



Which flavor of ice cream best represents you?

0



Fundamentals of Ecology

Week 7, Ecology Lecture 4

Cara Brook

February 18, 2025

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February 18, 2025

Office hours: On ZOOM

Friday, Feb 21, 2025

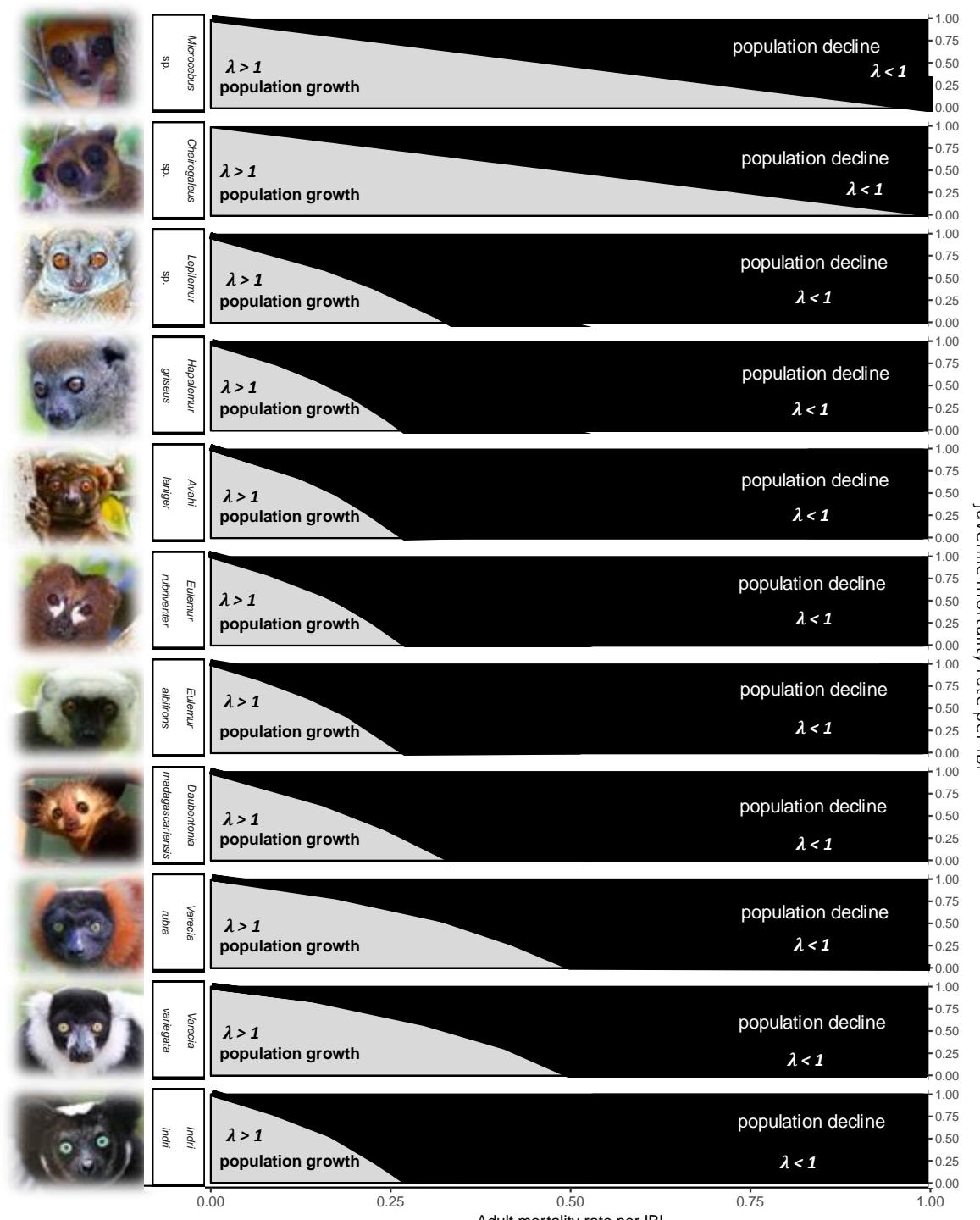
4-5pm

I will email out a link!

Learning objectives from Lecture 3

You should be able to:

- Know why/when a structured population model is needed
- From lab: know what elements of the transition matrix correspond to survival and fecundity for N^{th} age class and be able to identify the equation predicting the size of an age class in the next time interval
- Sketch graph of a demographic transition and corresponding population birth and death rates at different stages
- Predict the trajectory of a population (growing, shrinking, constant) by looking at its age pyramid
- Understand what a metapopulation is and why it matters
- Recognize and be able to apply Levins' metapopulation model equation
- Name and describe the 'metapopulation rescue effect'

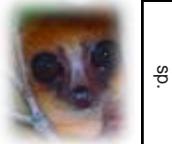


We plotted
zero-growth lines to
evaluate lemur
population trajectories
across different
mortality rates.

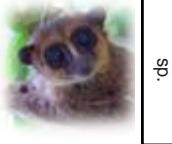
Smaller lemurs with
faster life histories are
resilient to **mortality**.

Bigger lemurs with **slower life histories** are particularly **vulnerable**.

We built a regional **metapopulation model** to simulate population dynamics into the future for a subset of species.



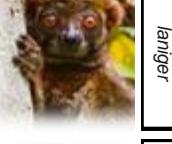
Microcebus
sp.



Cheirogaleus
sp.



Hapalemur
occidentalis



Avahi
laniger



Eulemur
albifrons



Varécia
variegata



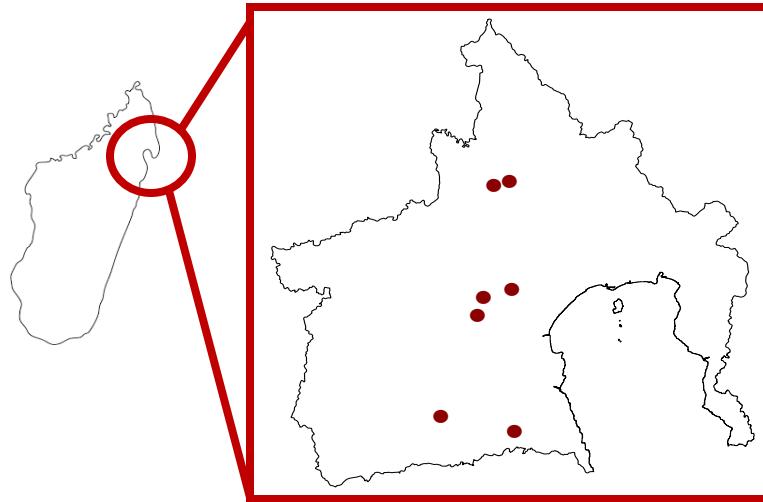
Indri
indri

We built a regional **metapopulation model** to simulate population dynamics into the future for a subset of species.



Assumptions:

- Starting population of 200 lemurs per site

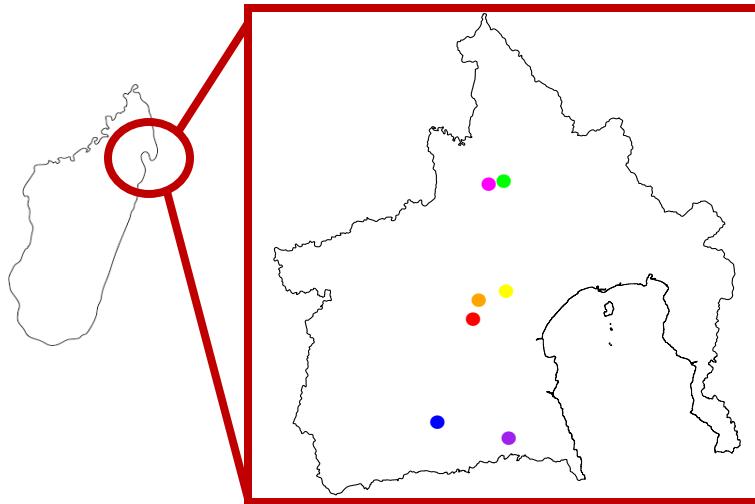


We built a regional **metapopulation model** to simulate population dynamics into the future for a subset of species.



Assumptions:

- Starting population of 200 lemurs per site
- Site-specific mortality rates derived from field studies

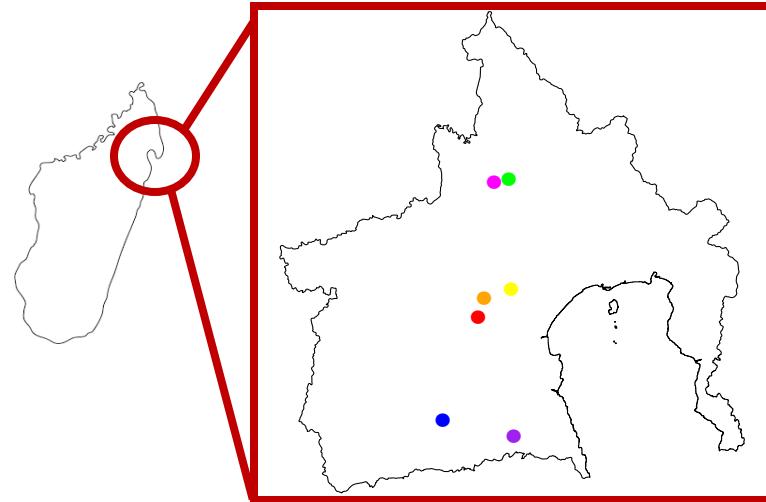


We built a regional **metapopulation model** to simulate population dynamics into the future for a subset of species.



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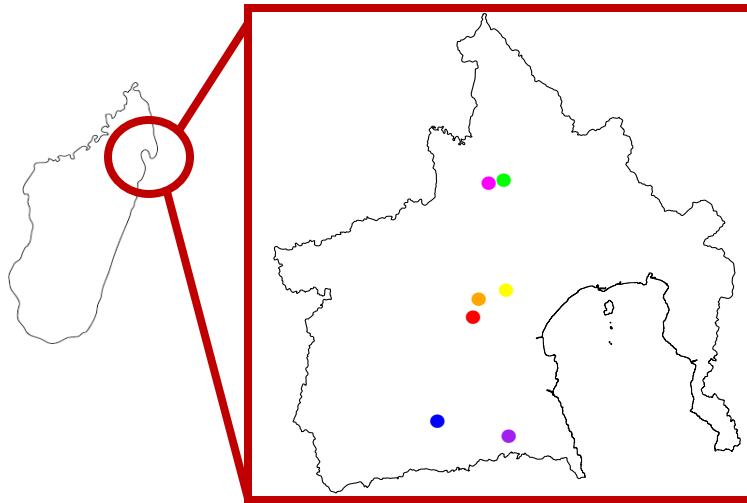


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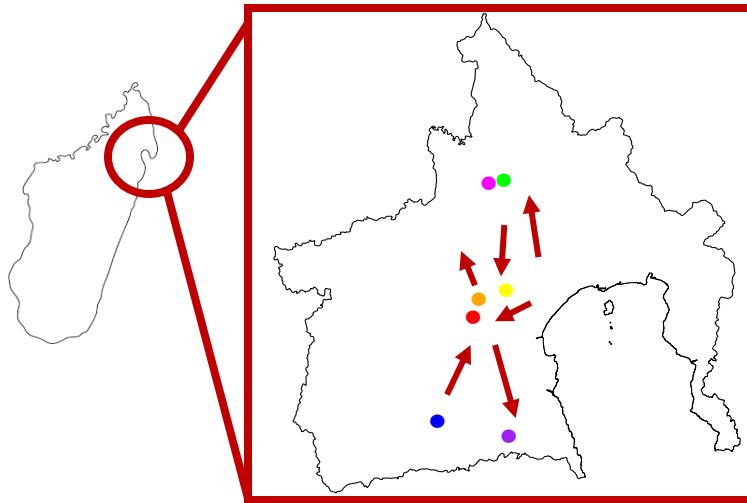


