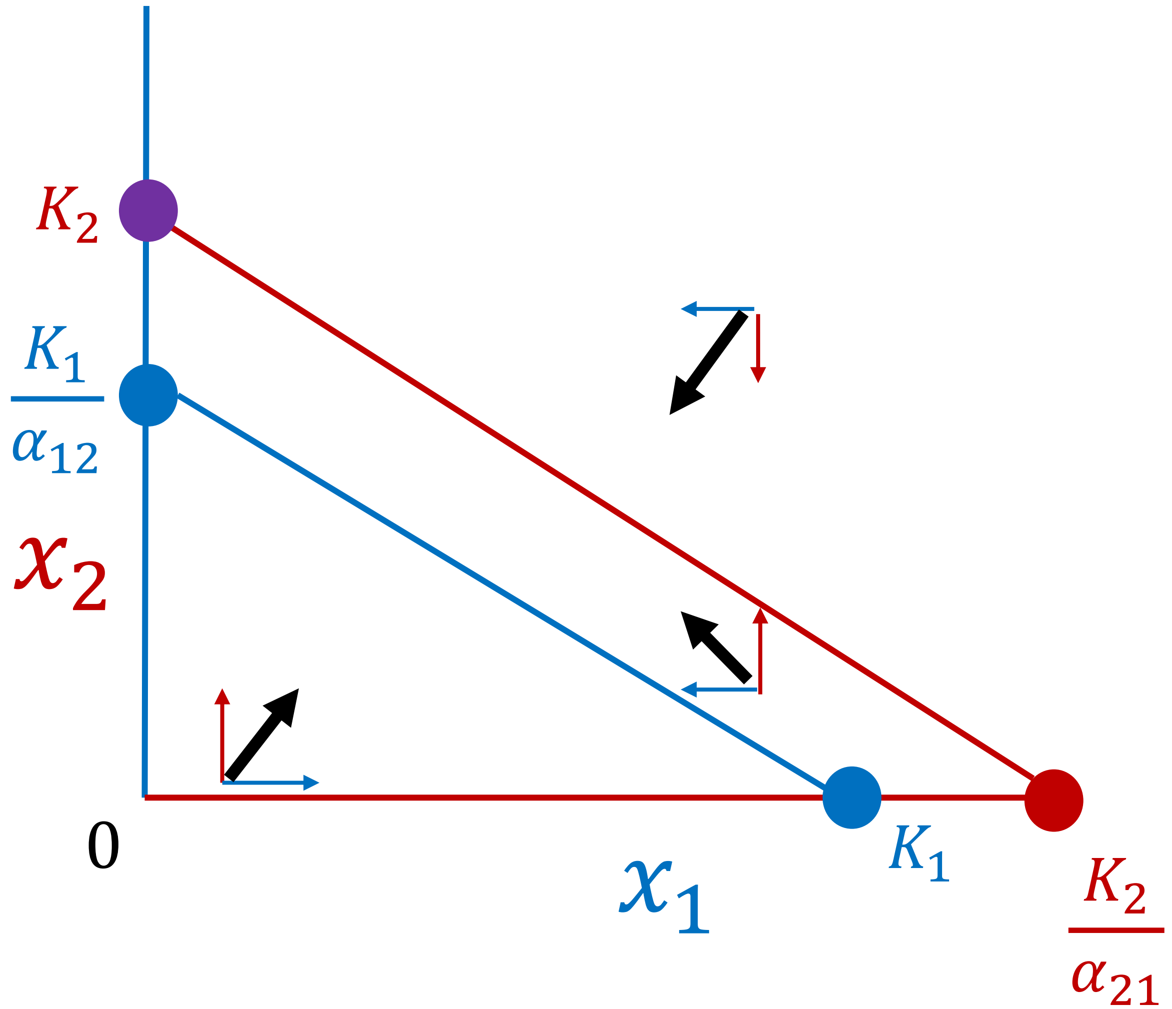
Case 3:

Species 2 outcompetes species 1

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

System collapses to equilibrium:

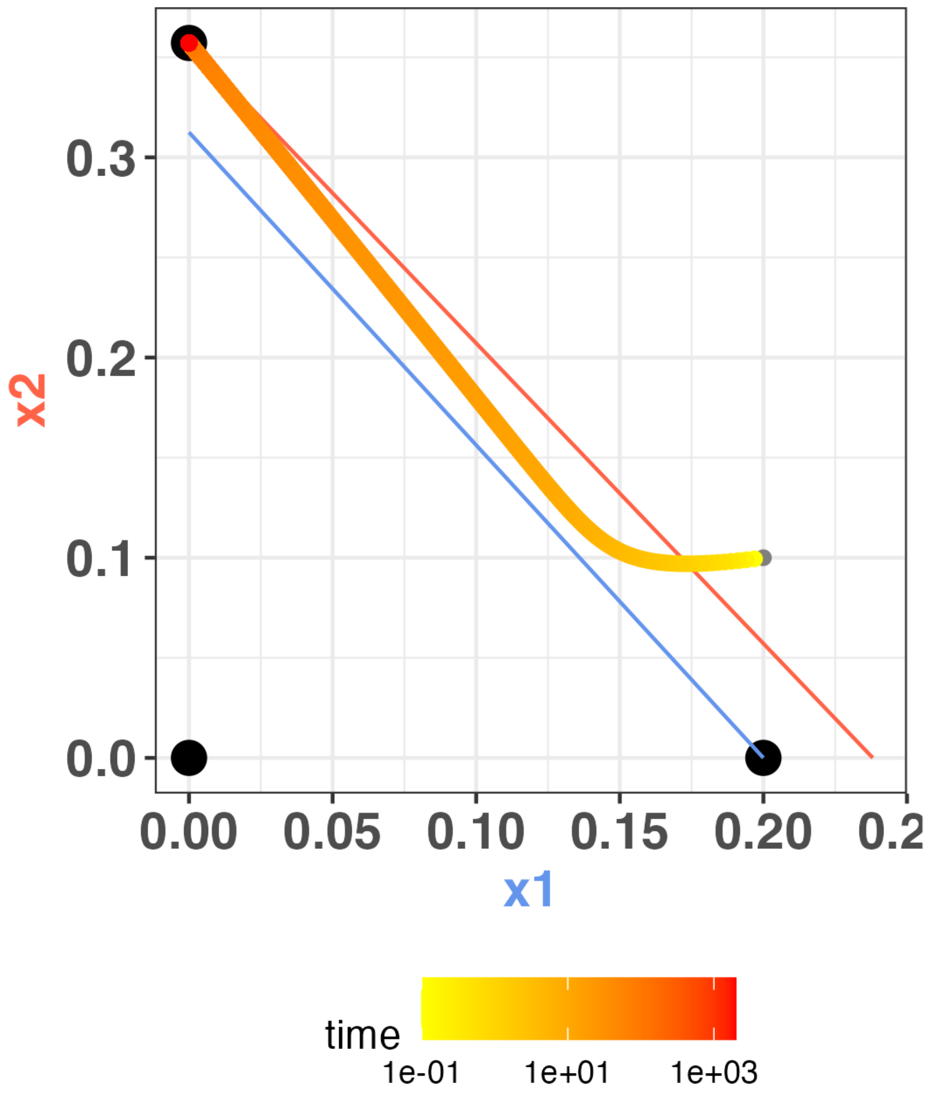
$$x_1^* = 0; \ x_2^* = K_2$$

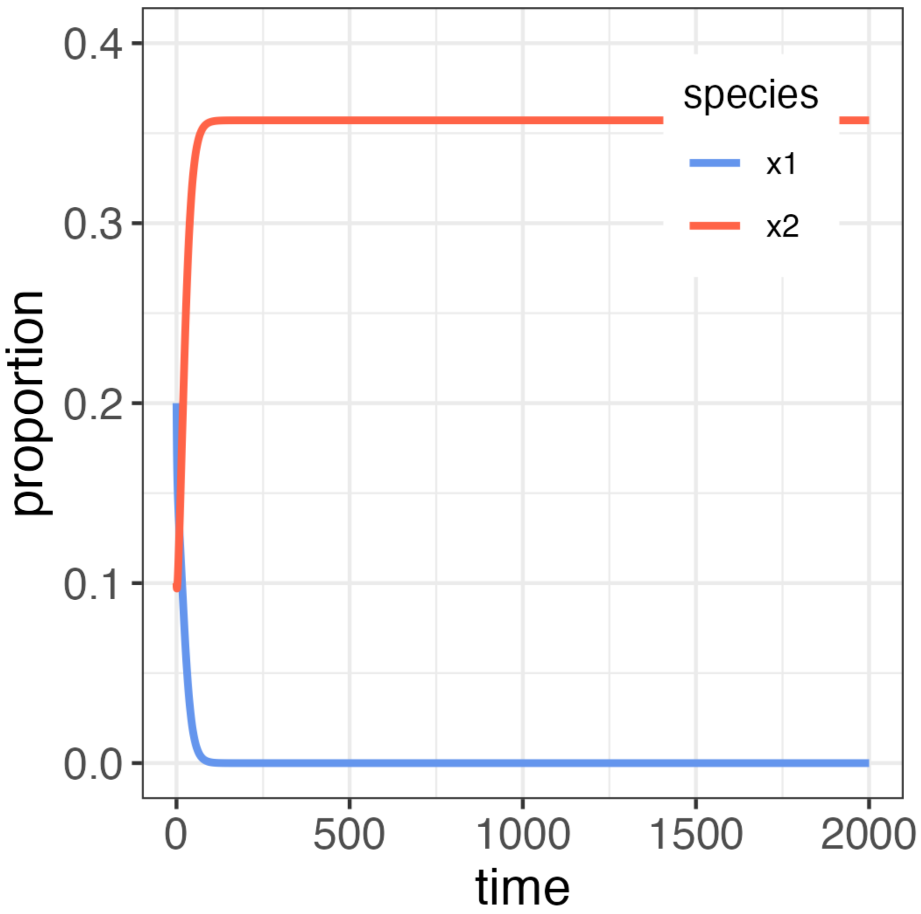


Case 3:

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

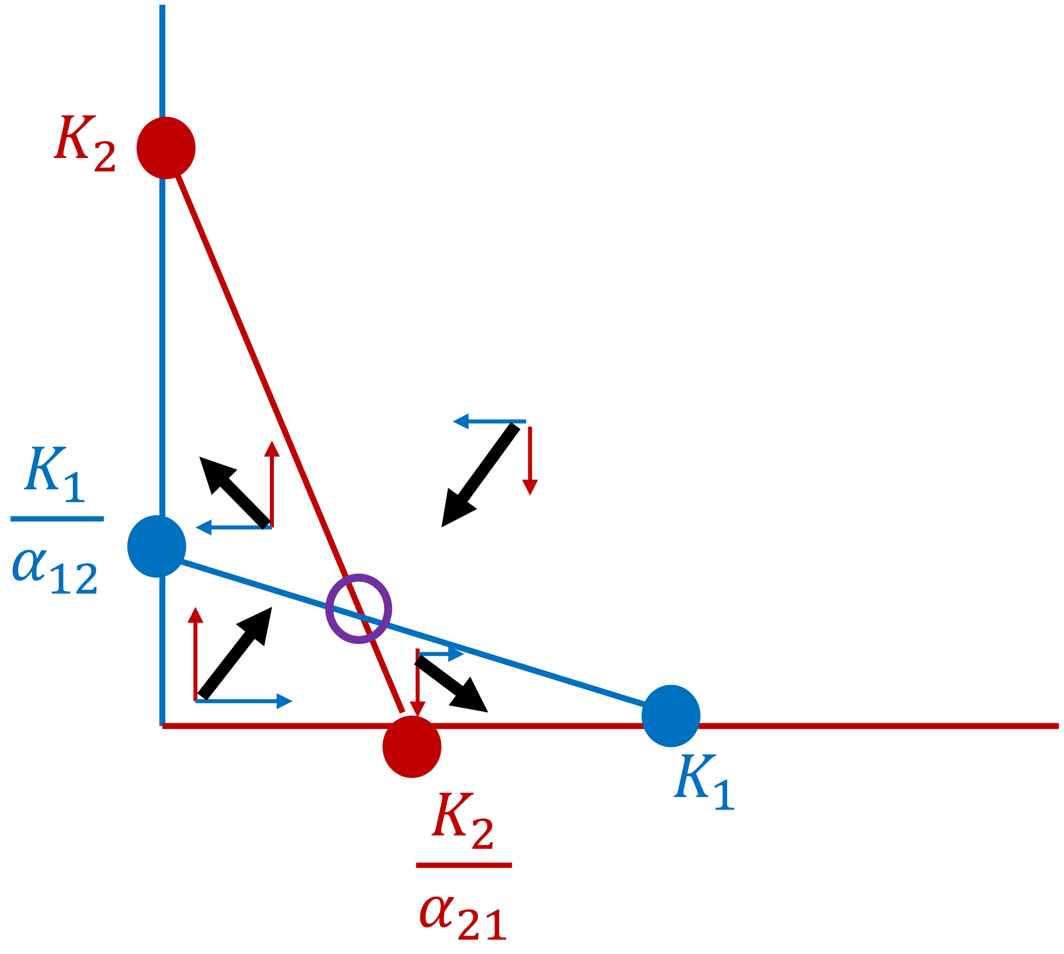
Aggressive interspecific competition.

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.