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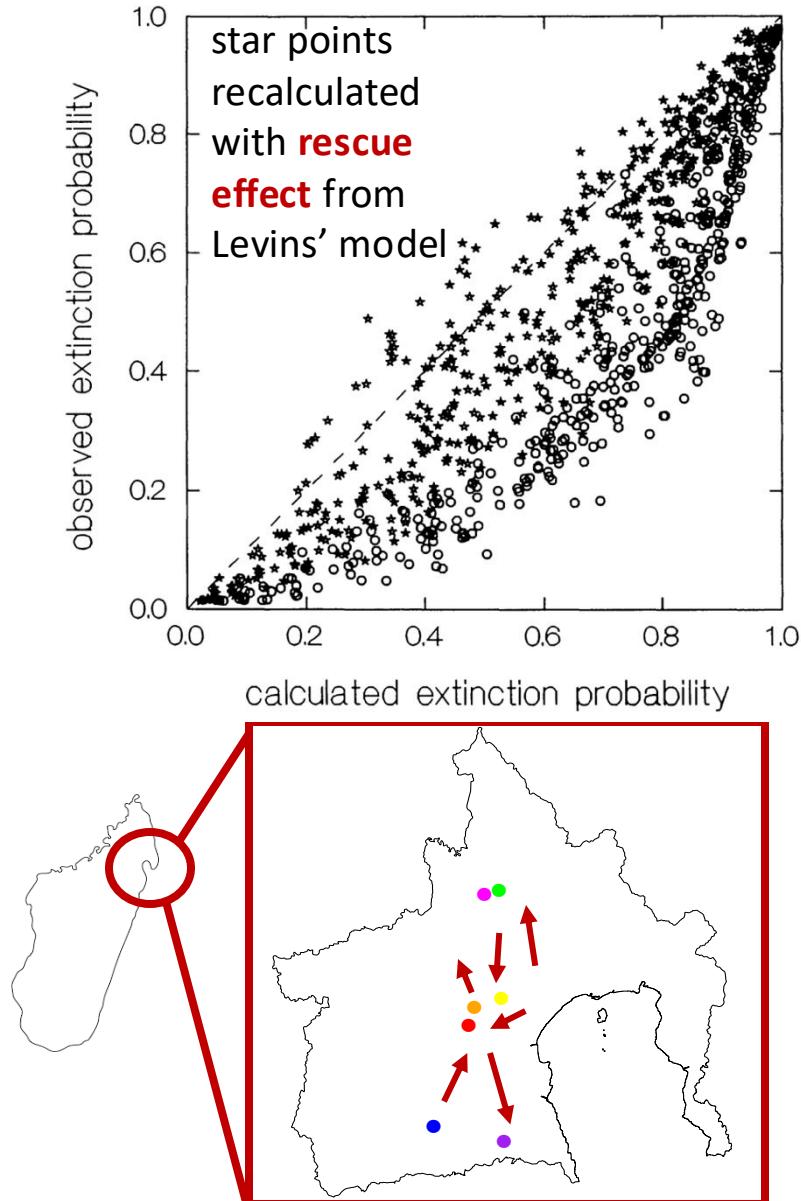
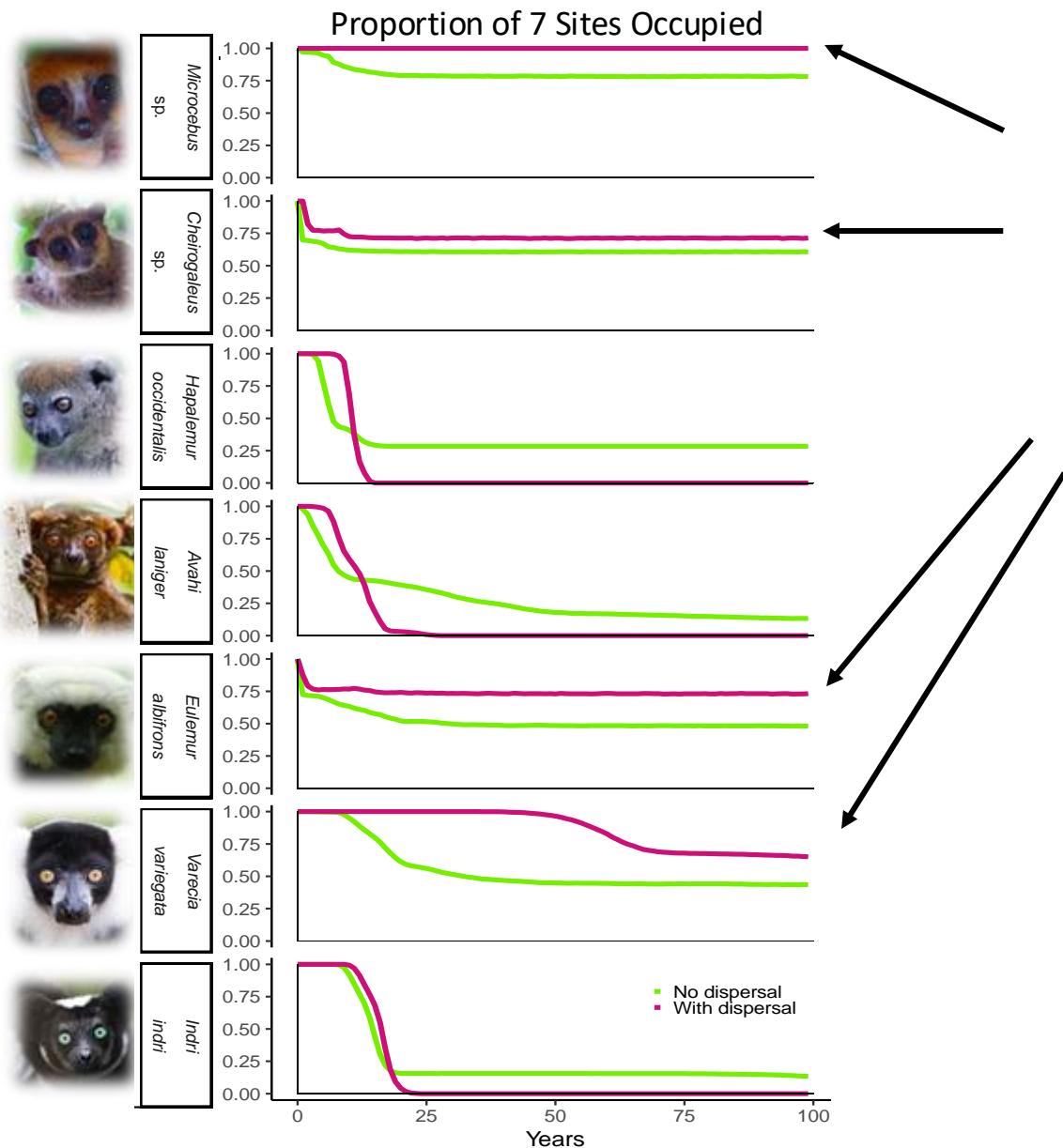


Assumptions:

- Starting population of 200 lemurs per site
- Site-specific mortality rates derived from field studies
- Density dependent effects on fecundity
- Compared **no dispersal scenarios** vs. scenarios allowing for **stochastic dispersal** mediated by geographic distance

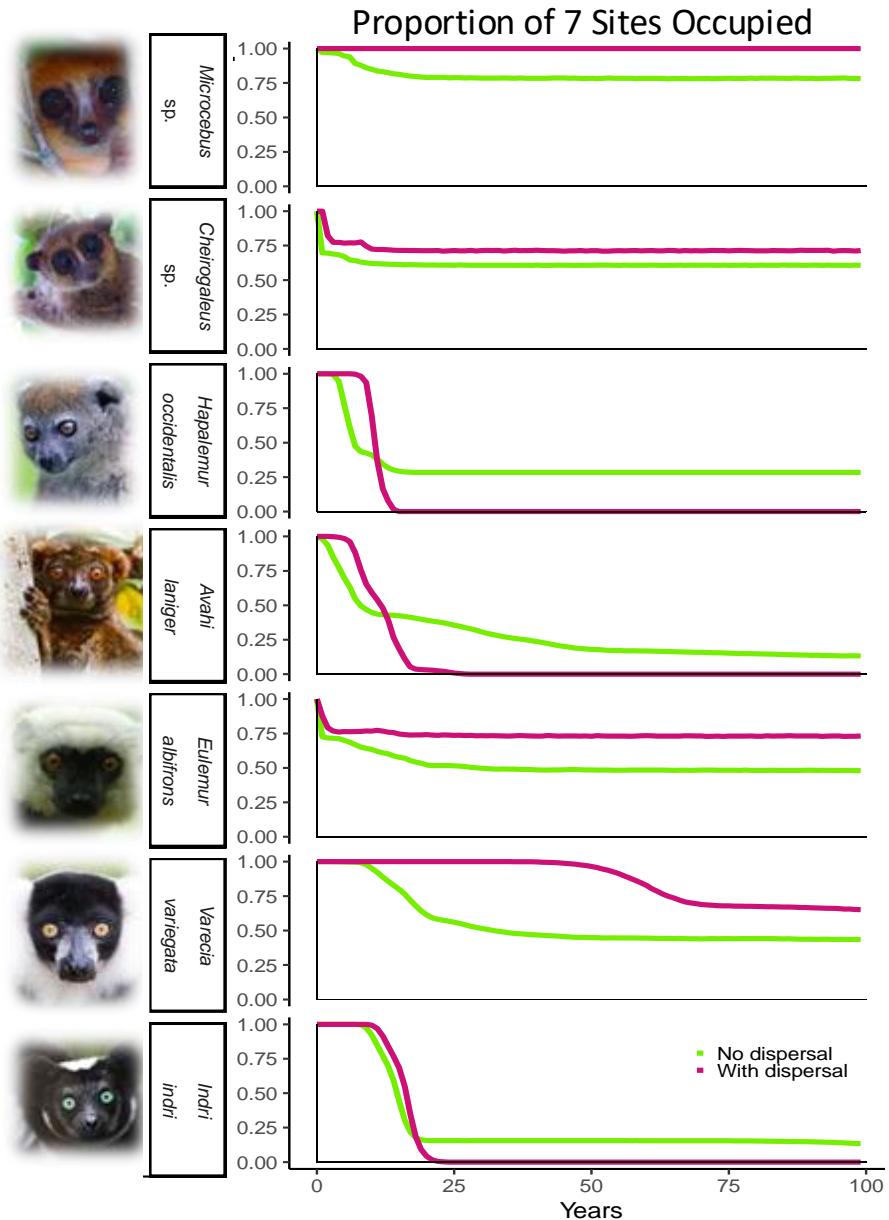


Dispersal sometimes promoted **rescue effects** as seen in Hanksi's work.



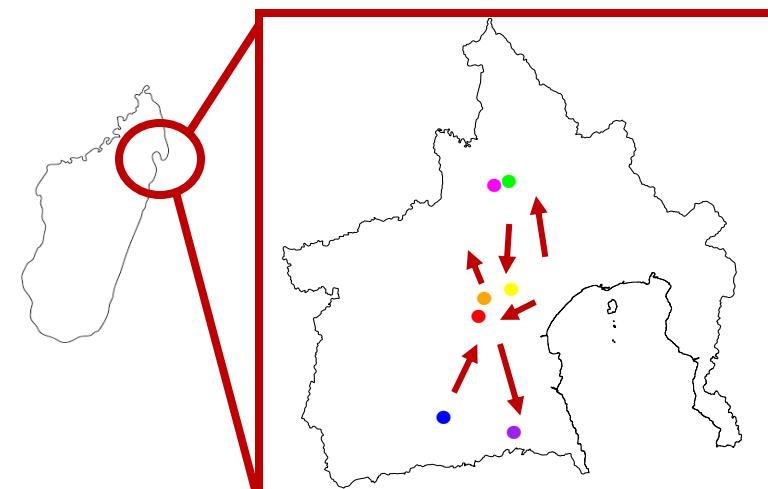
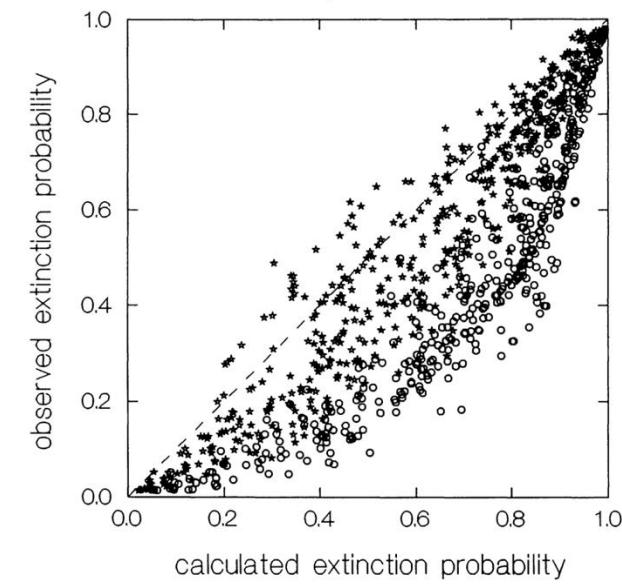
Brook et al. 2018. *Conservation Biology*.

Dispersal can drive **regional extirpation** if the majority of local sites function as **population sinks**.



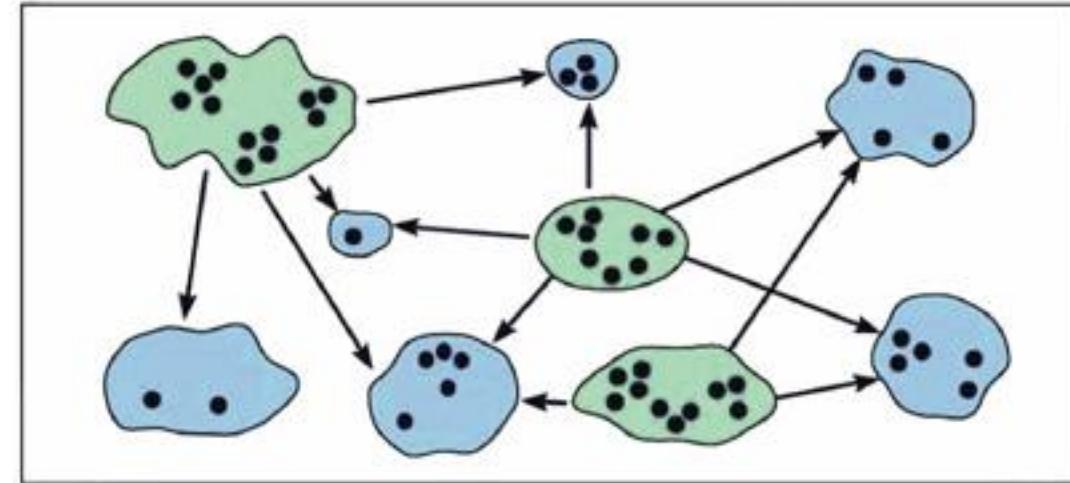
In contrast to the **rescue effect** observed in Hanski!

Metapopulation dynamics can drive regional declines in other cases!



Source-sink theory describes how variation in habitat may affect population dynamics.

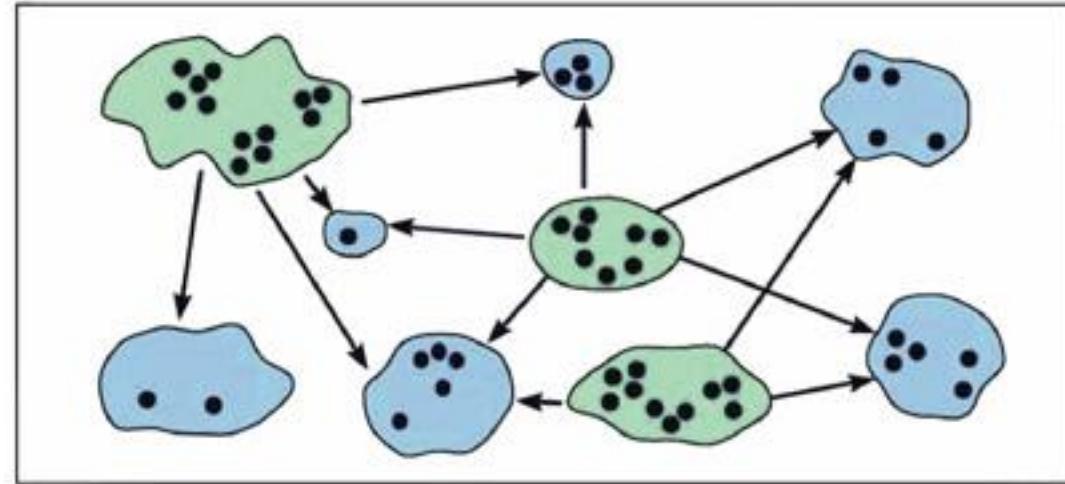
- Dispersal can drive **extinction** if the majority of sites function as **population sinks**.



- Individual within a local population
- Dispersal event
- Source population in a suitable habitat
- Sink population in a low-quality habitat

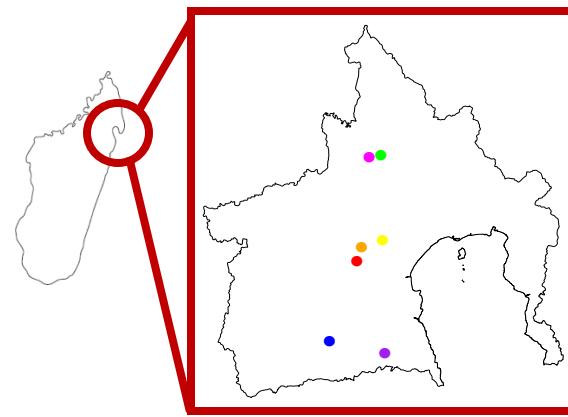
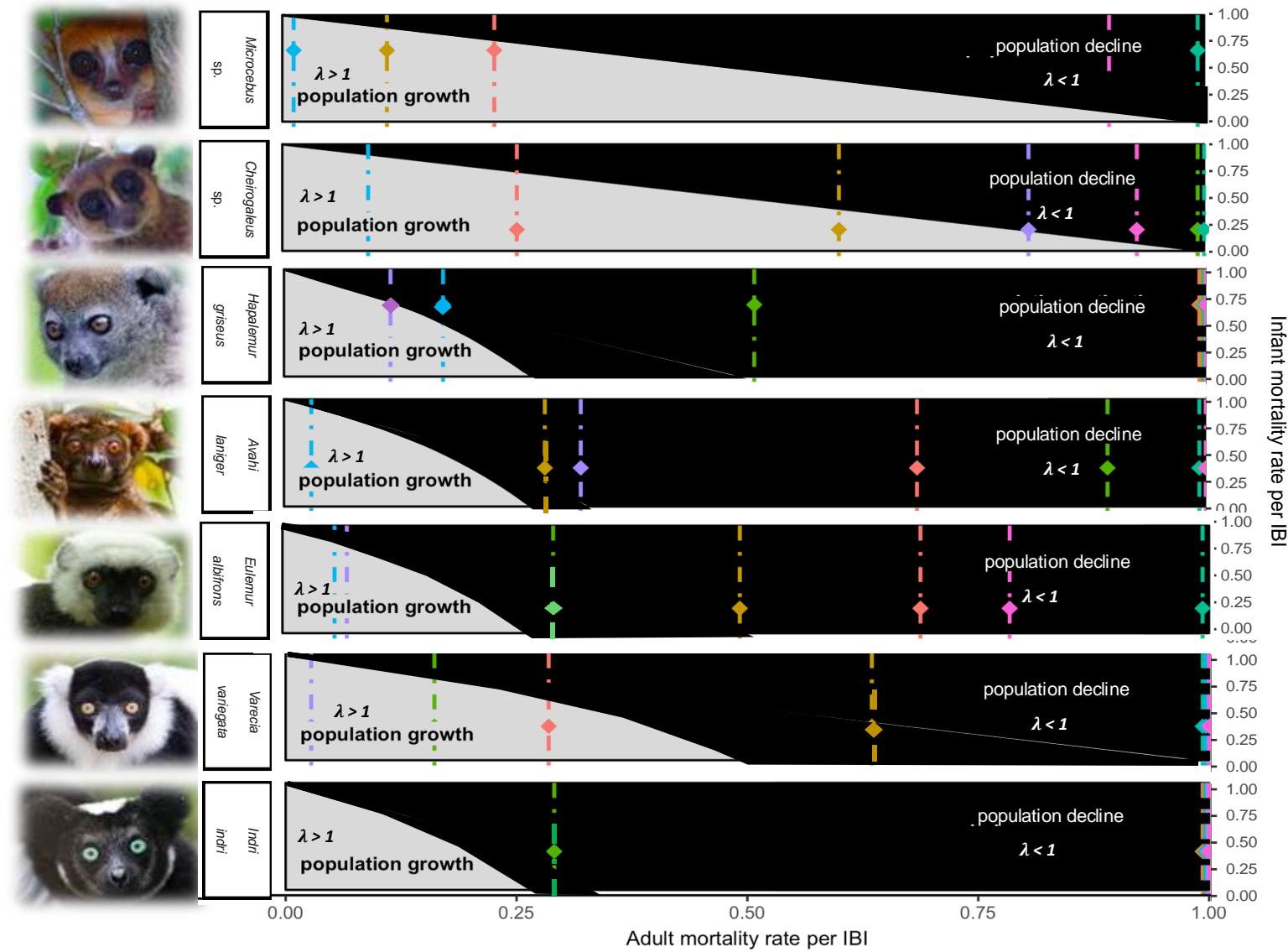
Source-sink theory describes how variation in habitat may affect population dynamics.

- Dispersal can drive **extinction** if the majority of sites function as **population sinks**.
- An **ecological trap** is an organism's preference for poor quality habitat
 - Ex: polarized light pollution & insect ovipositing



- Individual within a local population
 - Dispersal event
- Source population in a suitable habitat
○ Sink population in a low-quality habitat

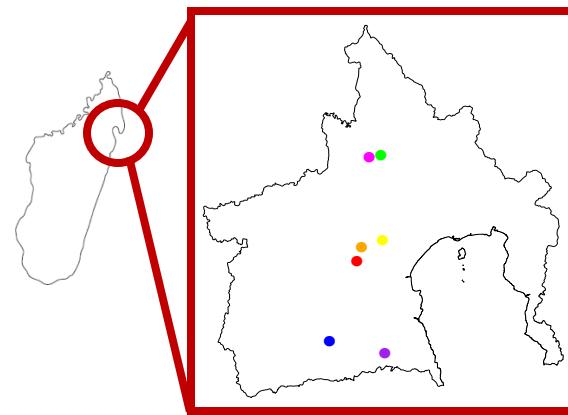
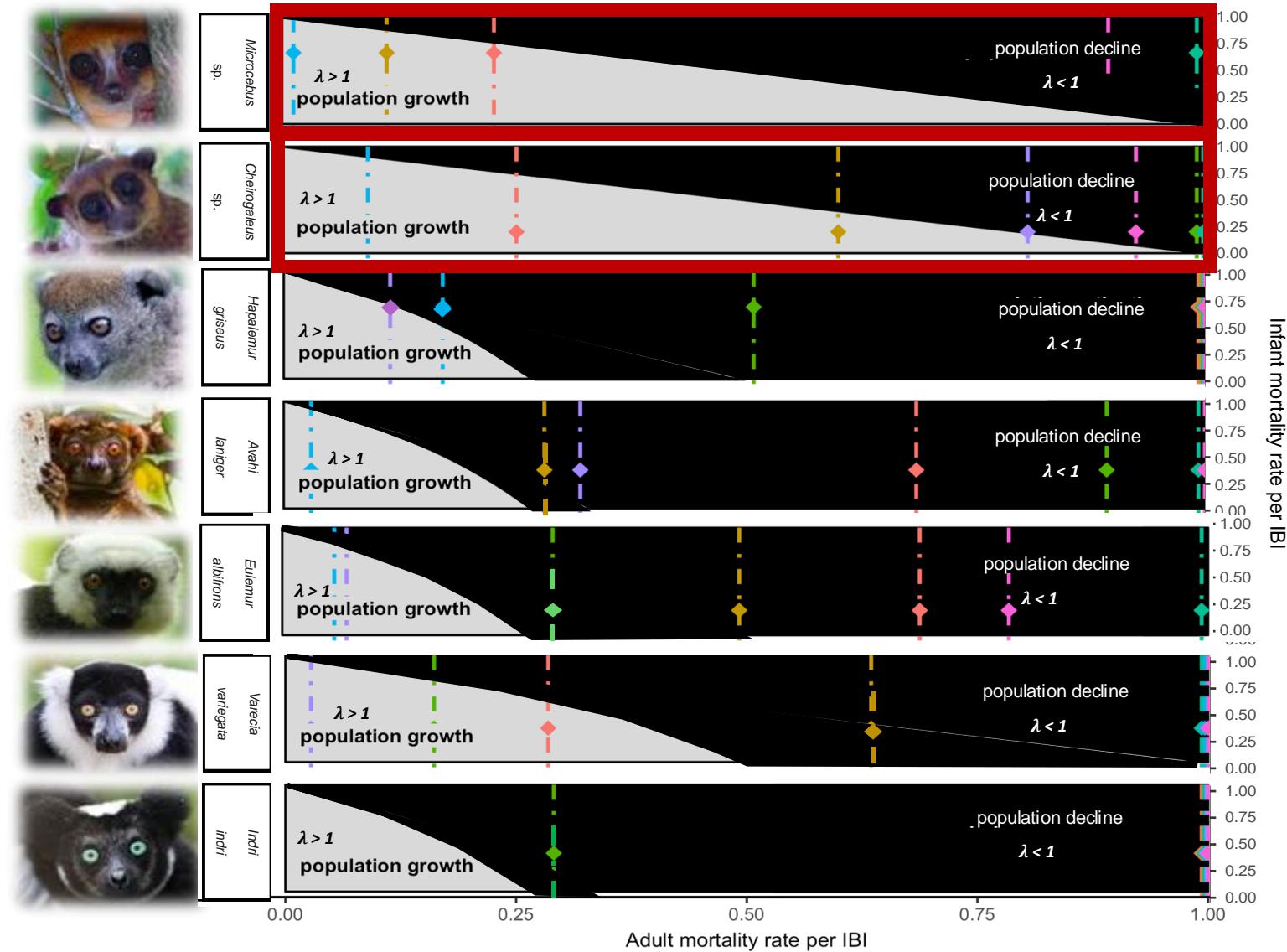
We also evaluated **excess mortality due to human hunting** to assess **harvest sustainability**.