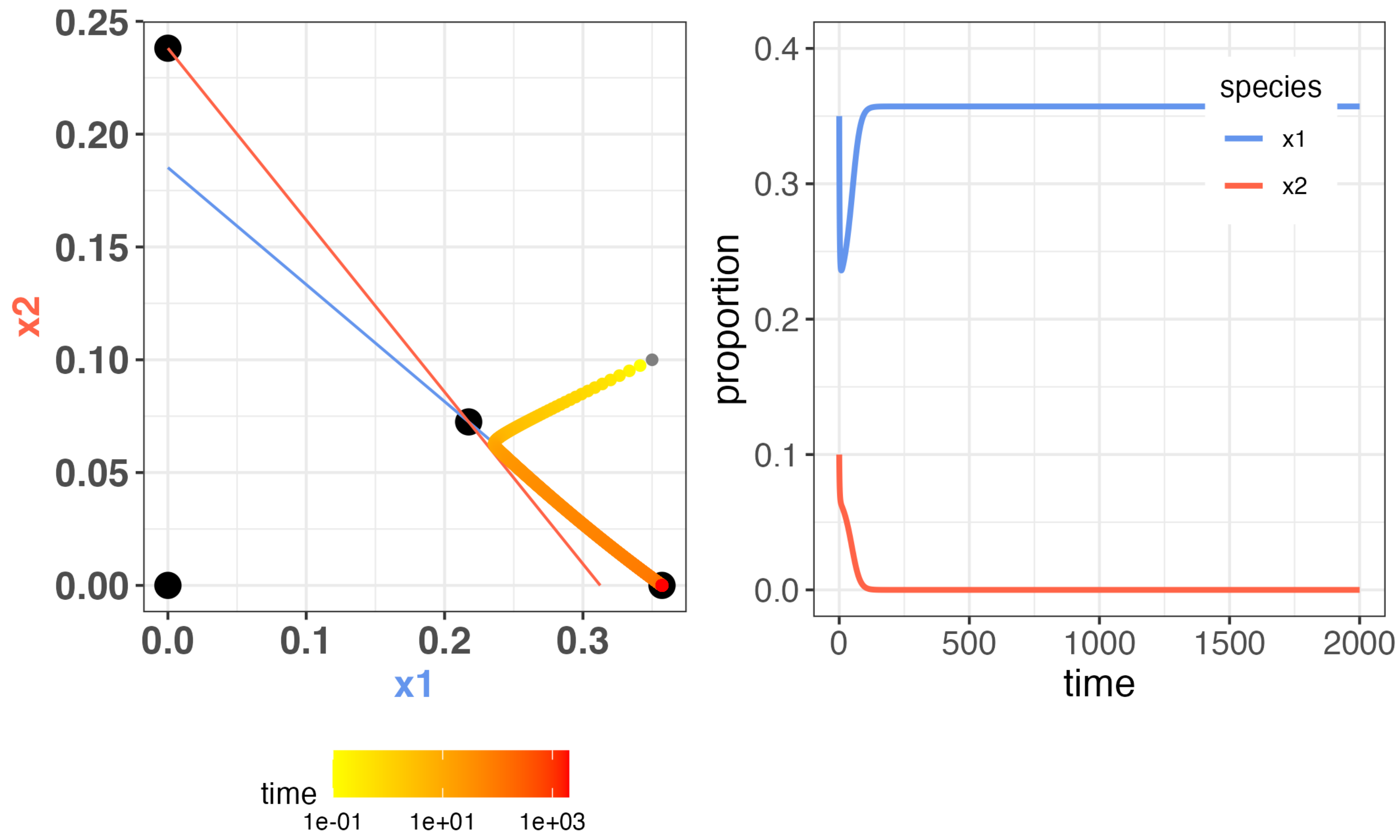


Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

Here, **x1 outcompetes x2**

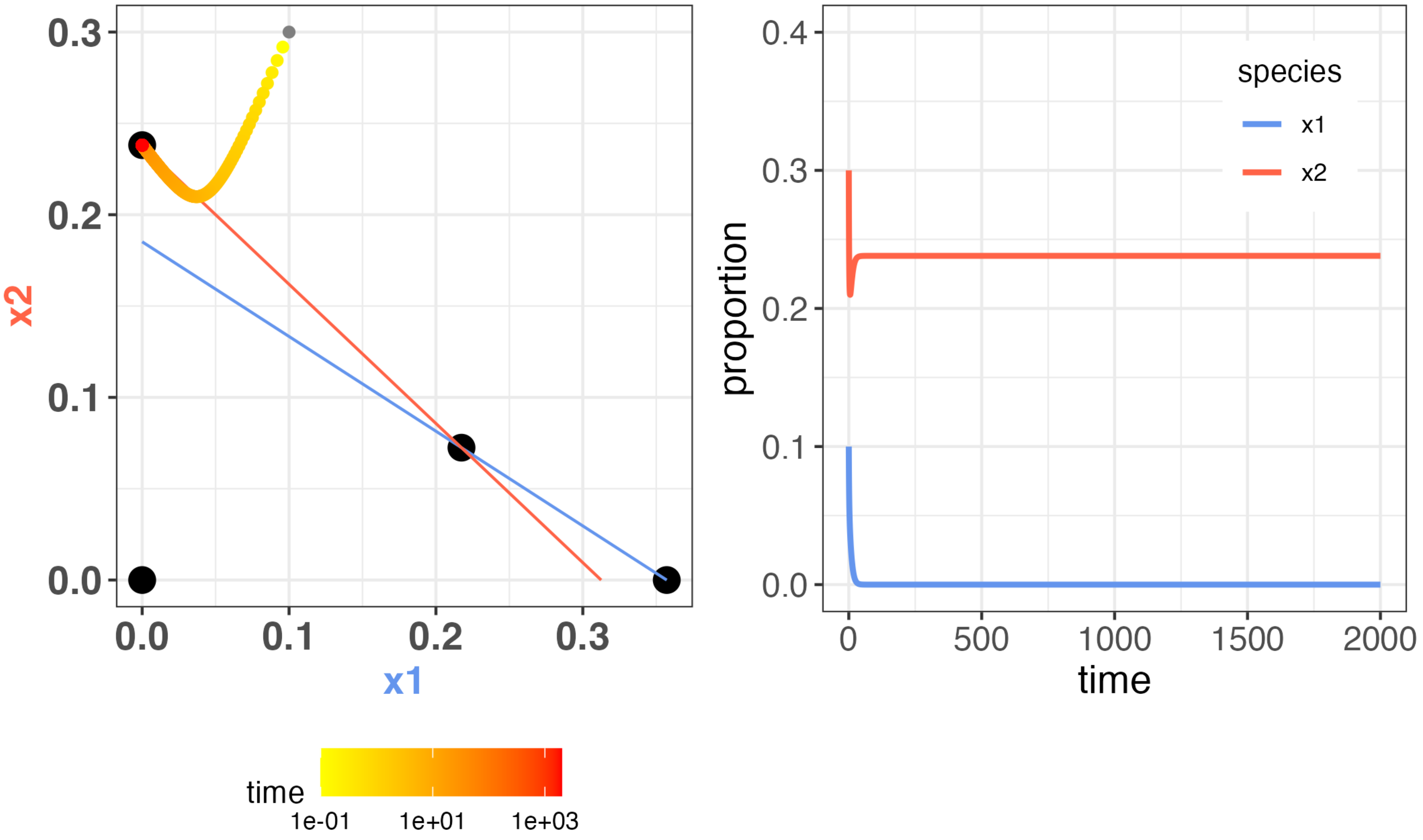


Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

Here, **x2 outcompetes x1**

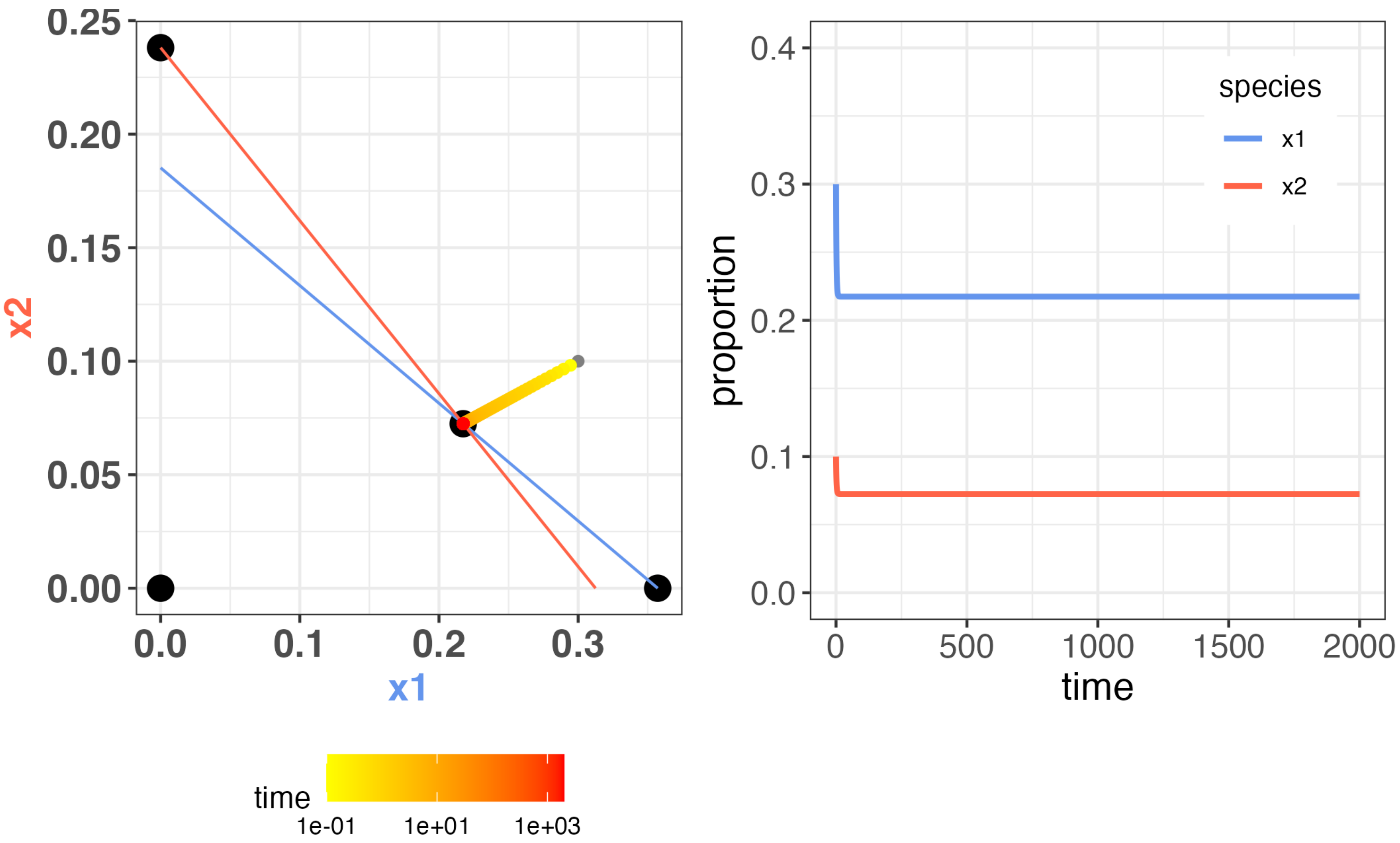


Case 4: Precedence

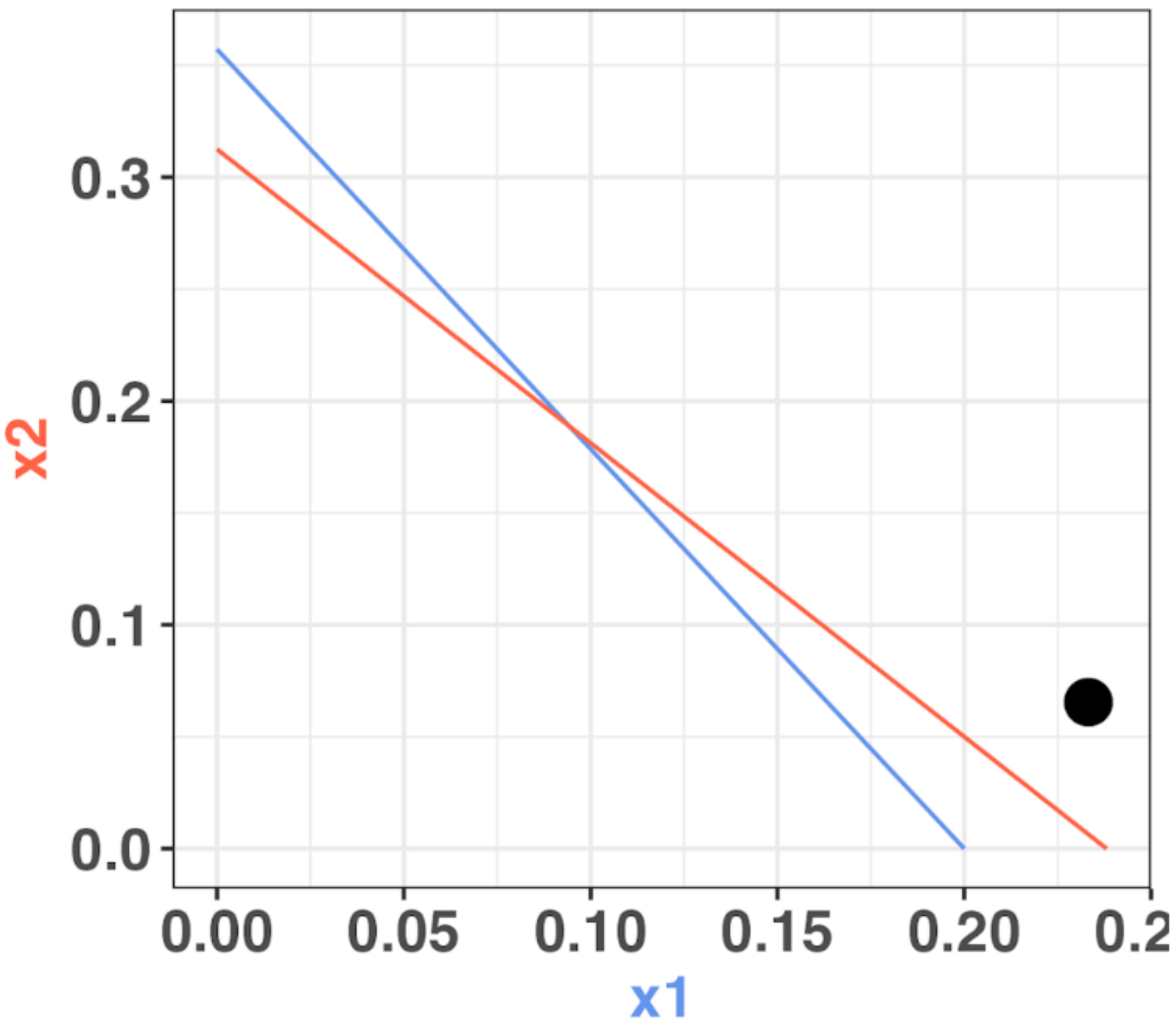
Aggressive interspecific competition.

Outcome depends on starting conditions.

Here, **coexistence**



Que 2. What will be the outcome of competition for a population with this nullcline sturcture, starting at the quantities shown by the black dot?