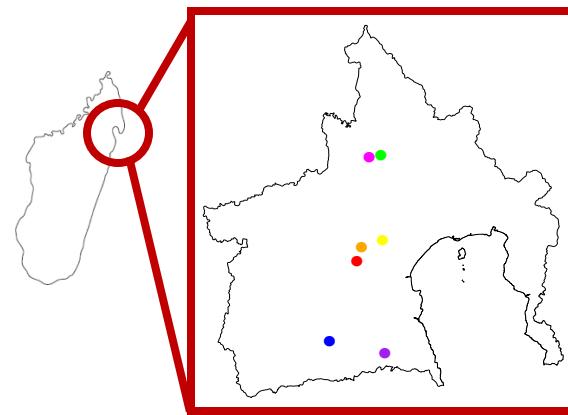
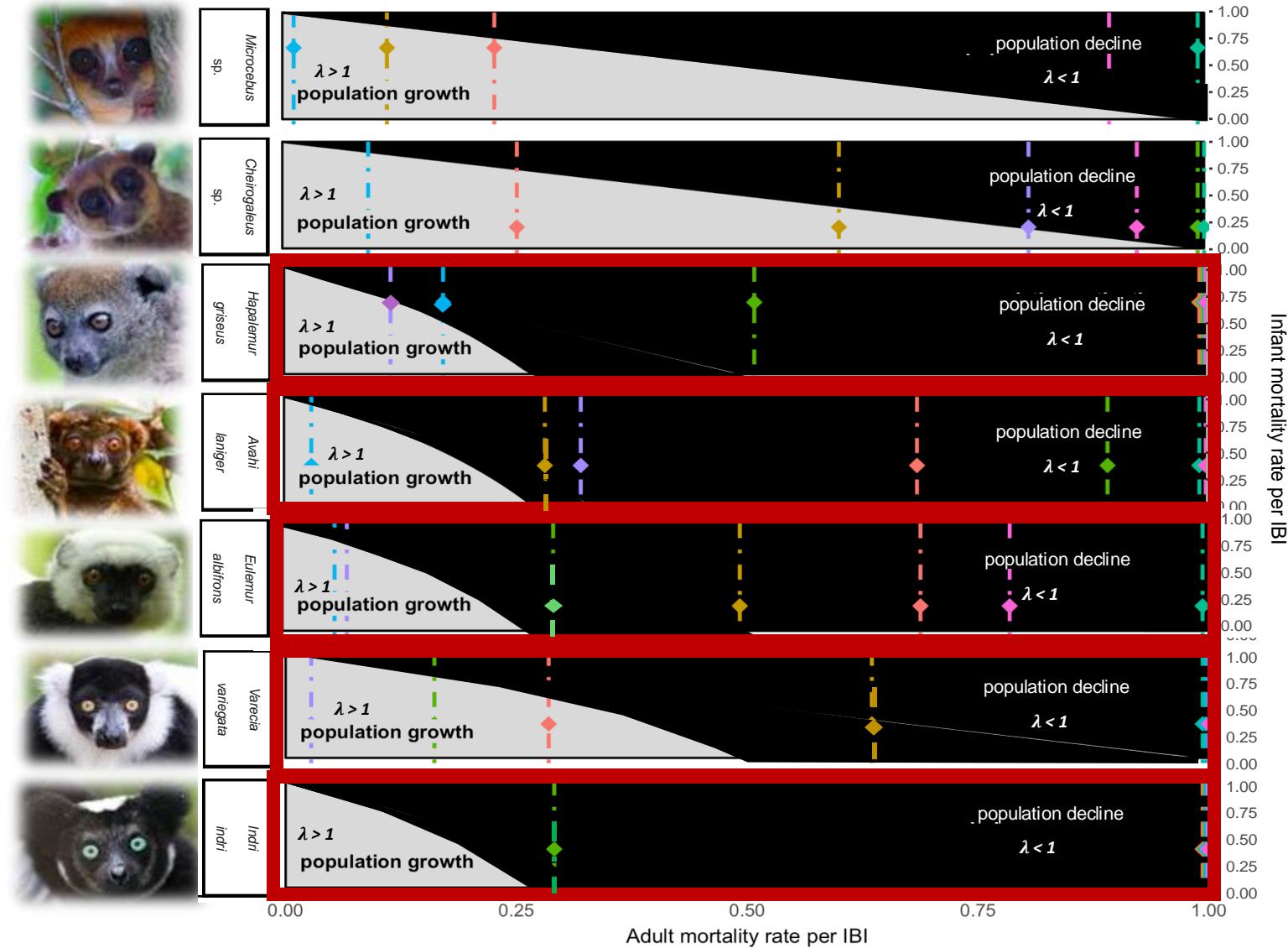
Colored vertical lines give **site-specific hunting rates** for adult lemurs.

Diamonds correspond to the intersection of that hunt rate with estimated juvenile mortality.

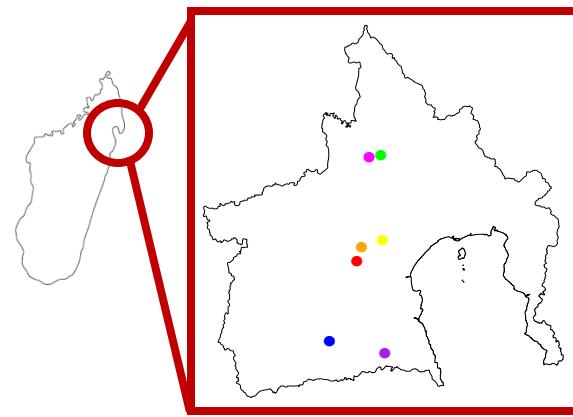
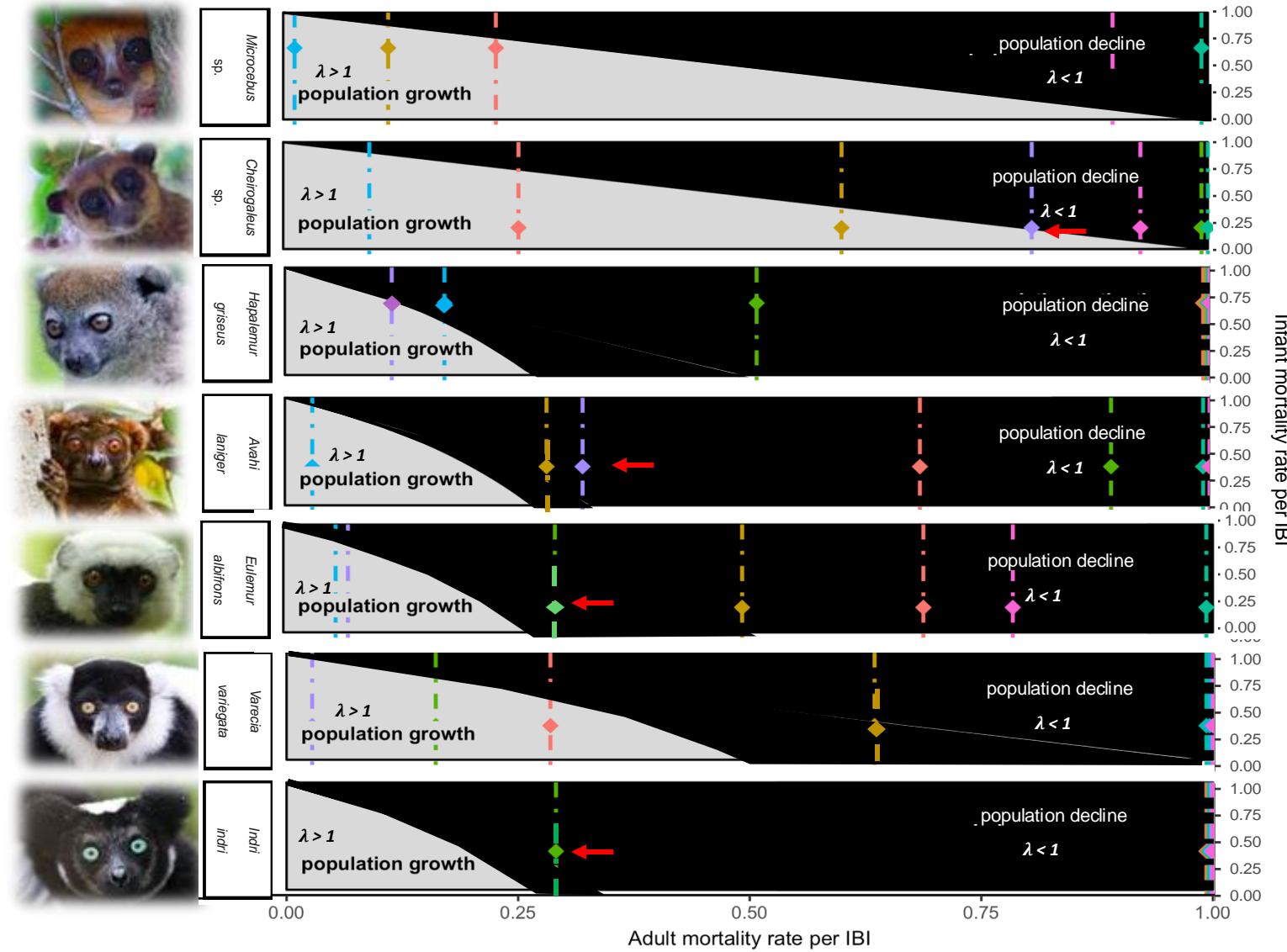
Small-bodied lemurs are largely harvested at sustainable rates on the Makira-Masoala peninsula.



By contrast, larger-bodied lemurs are severely threatened.