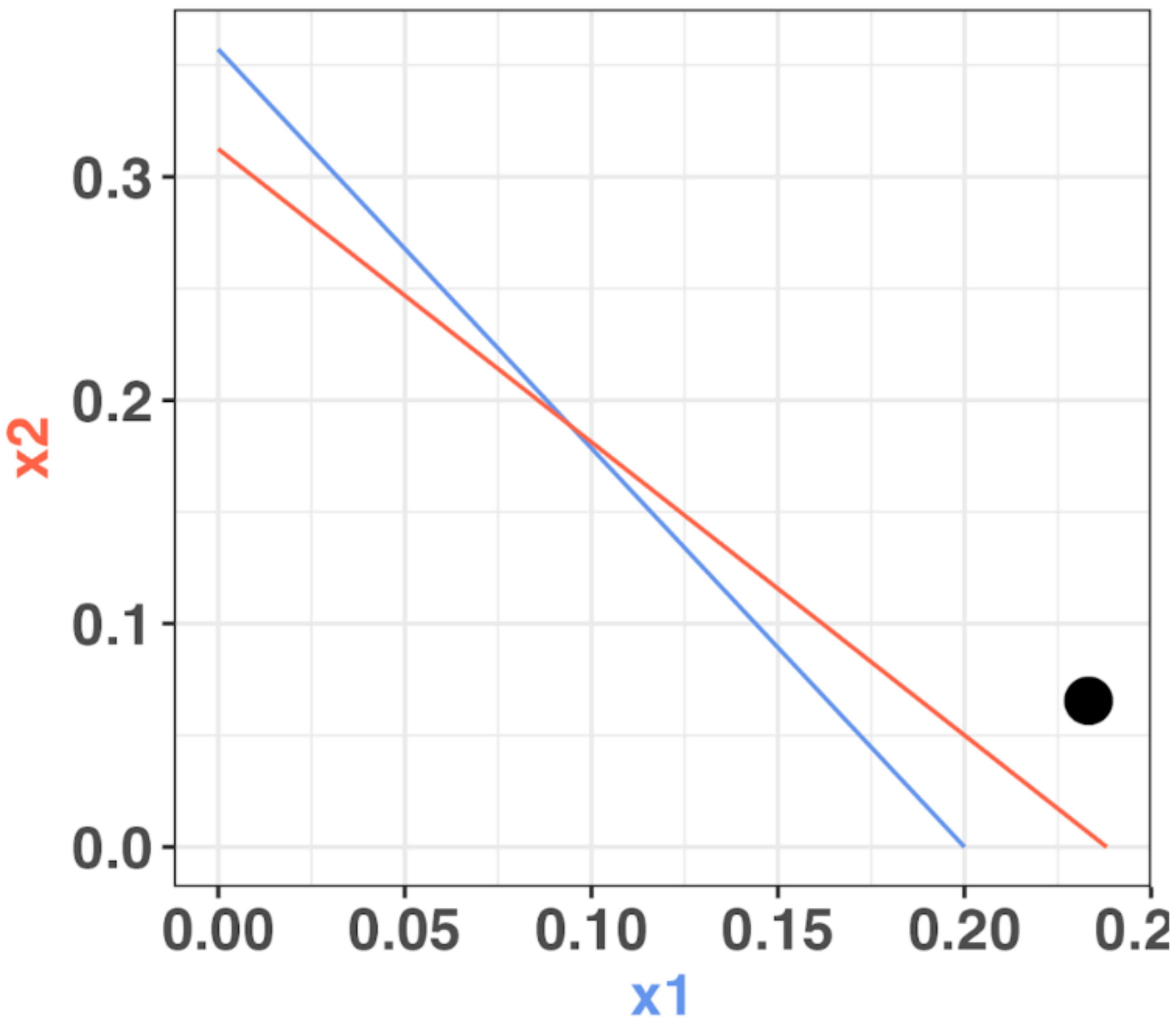
A Species x2 will outcompete x1, so we will end up at carrying capacity for x2 and extinction for x1.

B Species x1 will outcompete x2, so we will end up at carrying capacity for x1 and extinction for x2.

C Both species will coexist at the stable equilibrium.

D The outcome depends on the initial conditions.

Que 2. What will be the outcome of competition for a population with this nullcline sturcture, starting at the quantities shown by the black dot?



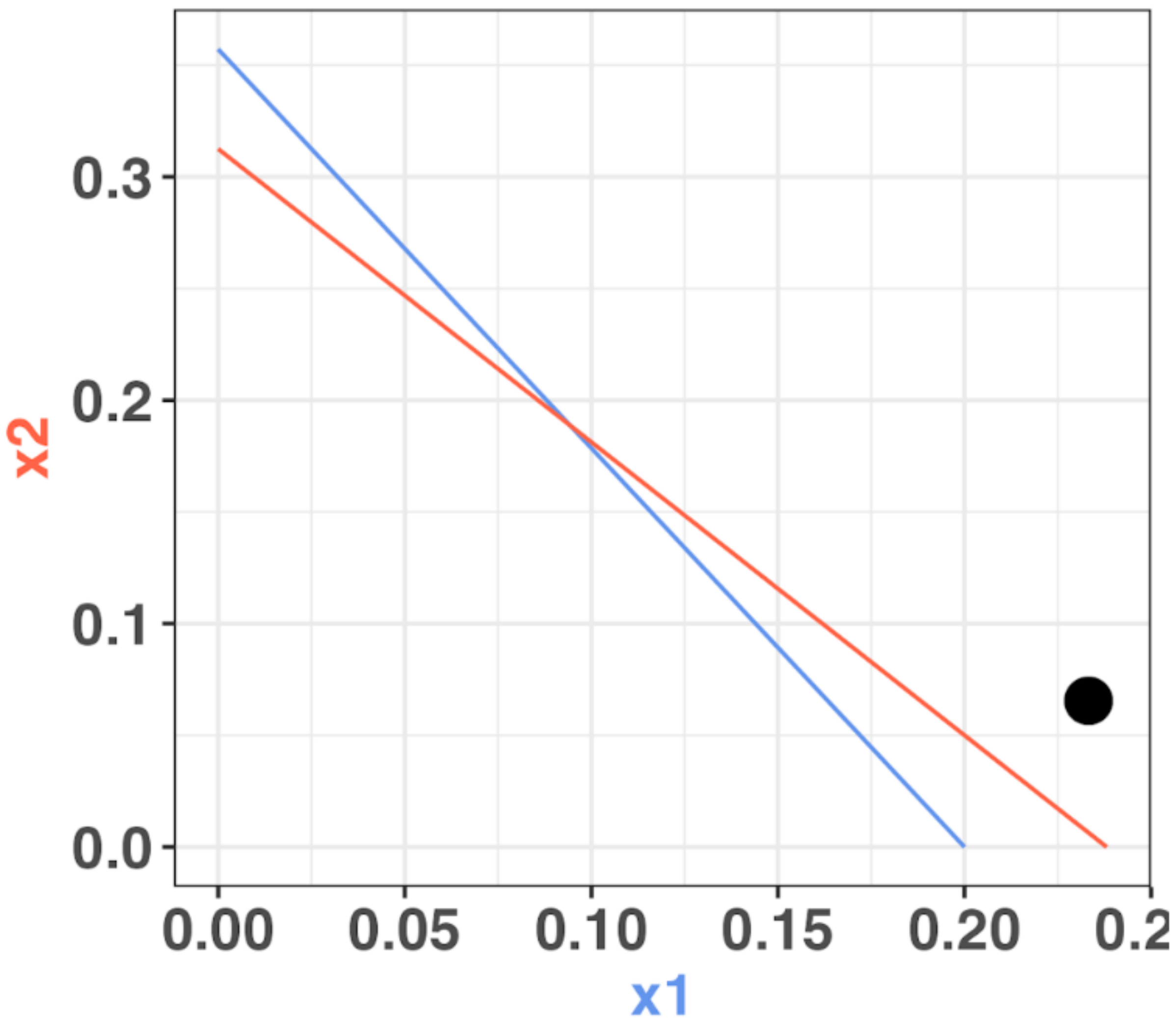
A Species x2 will outcompete x1, so we will end up at carrying capacity for x2 and extinction for x1. 0%

B Species x1 will outcompete x2, so we will end up at carrying capacity for x1 and extinction for x2. 0%

C Both species will coexist at the stable equilibrium. 0%

D The outcome depends on the initial conditions. 0%

Que 2. What will be the outcome of competition for a population with this nullcline sturcture, starting at the quantities shown by the black dot?



A Species x2 will outcompete x1, so we will end up at carrying capacity for x2 and extinction for x1. 0%

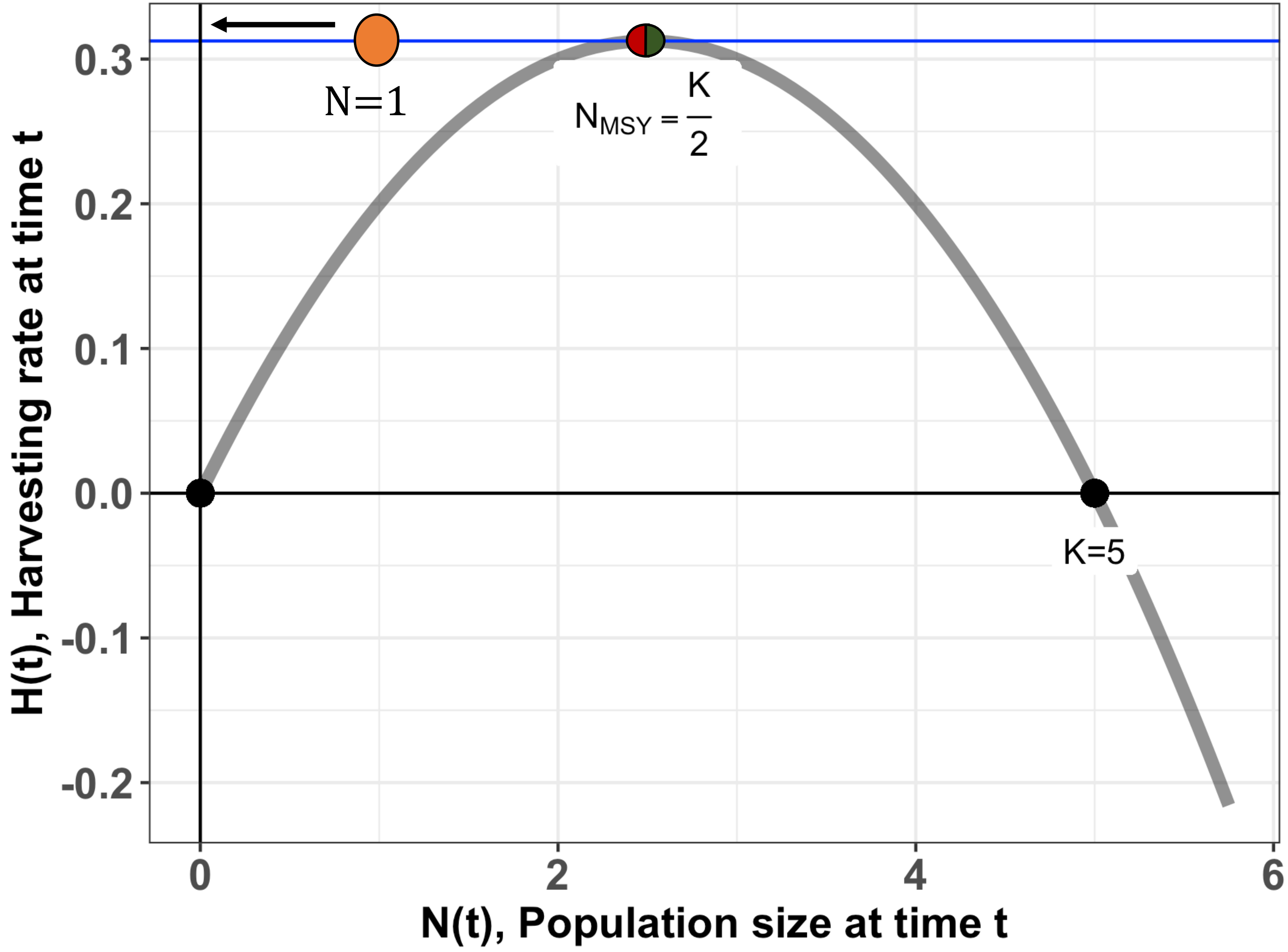
B Species x1 will outcompete x2, so we will end up at carrying capacity for x1 and extinction for x2. 0%

C Both species will coexist at the stable equilibrium. 0%

D The outcome depends on the initial conditions. 0%

Remember MSY, the semi-stable equilibrium:

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



K=5

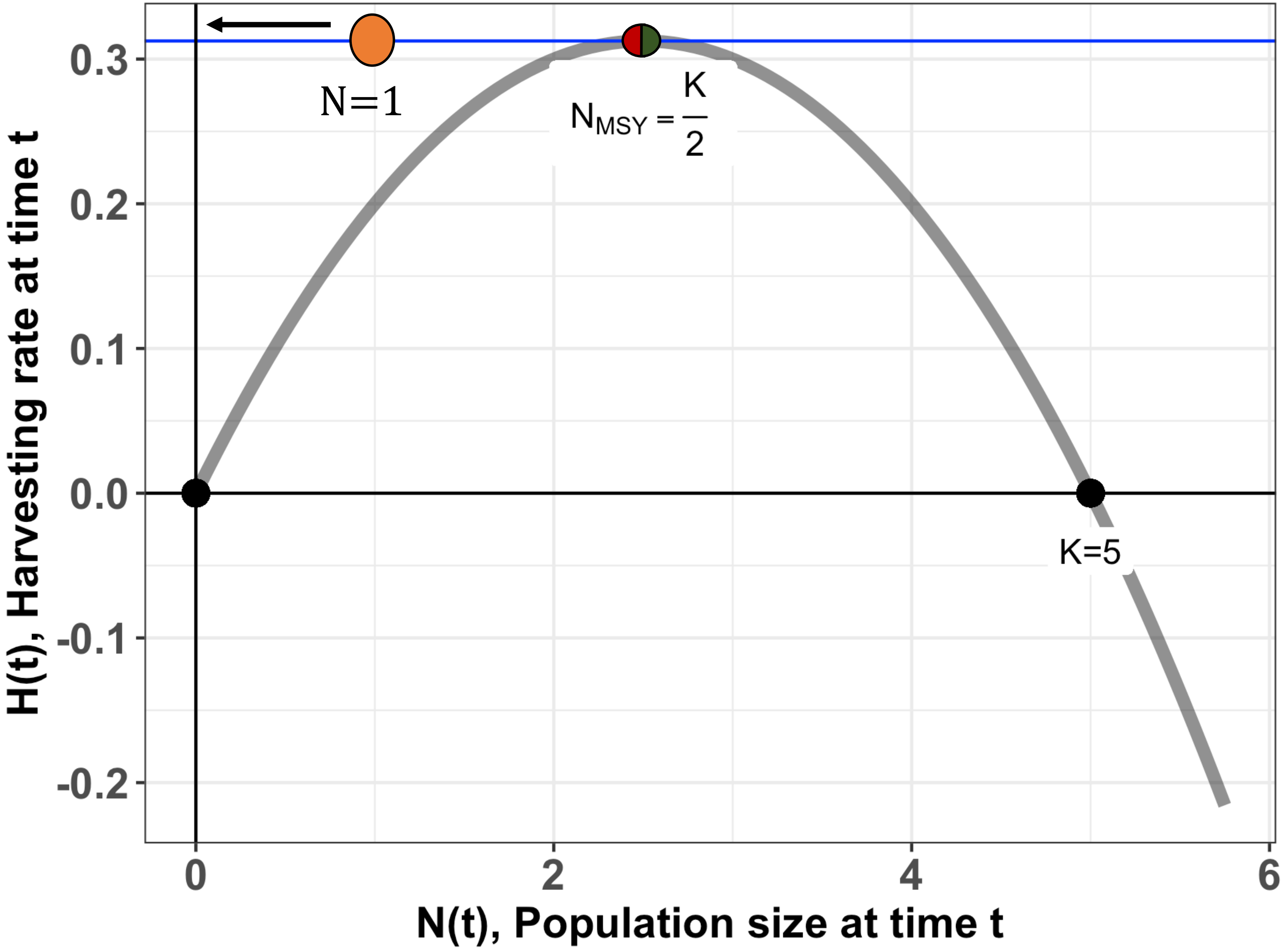
r=0.25

H=.3125

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

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

Remember MSY, the semi-stable equilibrium: $$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - H$$



K=5
r=0.25
H=.3125

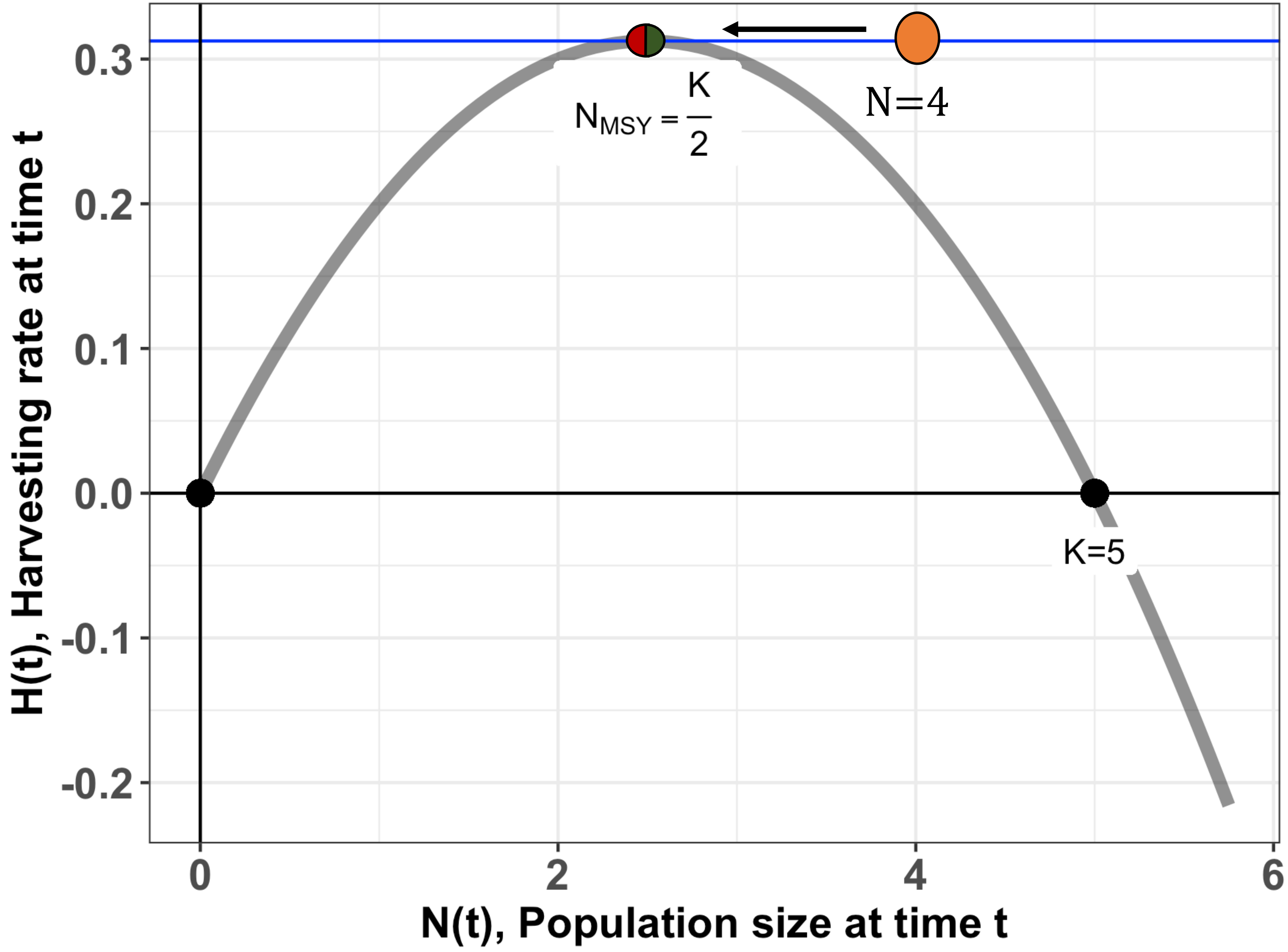
$$\frac{dN}{dt} = 0.25 * 1\left(1 - \frac{1}{5}\right) -.3125$$

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

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

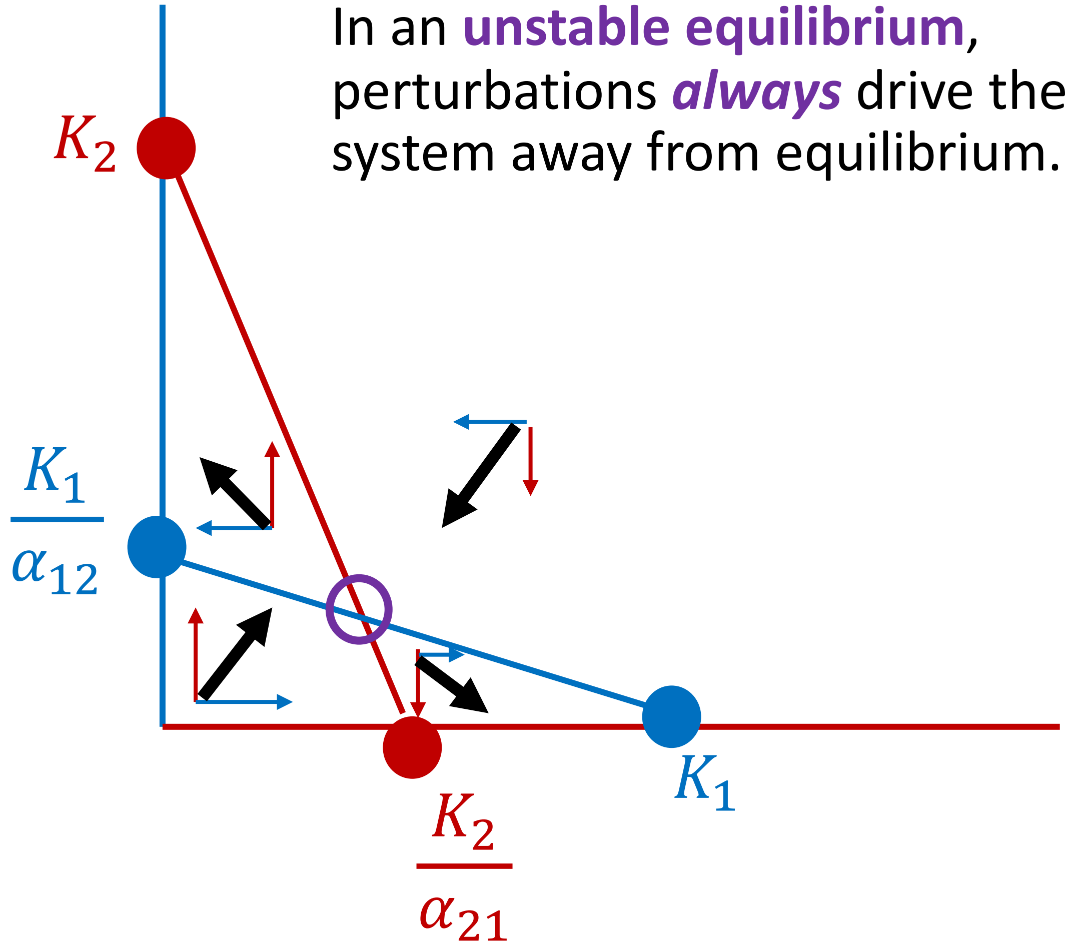
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

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

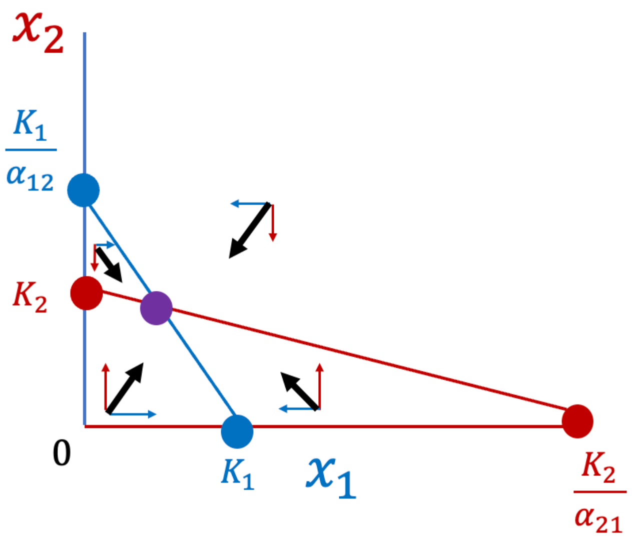
$$(\alpha_{12} * \alpha_{21} > 1)$$



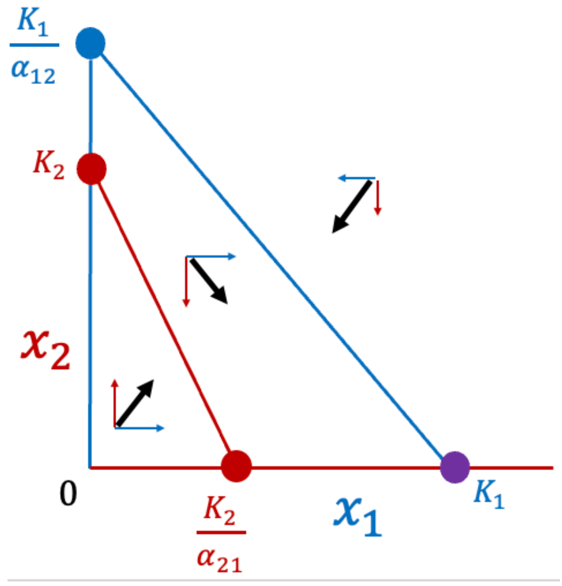
In an **unstable equilibrium**, perturbations ***always*** drive the system away from equilibrium.

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

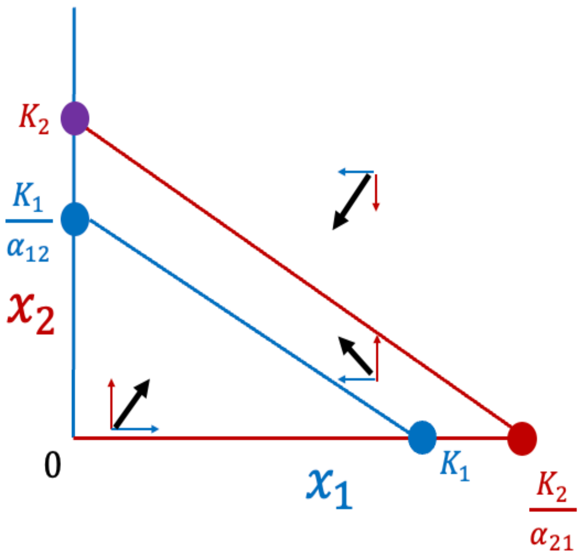
Case 1: Stable coexistence



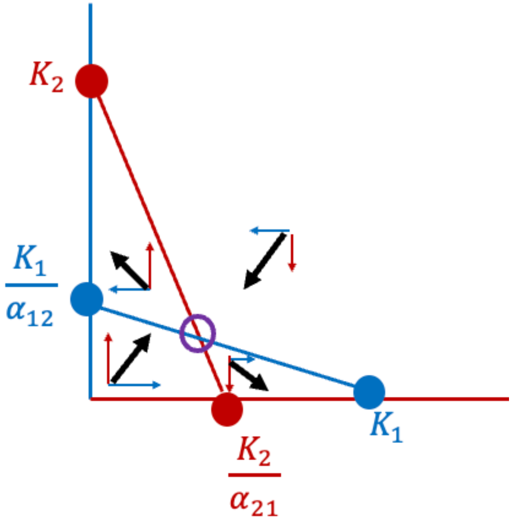
Case 2: Spp. 1 wins



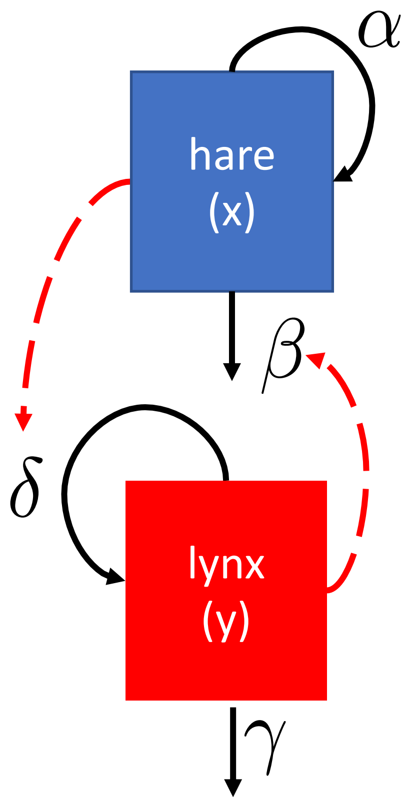
Case 3: Spp. 2 wins



Case 4: Precedence



Note the difference with a predator-prey model!

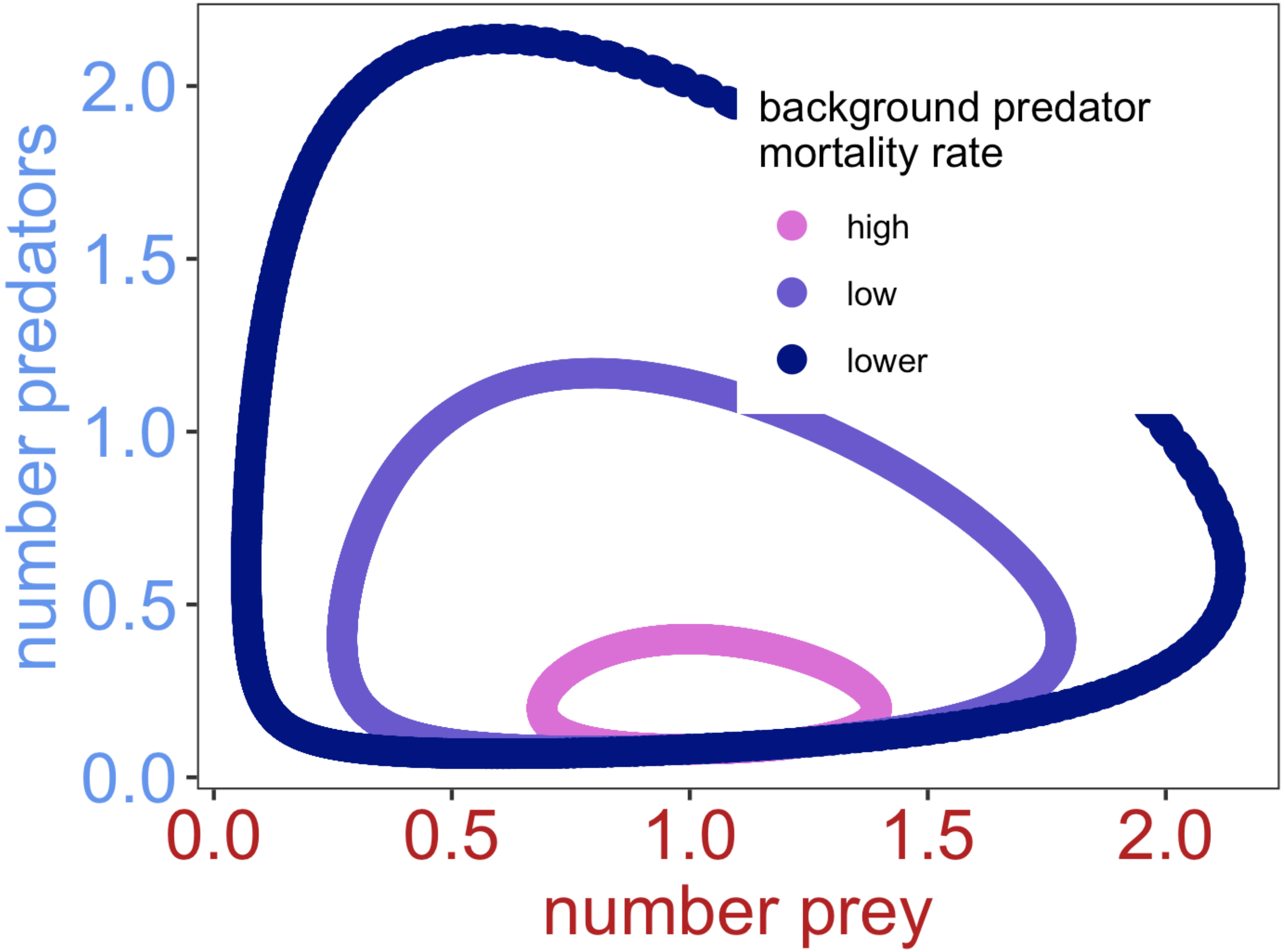


$$\frac{dx}{dt} = \alpha x - \beta xy$$

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

*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:

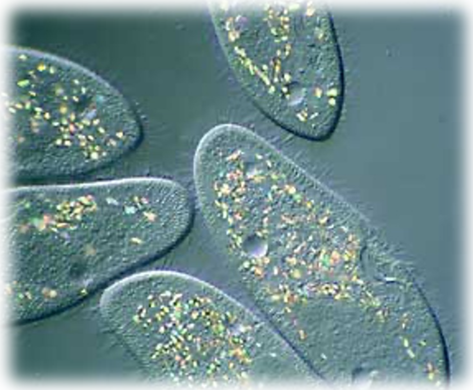
Museum of Vertebrate Zoology

University of California at Berkeley

"Neither can live while the other survives."