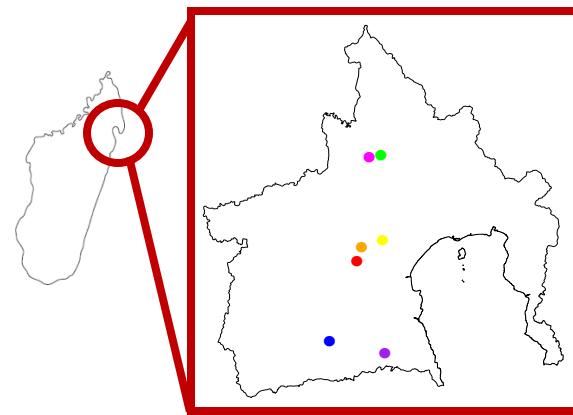
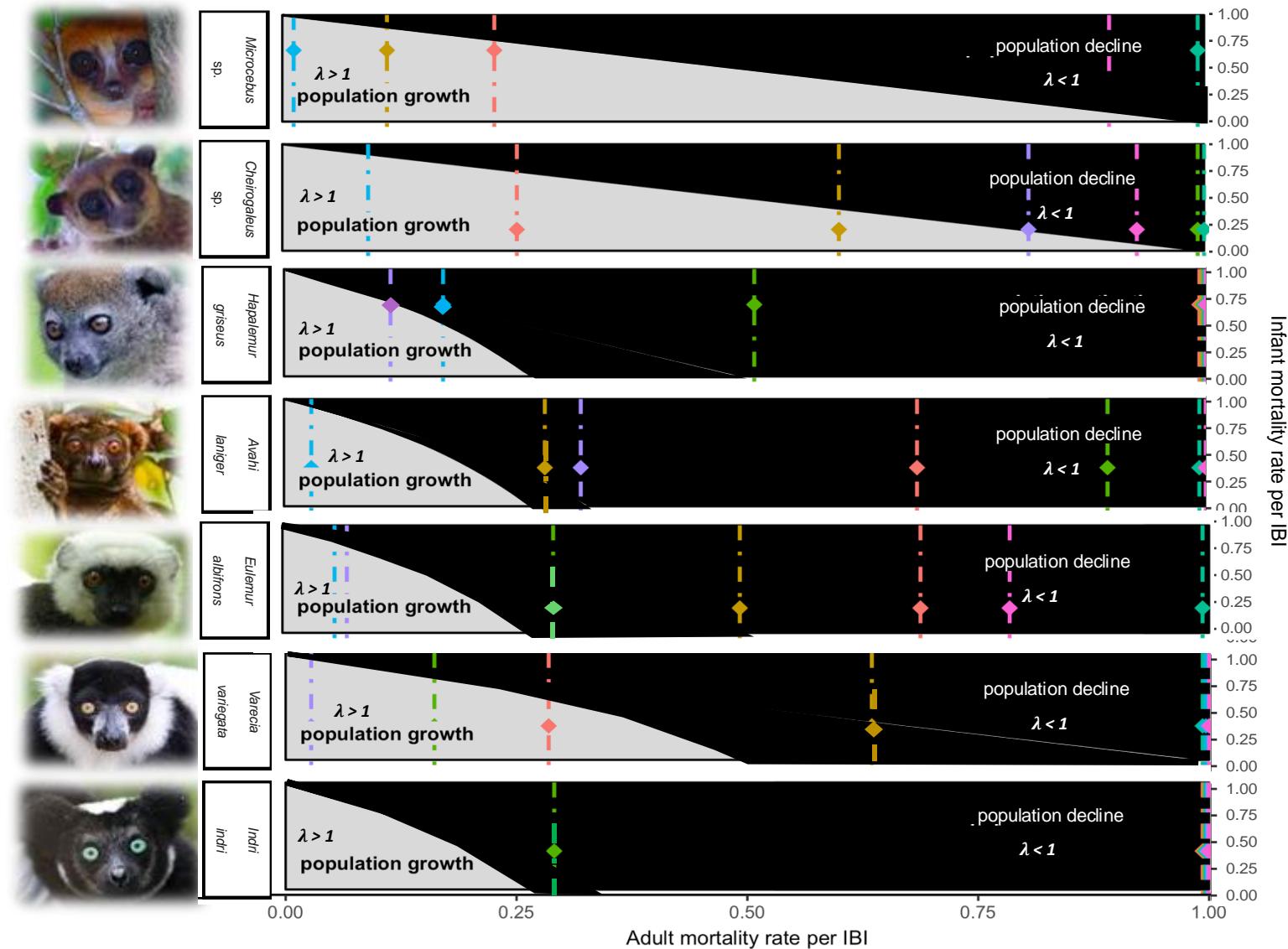
Harvesting near the zero-growth curve highlights the problems inherent with MSY!



Because of the **semi-stable equilibrium** at MSY, small (natural) decreases in N can be devastating:

- environmental **stochasticity**
- demographic **stochasticity**

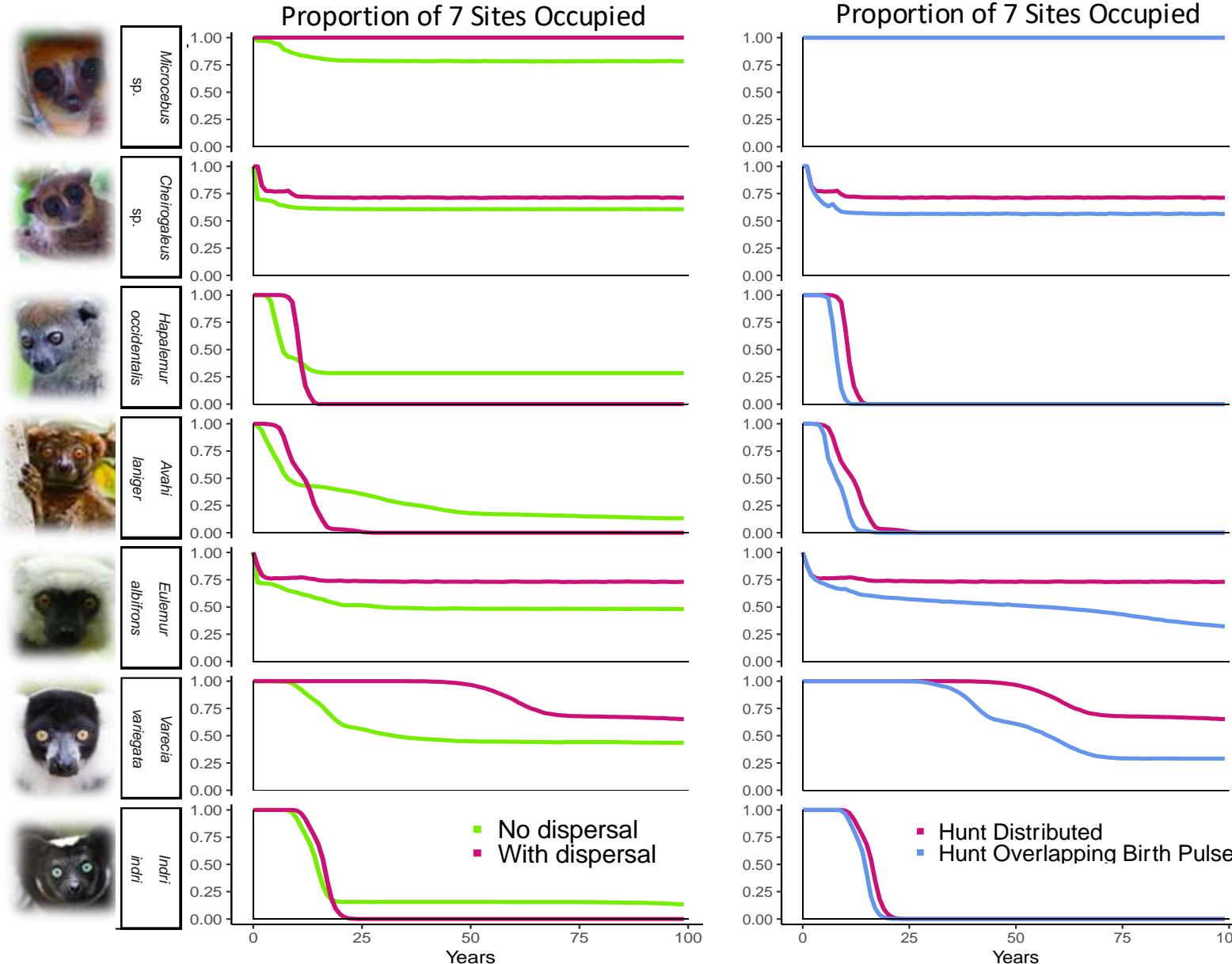
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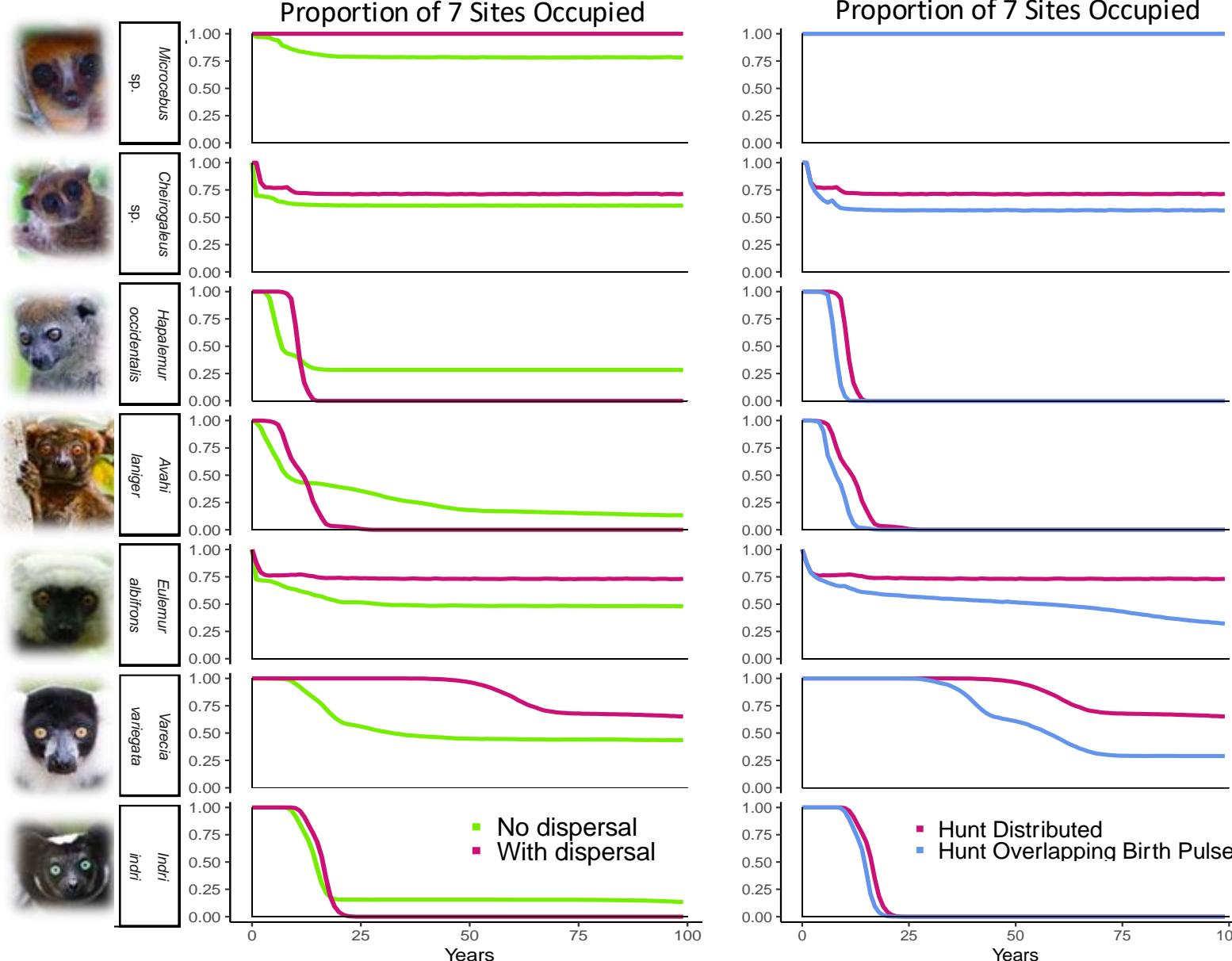
The '**Allee effect**' describes the correlation between population size and population 'fitness', often measured by the population rate of increase, λ .

Large animals tend to have **smaller population sizes**, which are often associated with **lower λ** .

Species are even **further threatened** when hunt seasonality overlaps the **annual birth pulse**.



Species are even **further threatened** when **hunt seasonality** overlaps the **annual birth pulse**.



Our lemur model highlights some of the earlier challenges discussed with modeling '**maximum sustainable yield**' in fisheries!

Simplest representations of MSY:

- Neglect population structure.
- Assume constant harvest.
- Ignore environmental and demographic stochasticity



Which of the following statements is correct?

A The greater the number...

0%

B Fragmentation c...

0%

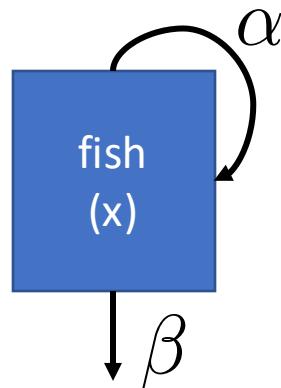
C Butterflies are goi...