- J.K. Rowling, 2003

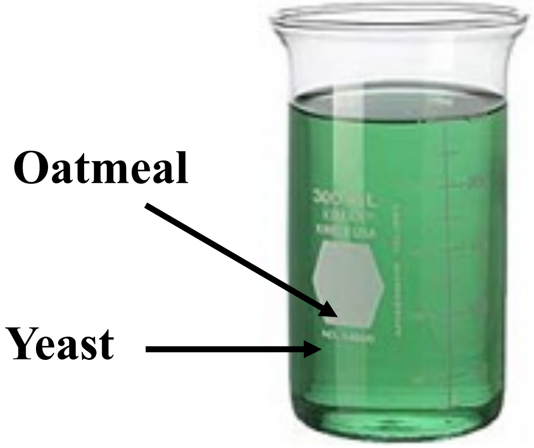
Principle of **competitive exclusion**



Paramecium aurelia

Paramecium caudatum

Paramecium bursaria



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

Gause first grew each species in isolation

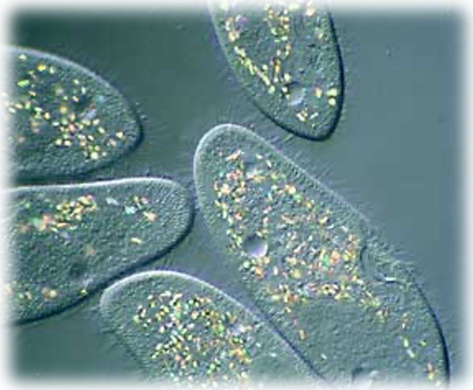
Paramecium aurelia

Paramecium caudatum

Paramecium bursaria

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

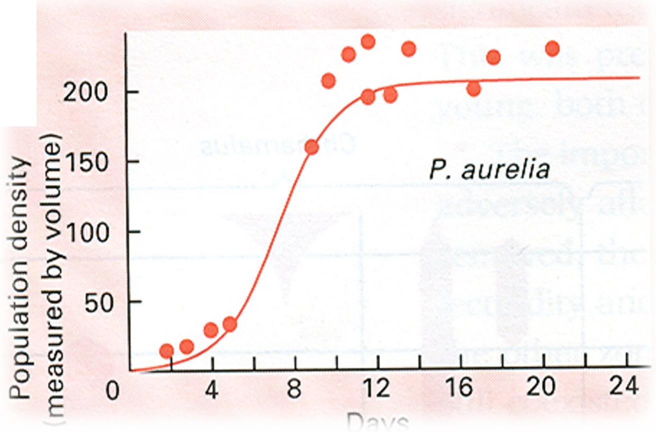
In isolation, each species grew logistically.

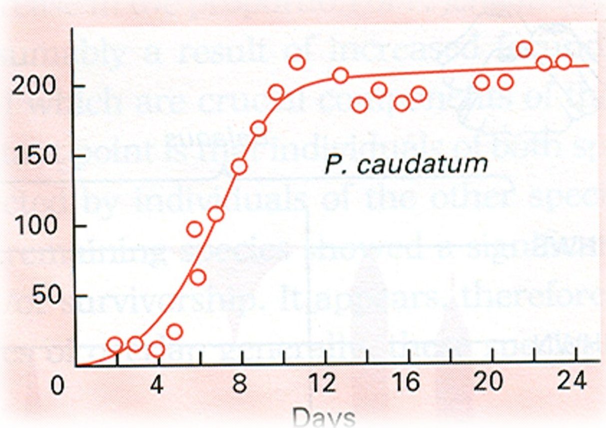


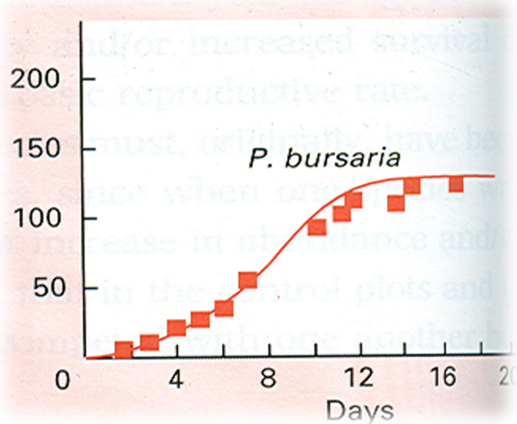
Paramecium aurelia

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.*

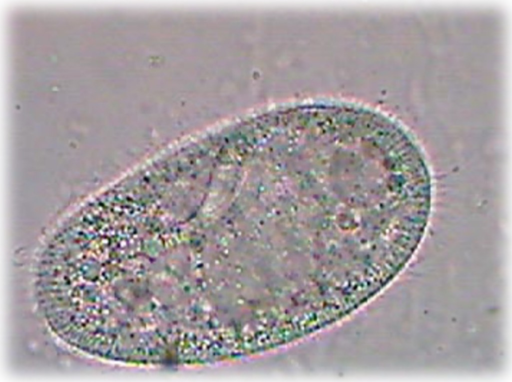
Competitive exclusion was observed:

Coexistence was observed:

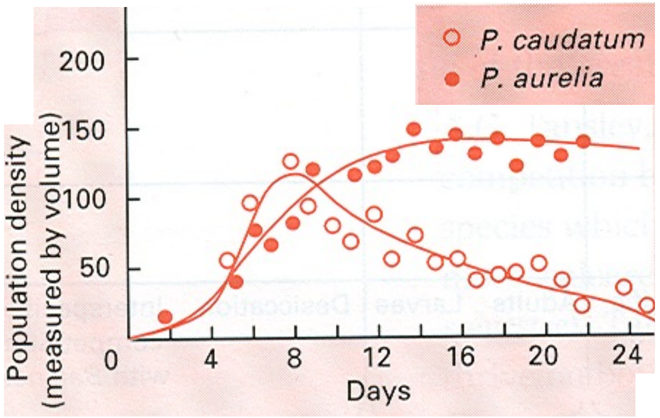
Paramecium aurelia

Paramecium caudatum

Paramecium caudatum

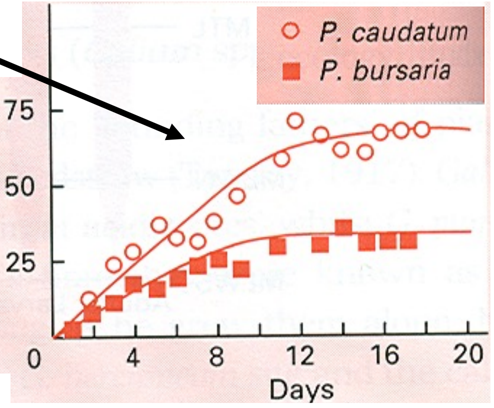


Paramecium bursaria



Species coexisted below each species' respective individual carrying capacity.

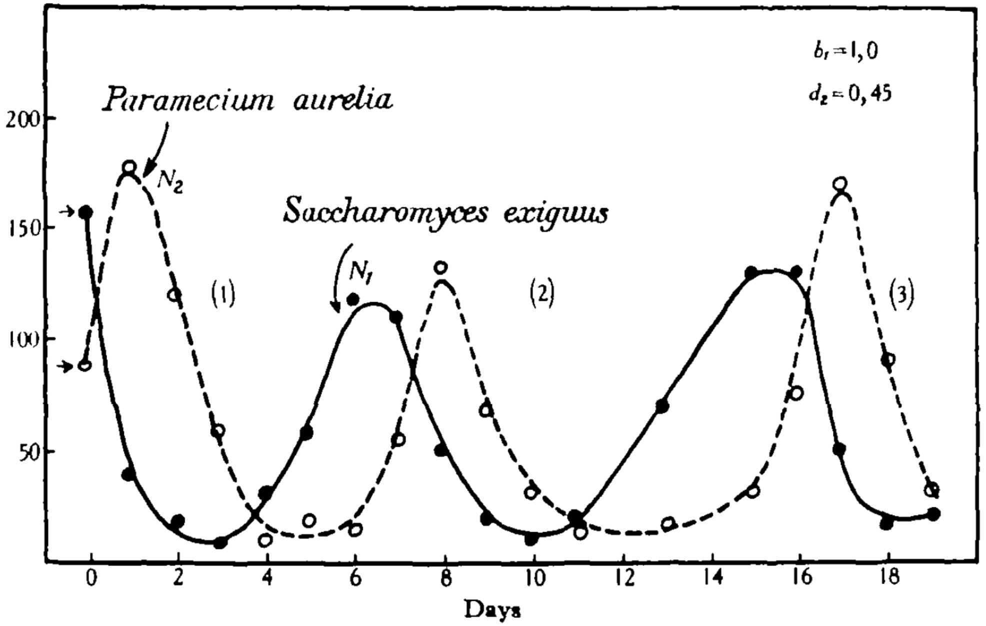
The two coexisting species were largely partitioned in space. *P. bursaria* ate yeast at the bottom and *P. caudatum* consumed bacteria suspended in the medium.

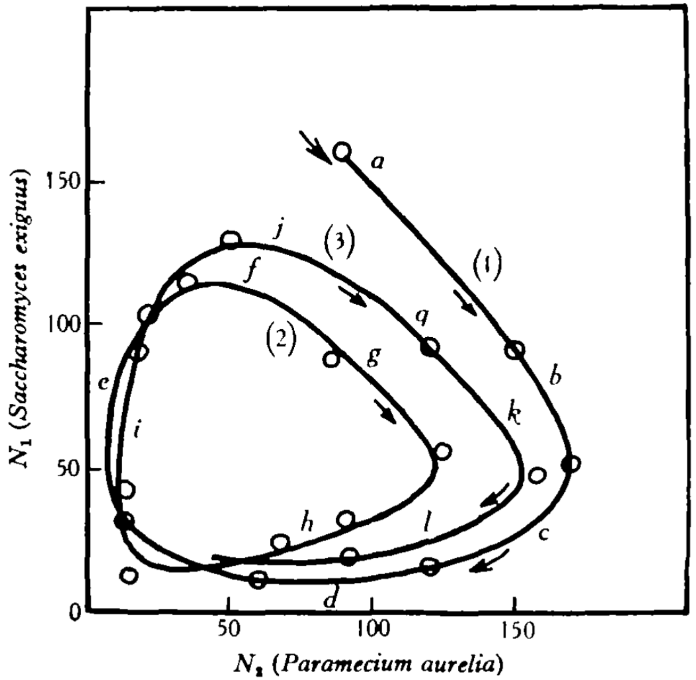


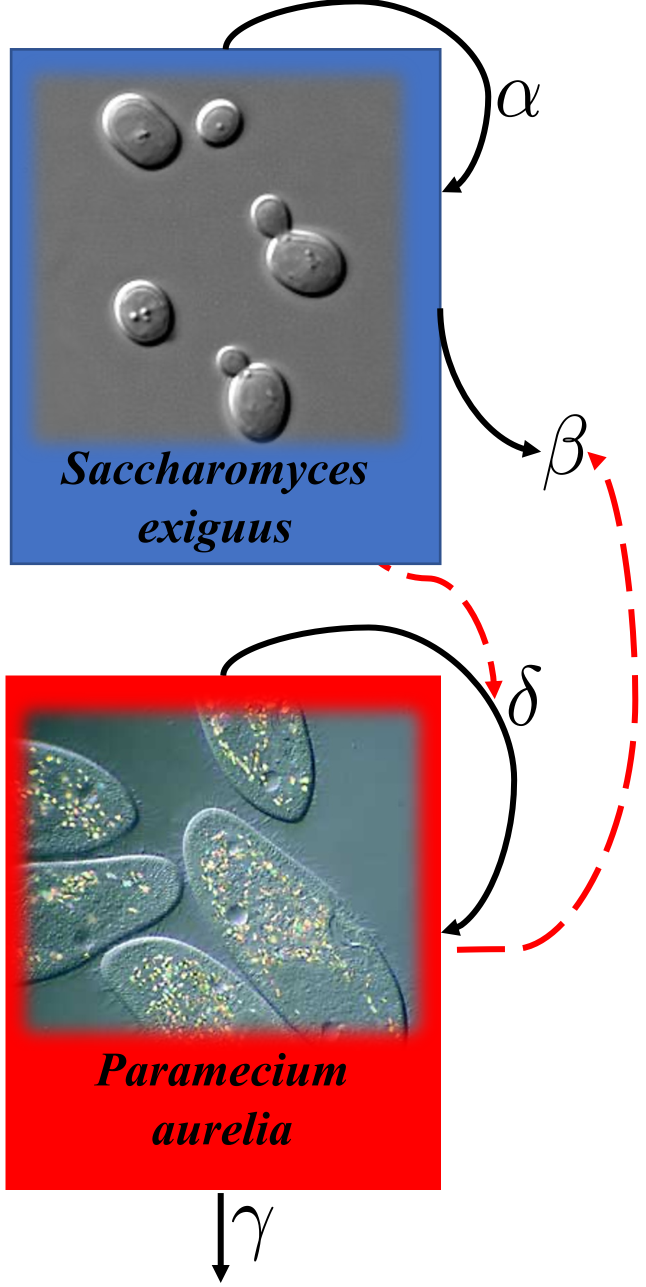
Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

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

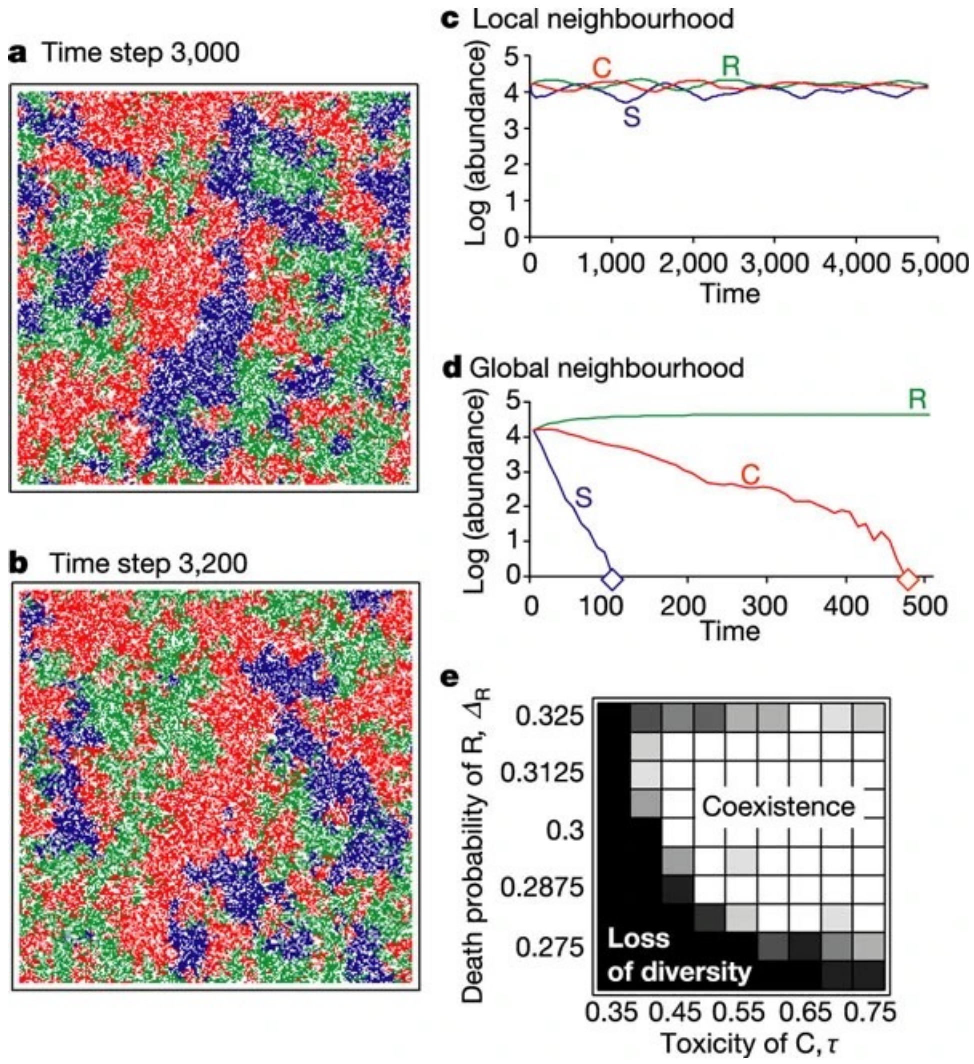






Gause 1935. *Science.*

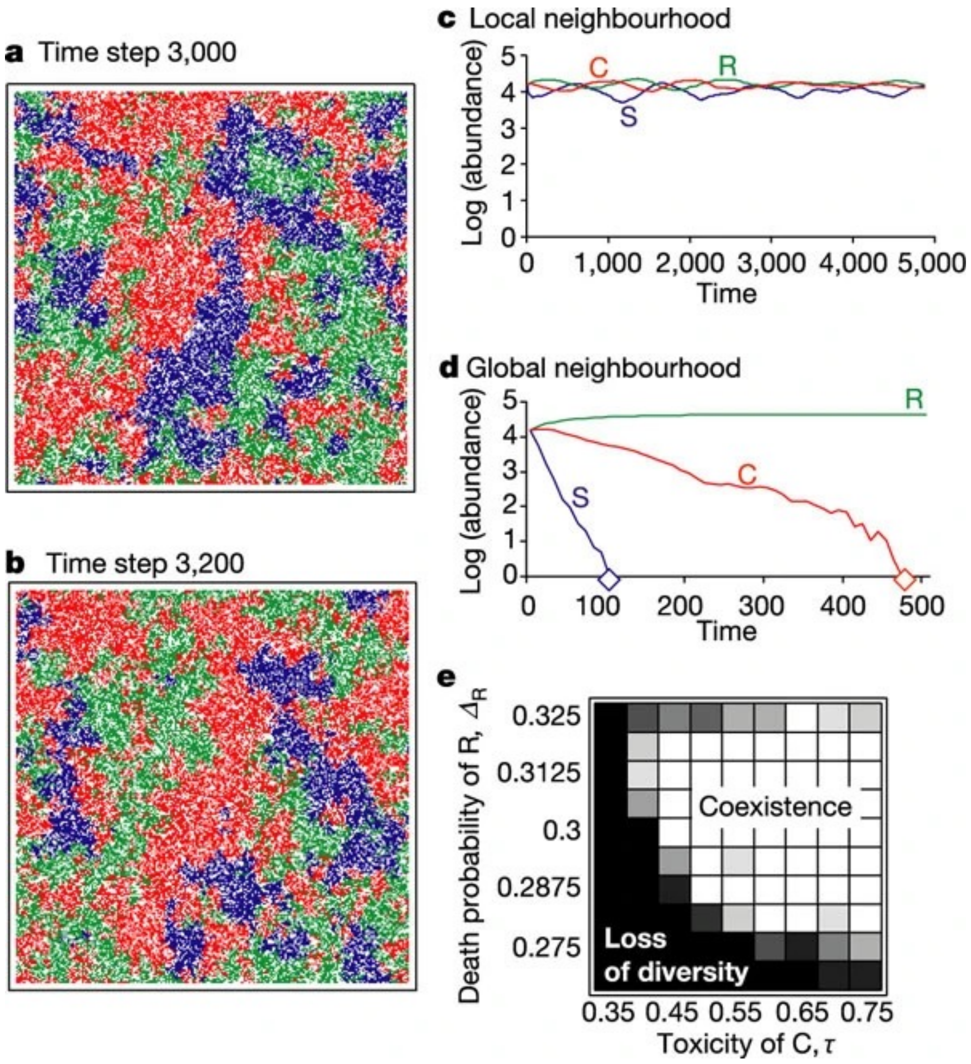
Sometimes **stochasticity** and **space** are all you need to ensure **coexistence** in a competitive environment