0%

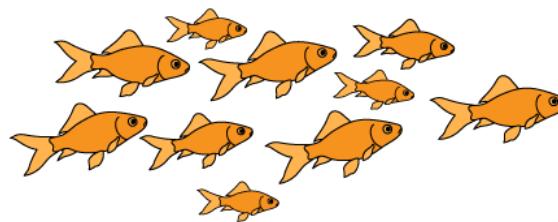
D Ecological traps oc...

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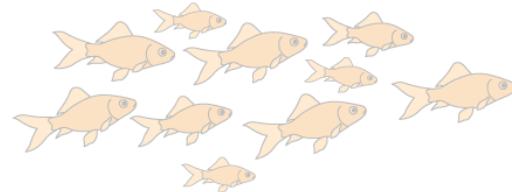
Population = multiple individuals of the same species (**conspecifics**) in the same habitat



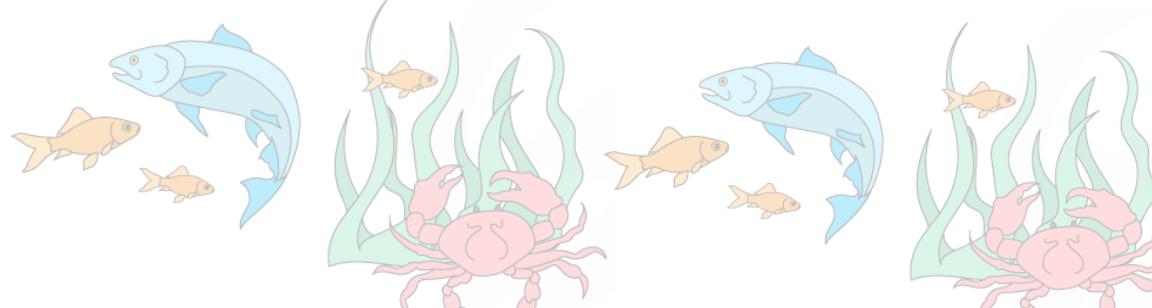
individual



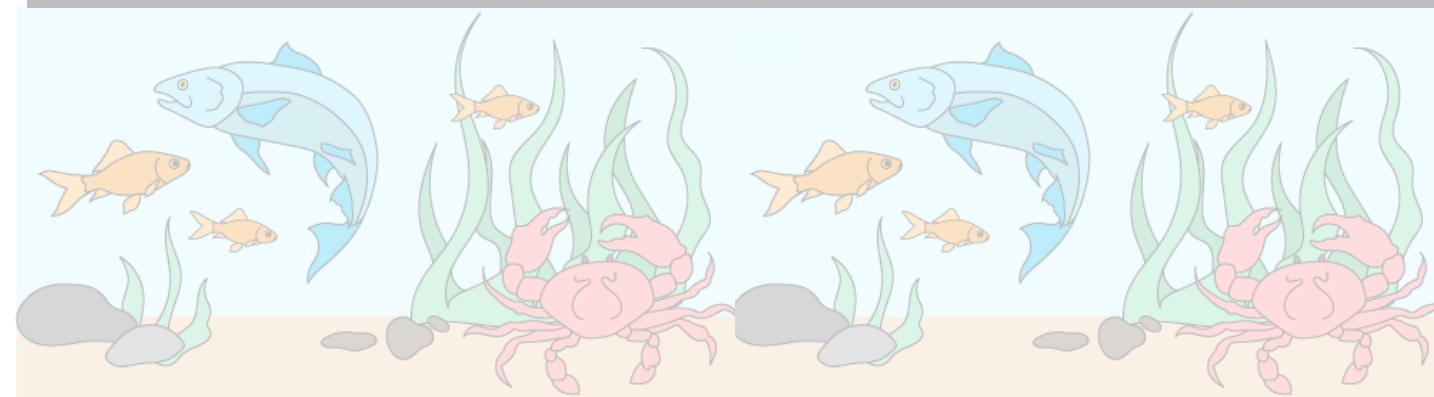
population



metapopulation



community



ecosystem

*How does the abundance of fish **change** through time?*

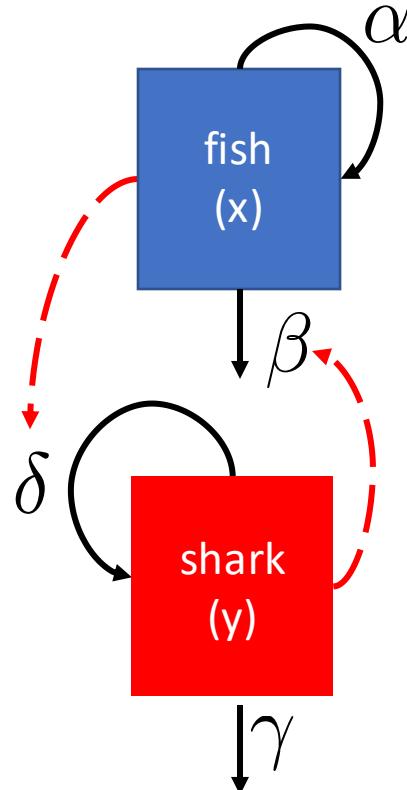
The logistic growth equation offers an explanation for population self-regulation, an example of **intraspecific competition**.

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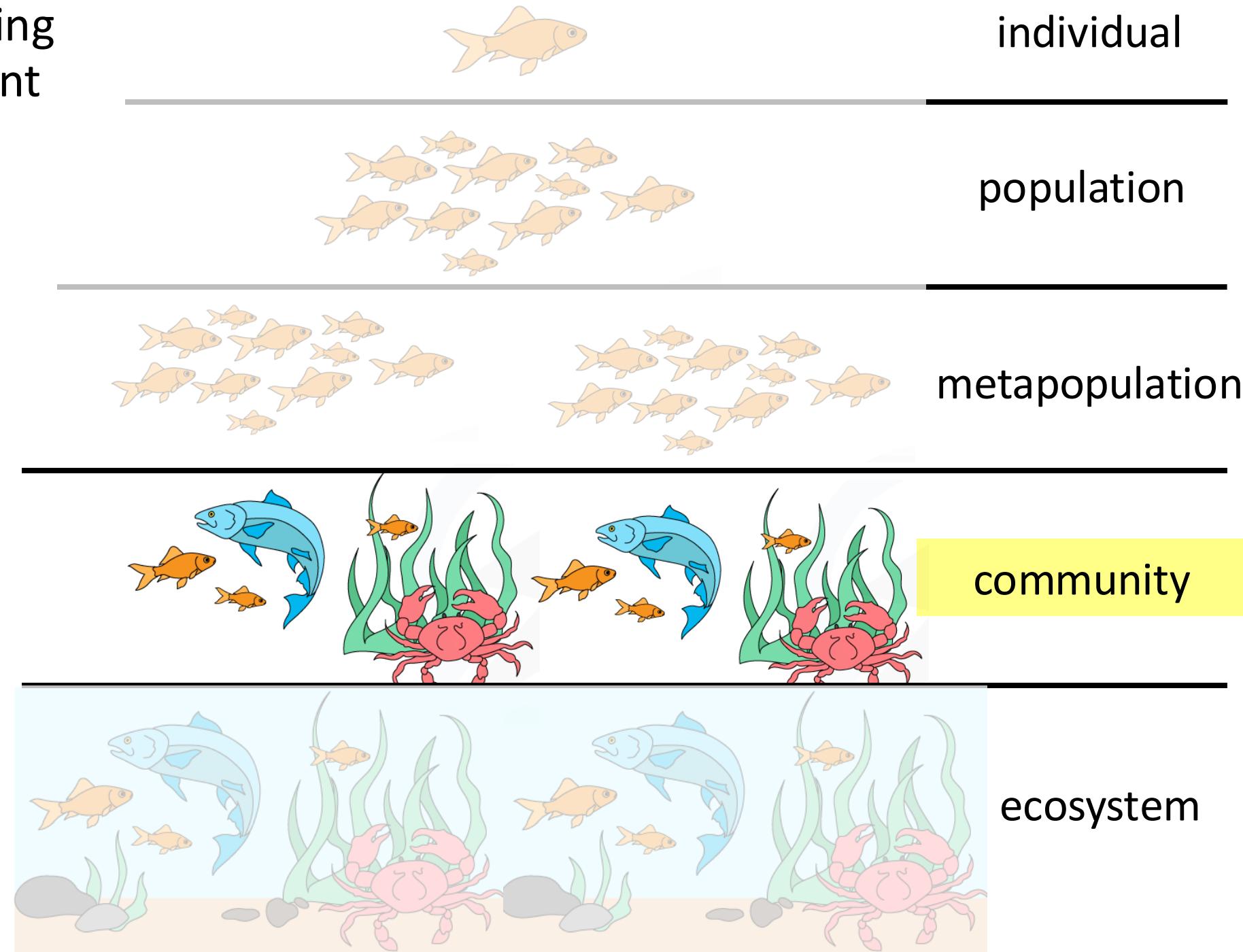


But ecology is the study of the **interactions** of organisms with each other and their environment, and in some cases, **interspecific interactions** are essential to understanding ecological systems.

Community = interacting populations of different species

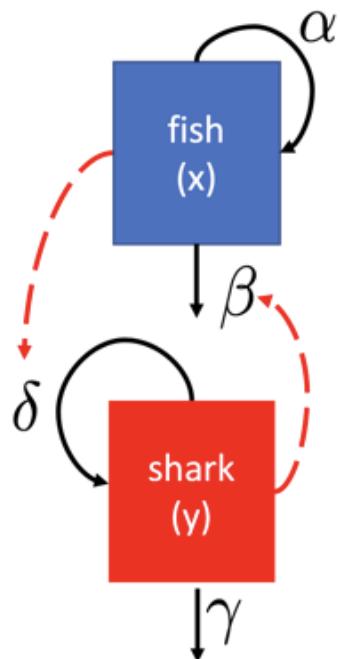


How does fish abundance **vary** with changes in shark abundance?





What are the state variables in this predator-prey system?



A β and γ

0%

B α and δ

0%

D fish (x) and sharks (y)

0%

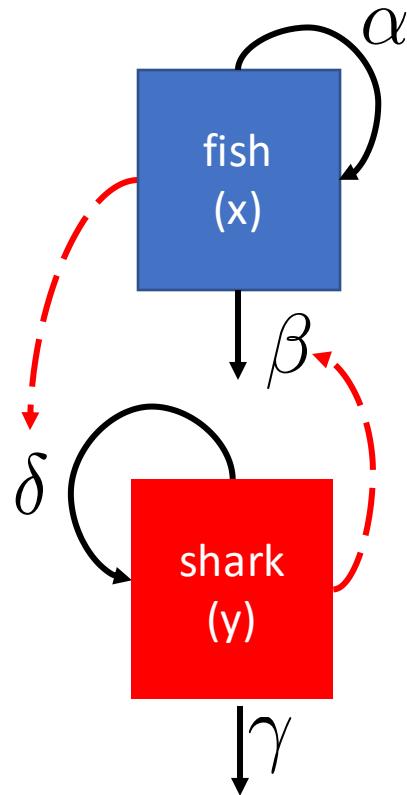
E The red dashed lines

0%

C Both "A" and "B"

0%

The Lotka-Volterra predator-prey model



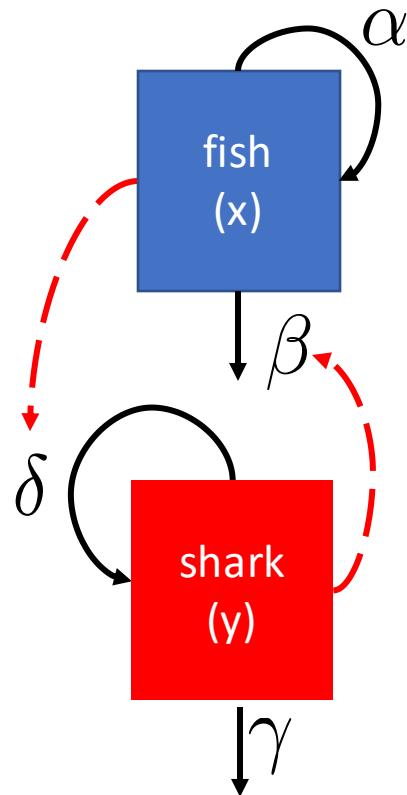
$$\frac{dx}{dt} = \alpha x - \beta xy$$

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

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

- First proposed by Polish-born American mathematician & chemist, Alfred J. Lotka, in 1920 to explain autocatalytic chemical reactions.