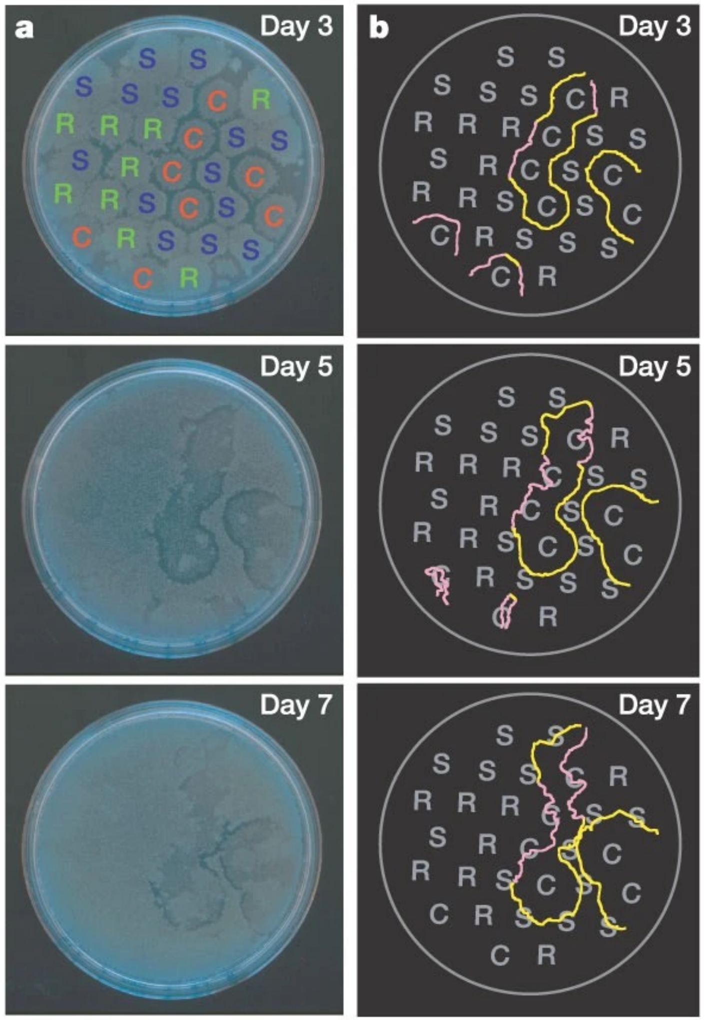


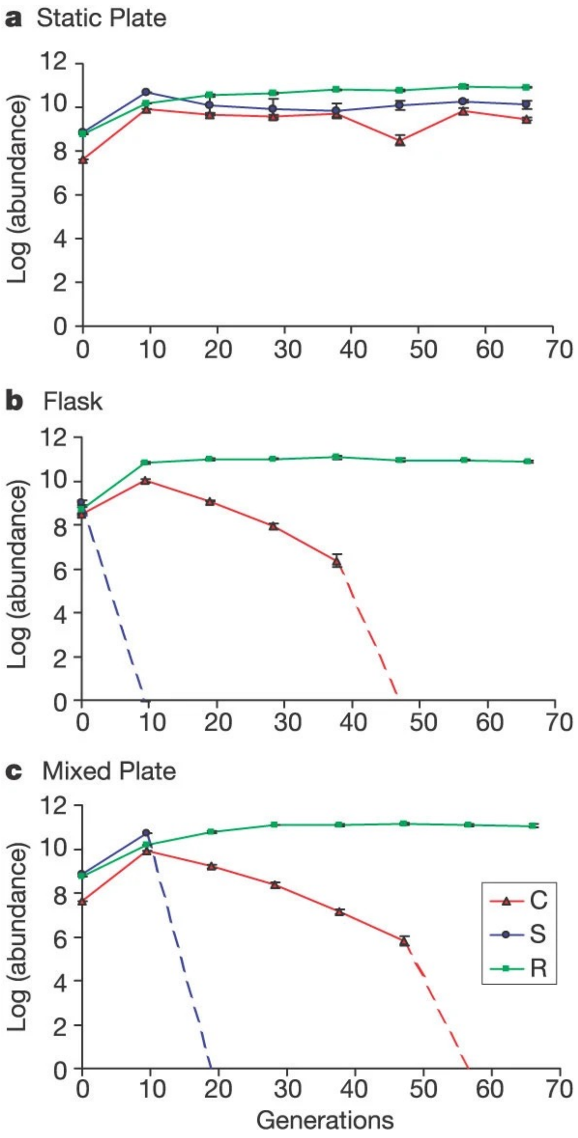
Kerr et al. 2002. *Nature.*

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



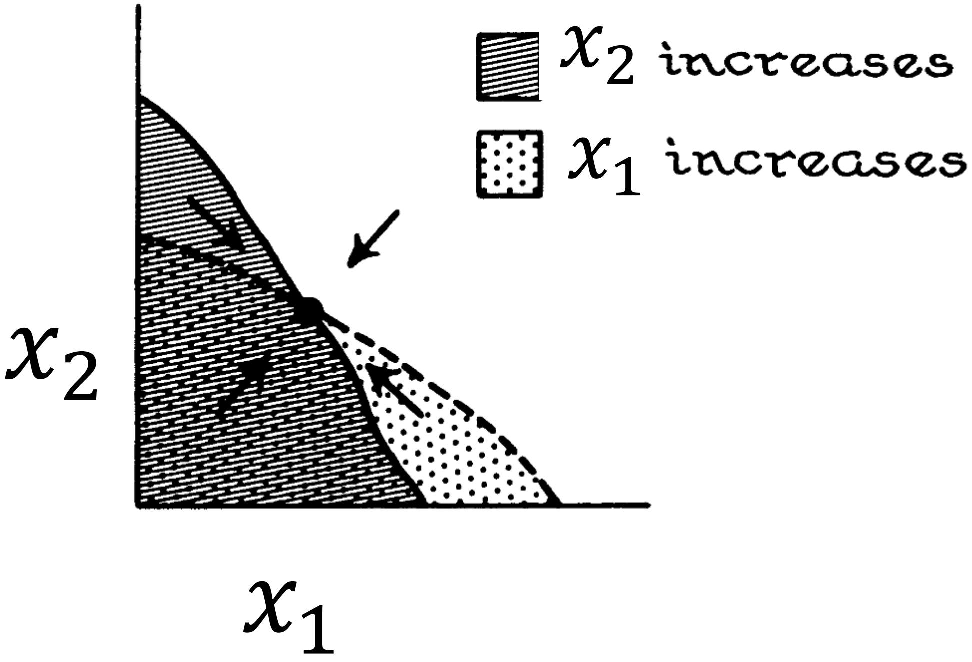




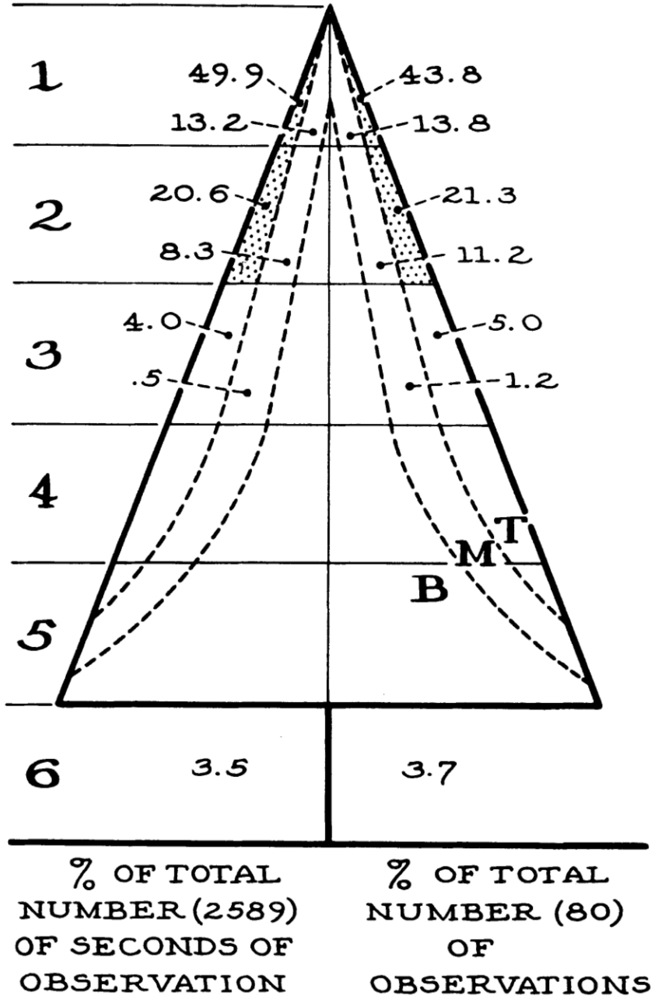
Kerr et al. 2002. *Nature.*

Niche partitioning enables organisms to avoid competitive exclusion

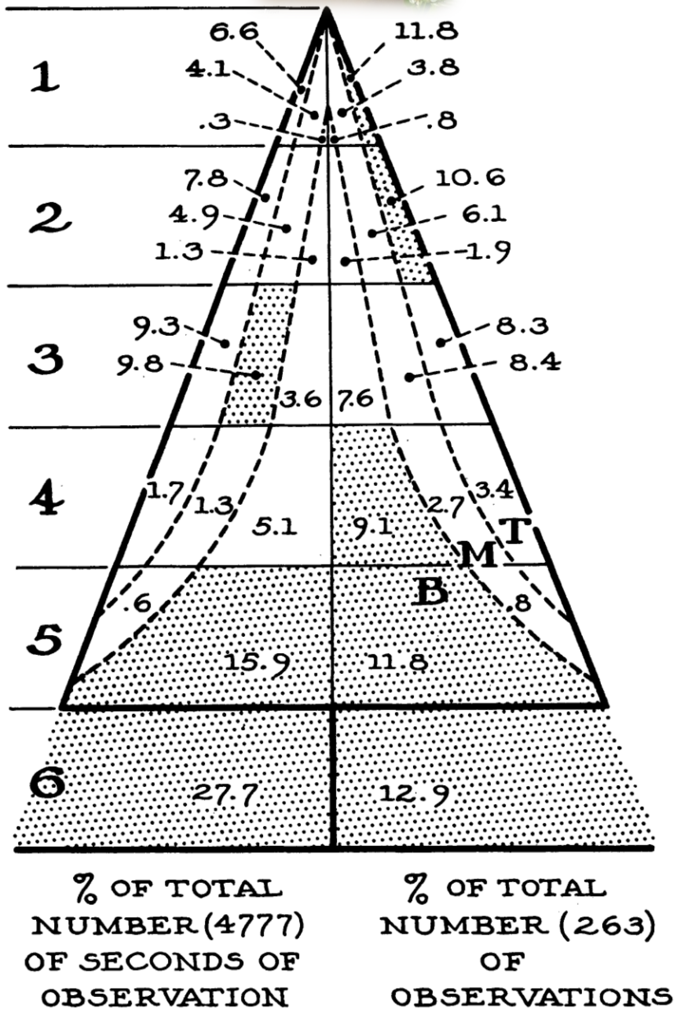
Niche: a match of a species to a specific environmental condition



Cape May Warbler



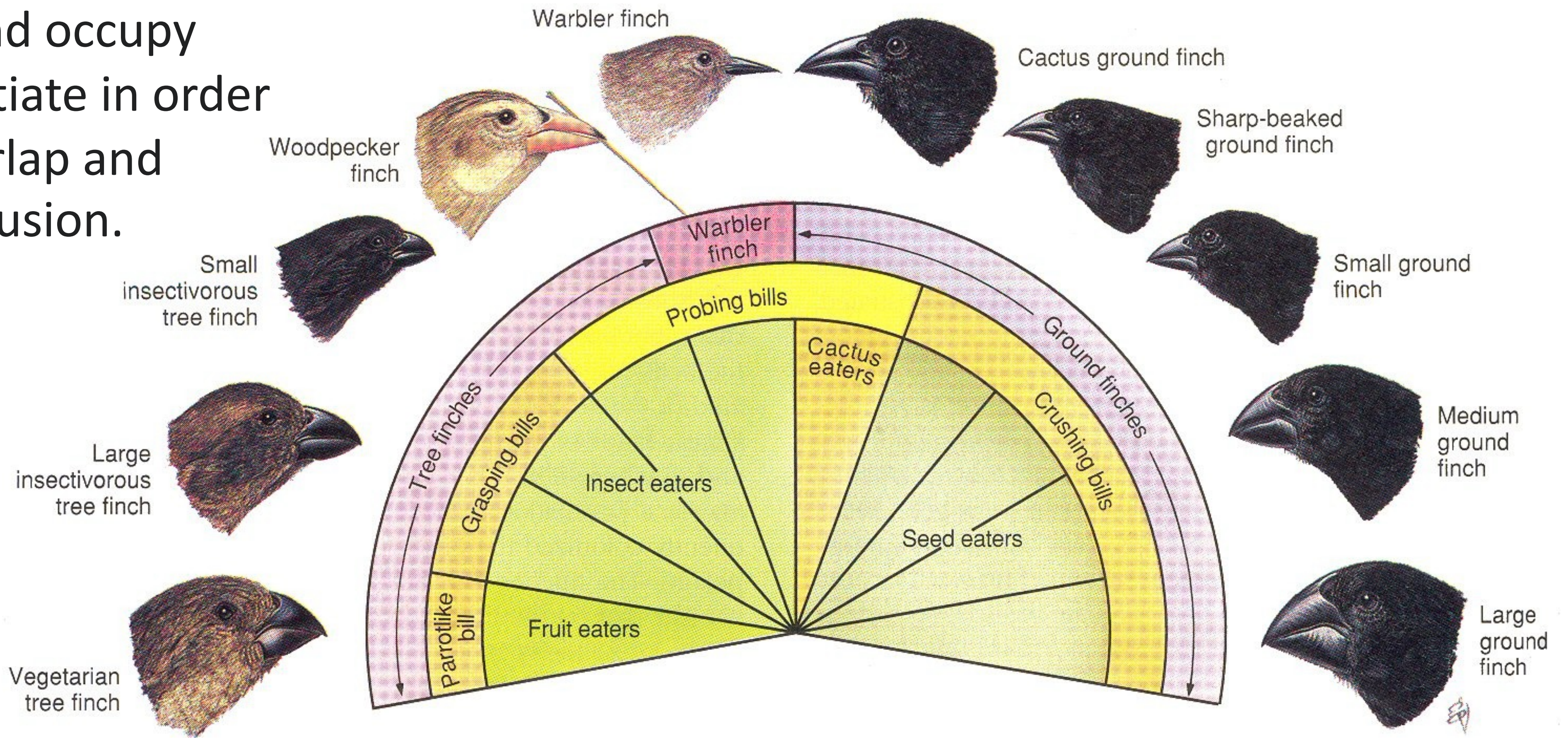
Myrtle Warbler



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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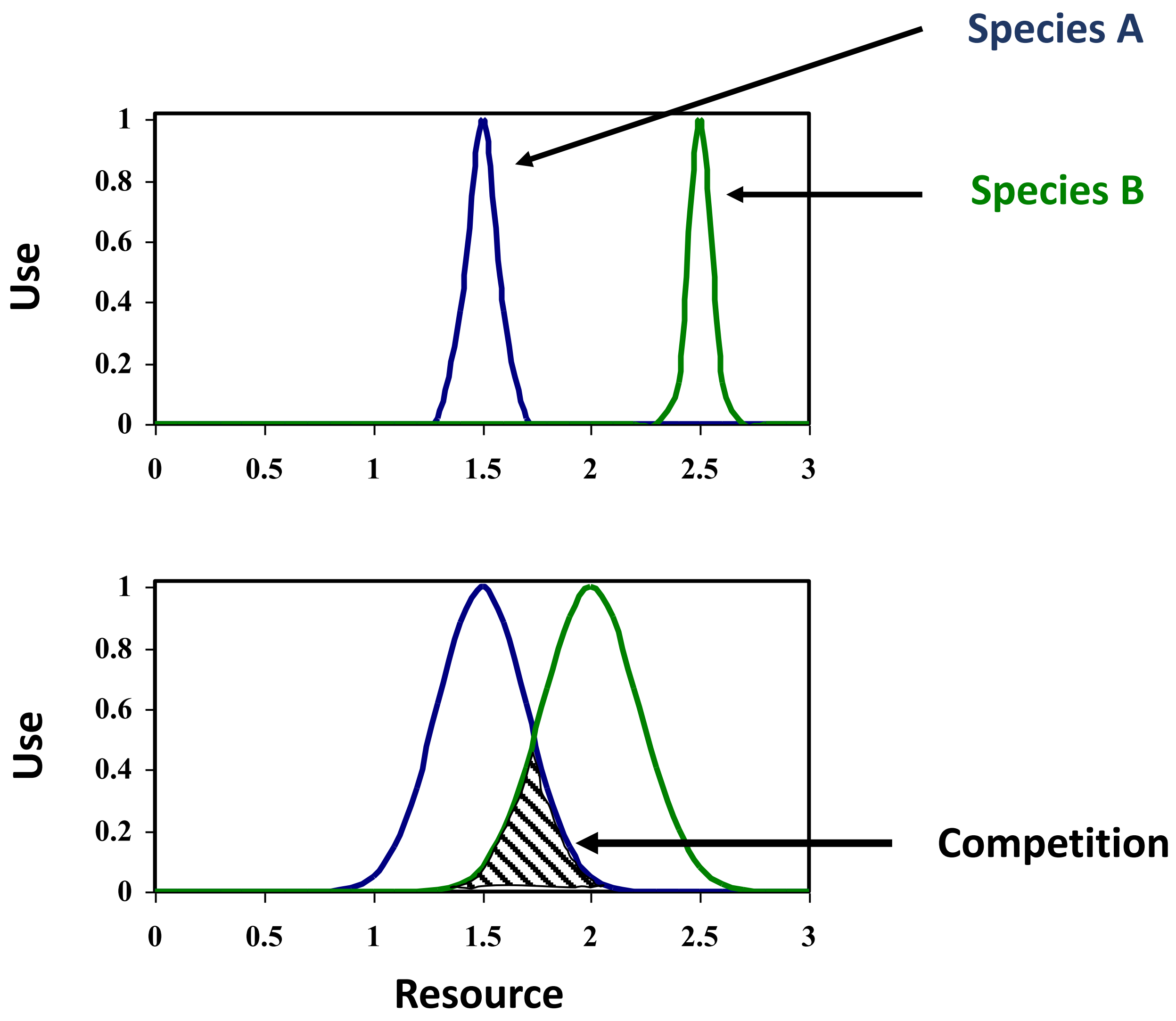
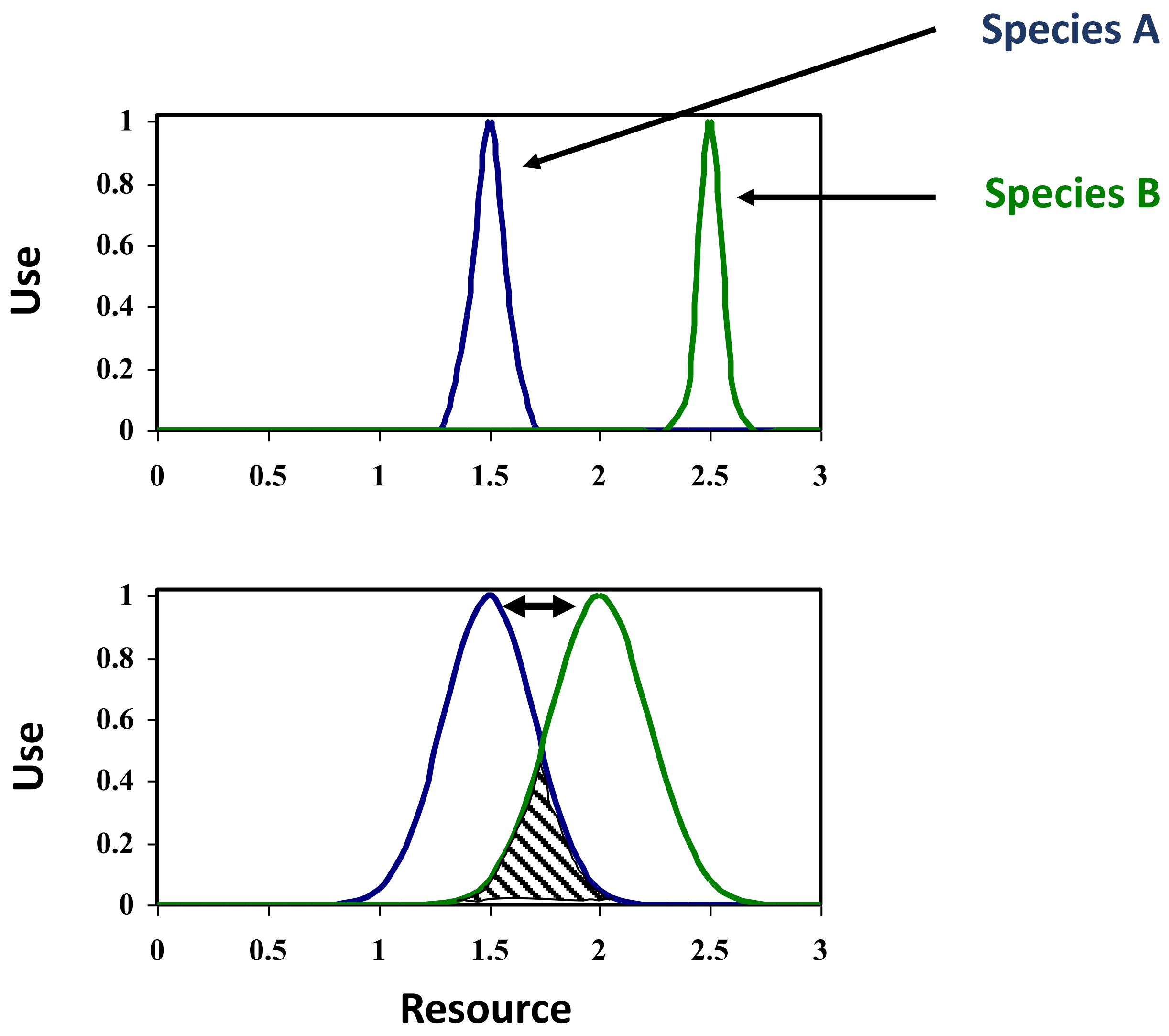


When niches overlap, competition results

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.