The Lotka-Volterra predator-prey model

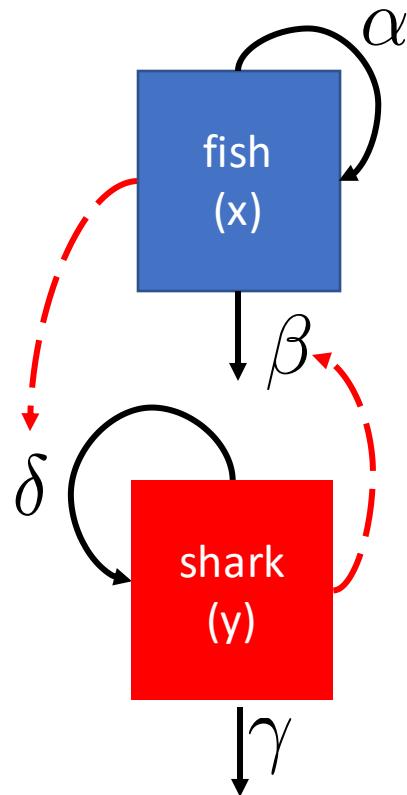


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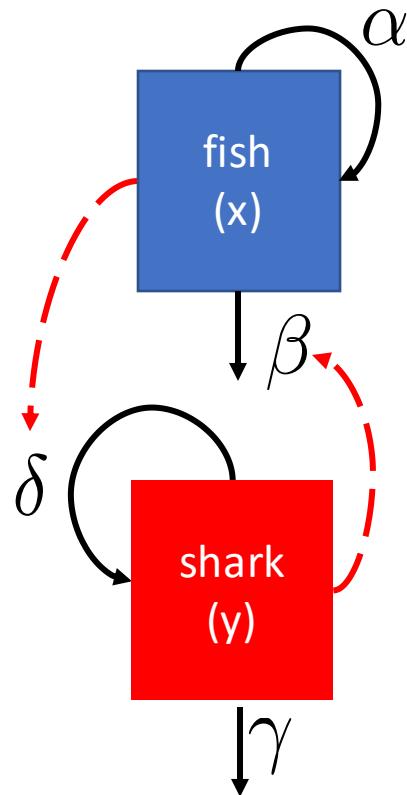


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The Lotka-Volterra predator-prey model

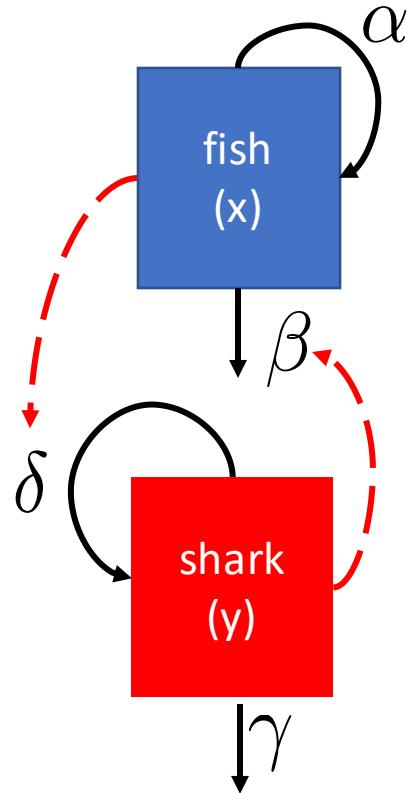


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- Idea that **interspecies interactions** regulate populations

The Lotka-Volterra predator-prey model



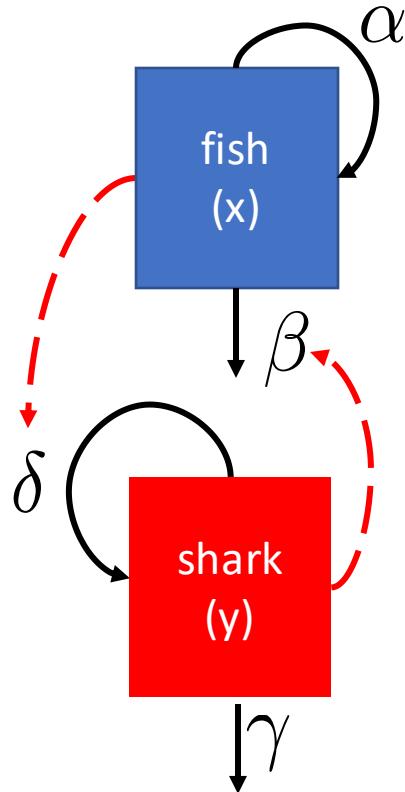
growth rate of prey,
independent of predator

$$\frac{dx}{dt} = \underbrace{\alpha x}_{\text{growth rate}} - \beta xy$$

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

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The Lotka-Volterra predator-prey model



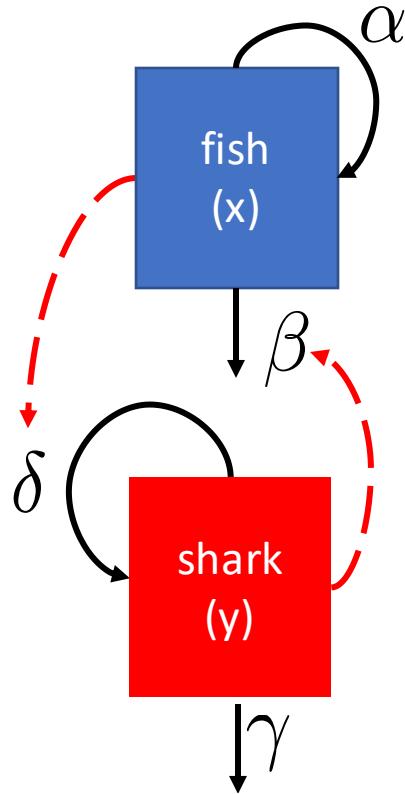
growth rate of prey,
independent of predator

$$\left. \begin{aligned} \frac{dx}{dt} &= \alpha x - \beta xy \\ \frac{dy}{dt} &= \delta xy - \gamma y \end{aligned} \right\}$$

death rate of prey,
depends on
abundance of
predator

*How does **fish**
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The Lotka-Volterra predator-prey model



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growth rate of prey,
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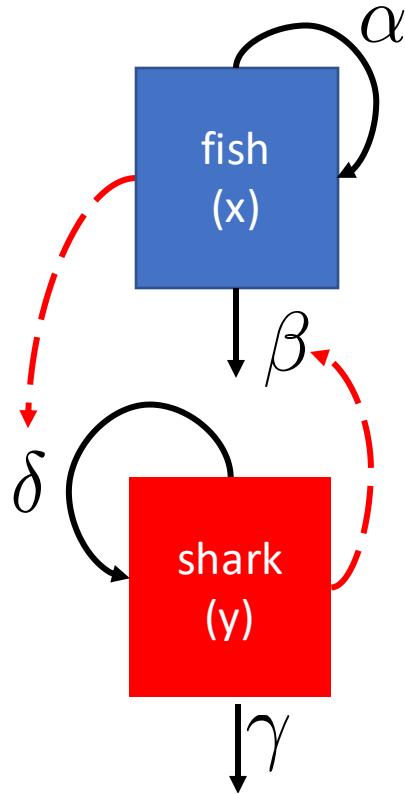
$$\frac{dx}{dt} = \alpha x - \beta xy \quad \left. \right\}$$

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

growth rate of
predator, depends on
abundance of prey
(and efficiency of
consumption)

death rate of prey,
depends on
abundance of
predator

The Lotka-Volterra predator-prey model



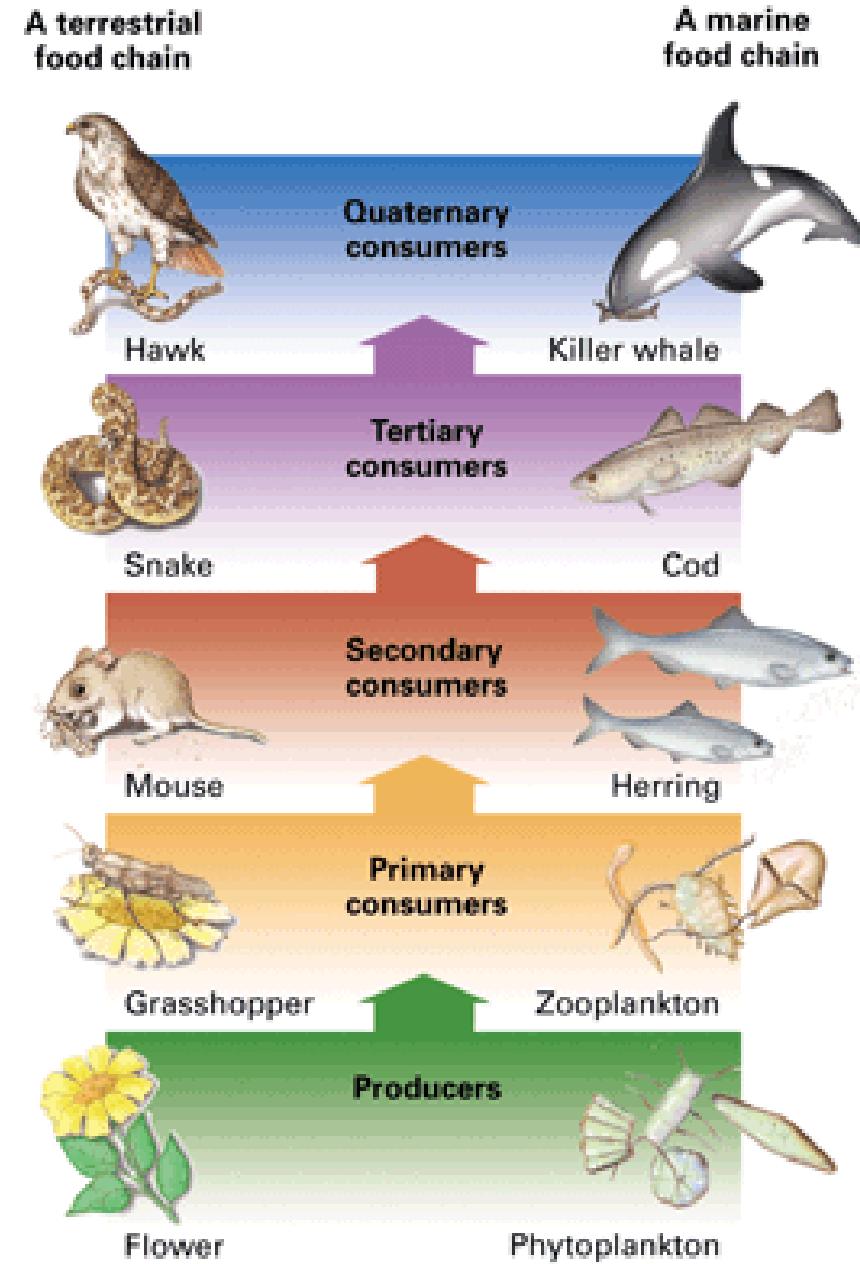
*How does **fish** abundance **vary** with changes in **shark** abundance?*

growth rate of prey,
independent of predator

$$\frac{dx}{dt} = \underbrace{\alpha x}_{\text{growth rate of prey, independent of predator}} - \underbrace{\beta xy}_{\text{death rate of prey, depends on abundance of predator}}$$