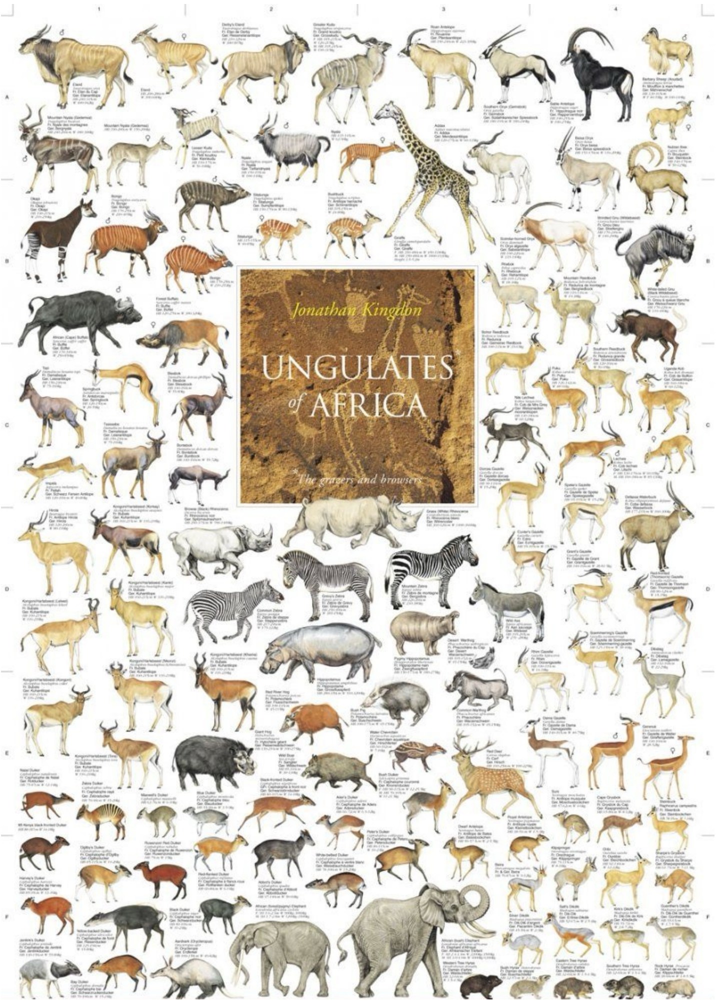
Grant & Grant 2006. *Science.*

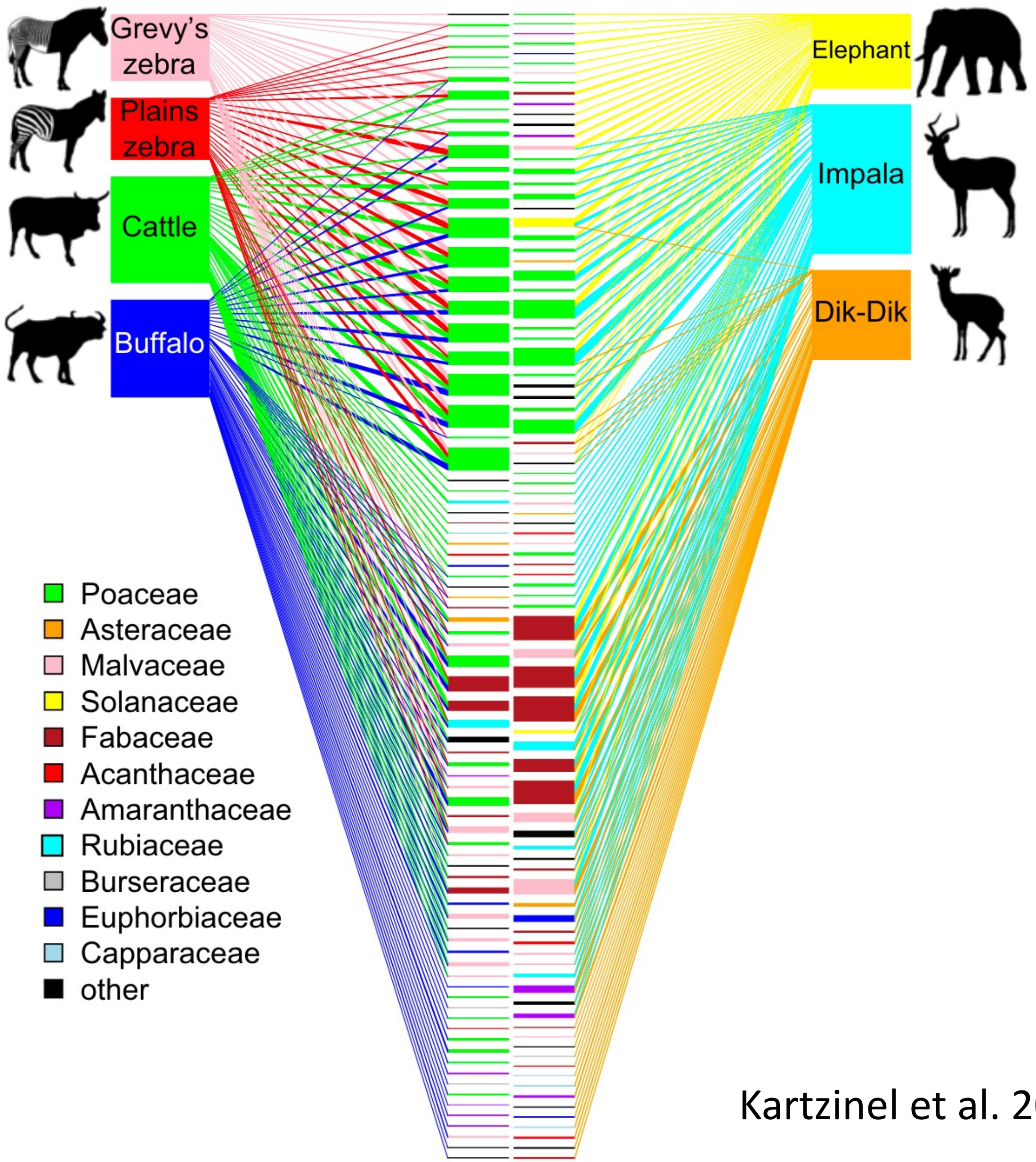


Character displacement forces niches apart.

Niche partitioning enables organisms to avoid competitive exclusion

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

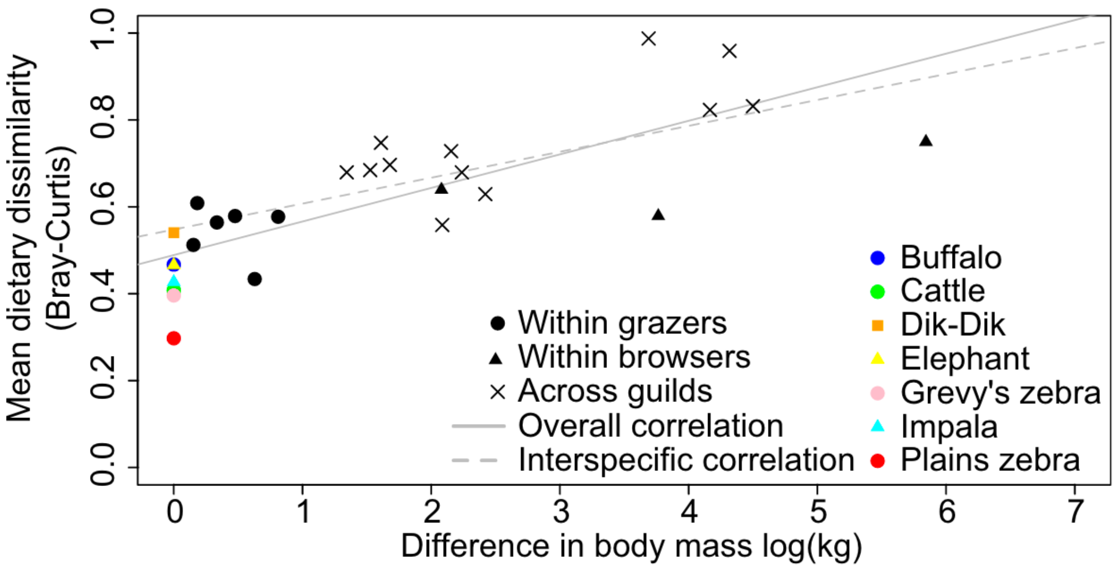


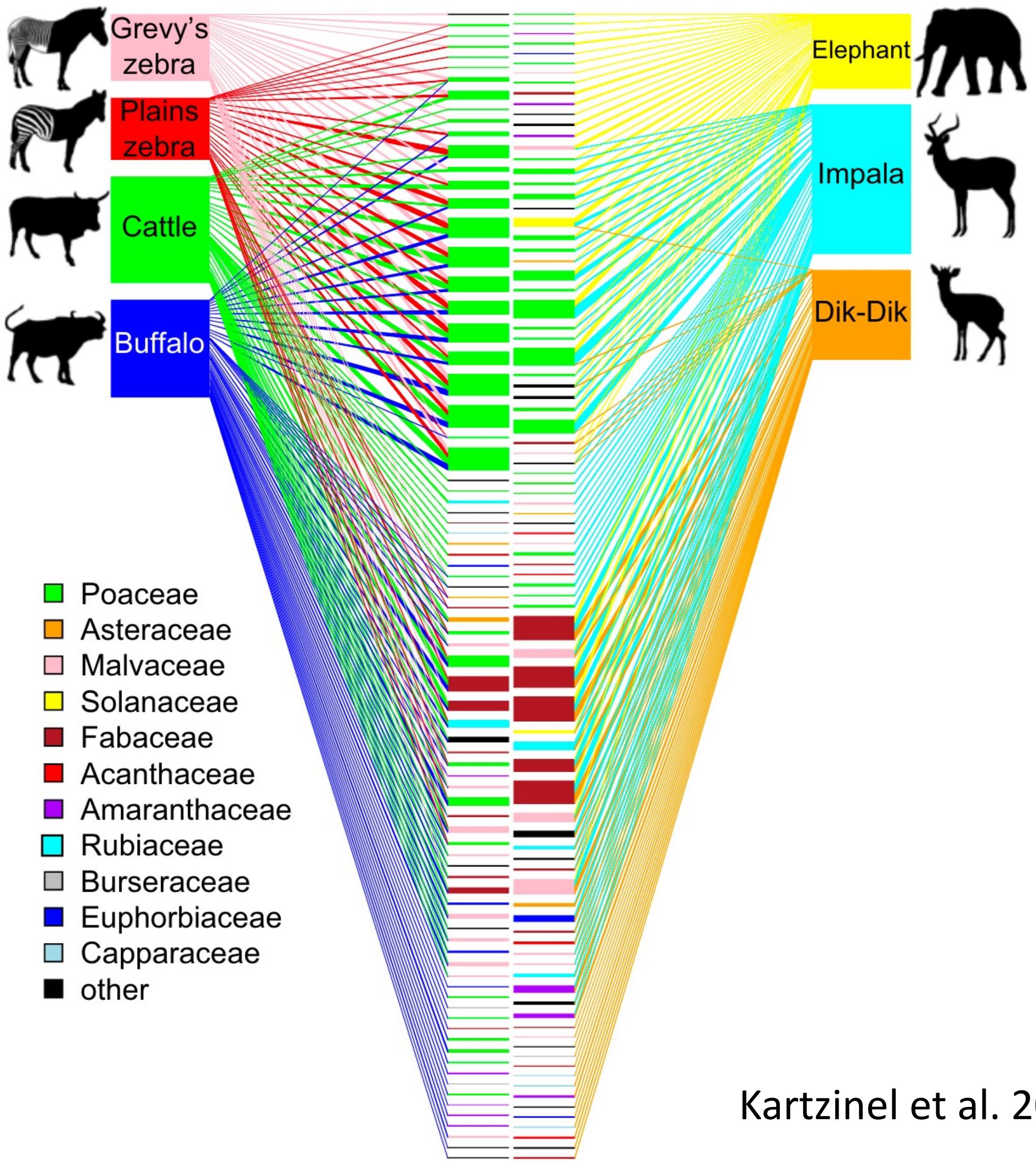


Kartzinel et al. 2015. *PNAS.*

Niche partitioning enables organisms to avoid competitive exclusion

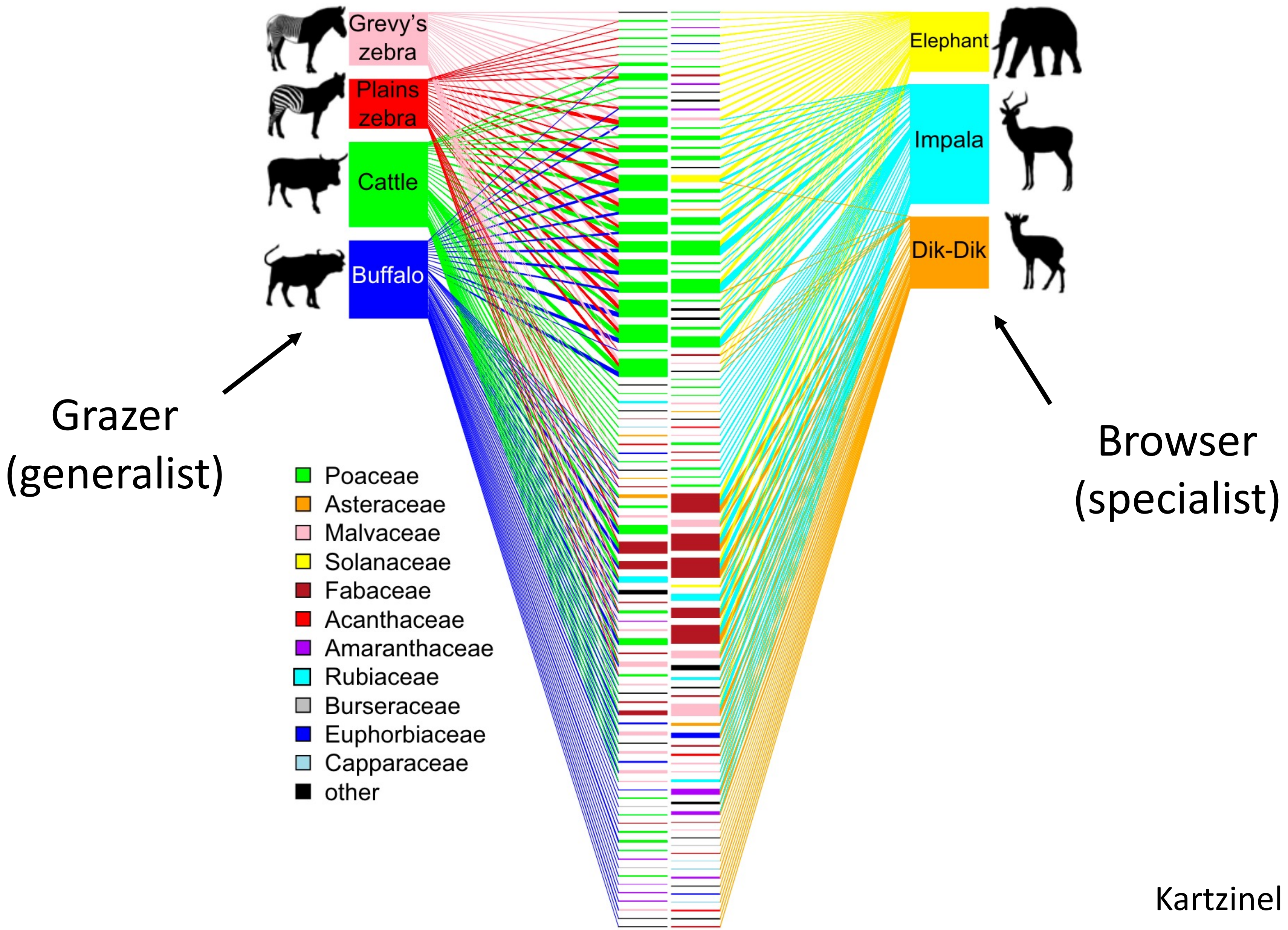
Dietary overlap is higher in similar-sized mammals





Kartzinel et al. 2015. *PNAS.*

Consumer resource partitioning in the African savanna



Kartzinel et al. 2015. *PNAS.*

Que. 3 "Complete competitors cannot coexist" unless:

0

a. there is a precedence effect

b. space, low dispersal, and stochasticity are important

c. there is character displacement

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