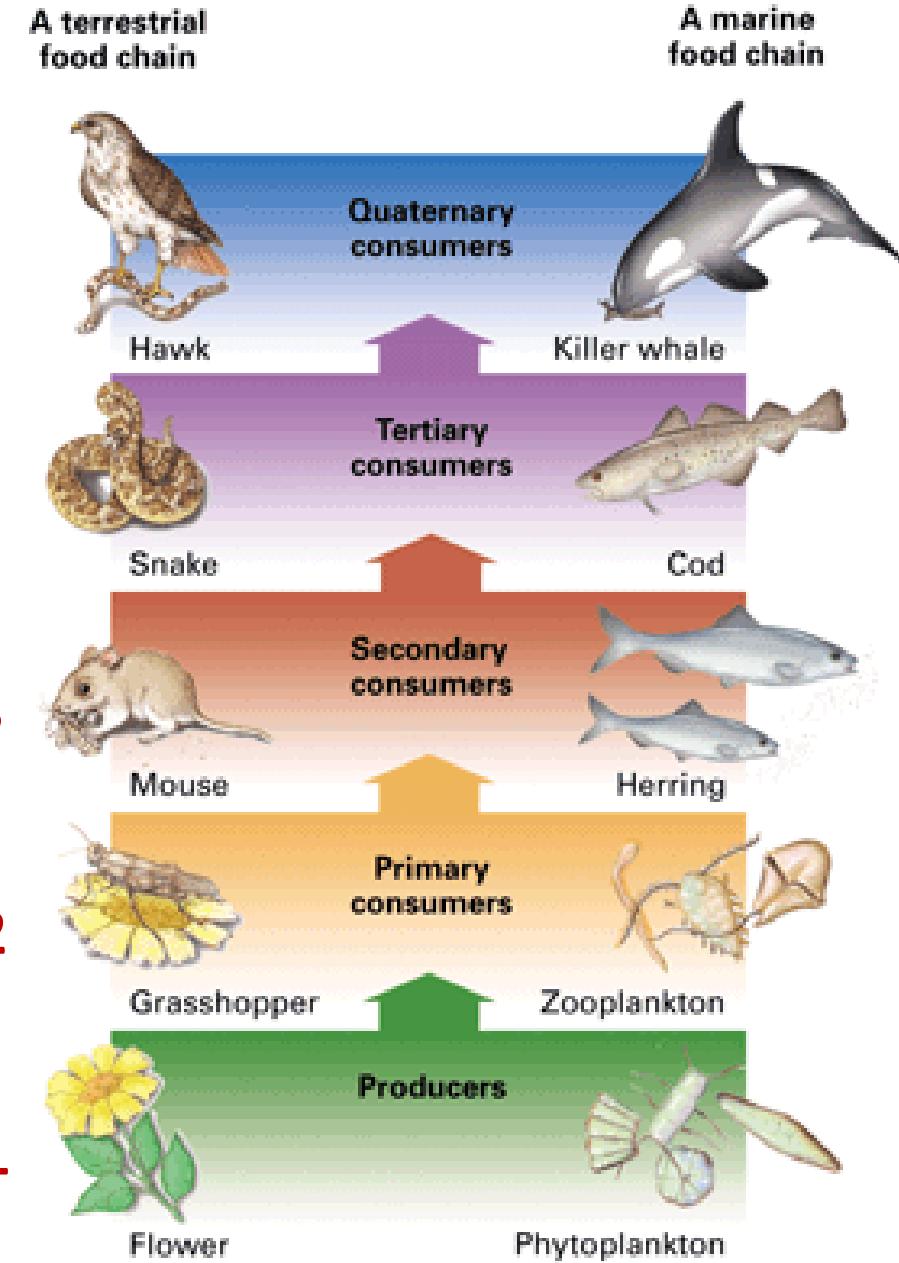
$$\frac{dy}{dt} = \underbrace{\delta xy}_{\text{growth rate of predator, depends on abundance of prey (and efficiency of consumption)}} - \underbrace{\gamma y}_{\text{death rate of predator, independent of prey}}$$

Trophic levels are levels in the food chain, grouped by energy transfer.



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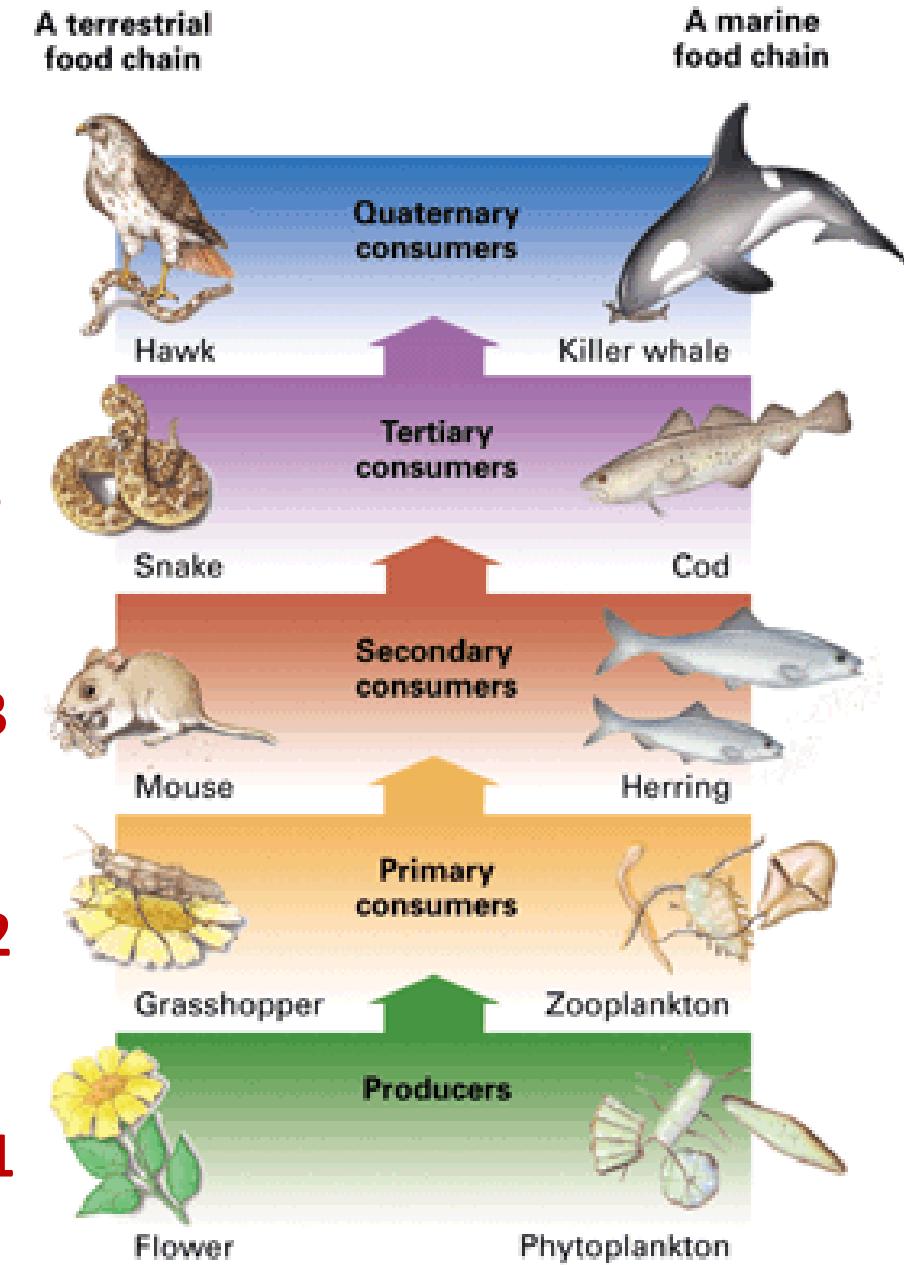
Each trophic level is given a number corresponding to **how many steps it is away from the start of the chain**.



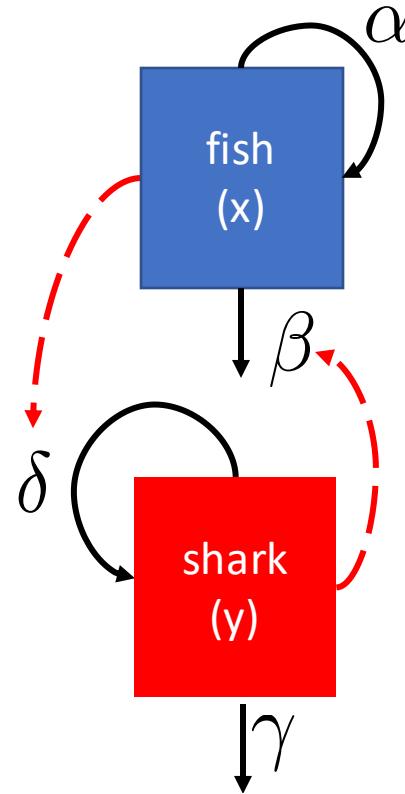
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Energy efficiency is the term used to describe the transfer of energy moving up a trophic level.



The Lotka-Volterra predator-prey model



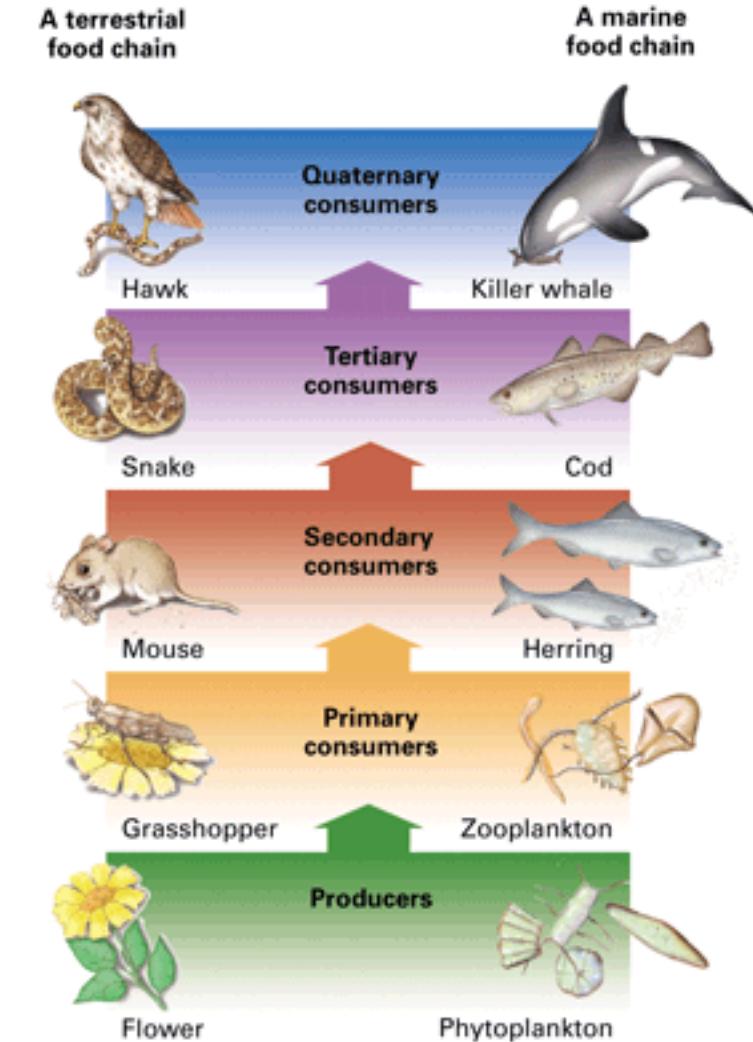
How does **fish** abundance **vary** with changes in **shark** abundance?

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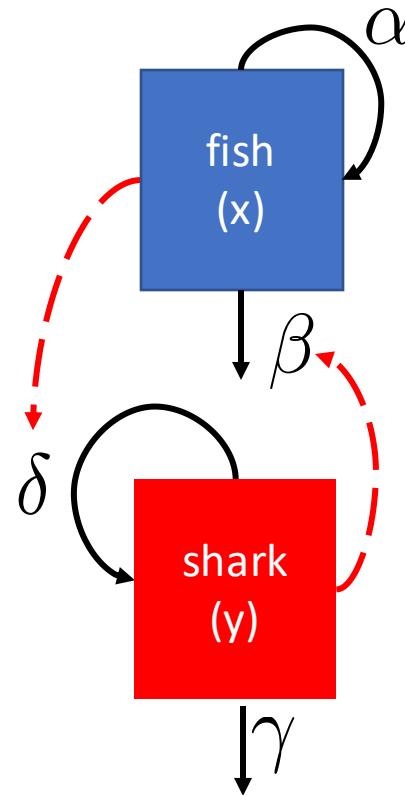
$$\frac{dy}{dt} = \delta xy - \gamma y$$

Bottom-up processes describe ecosystems regulated via production from lower trophic levels.

Top-down processes describe ecosystems regulated via consumption from higher trophic levels.



The Lotka-Volterra predator-prey model



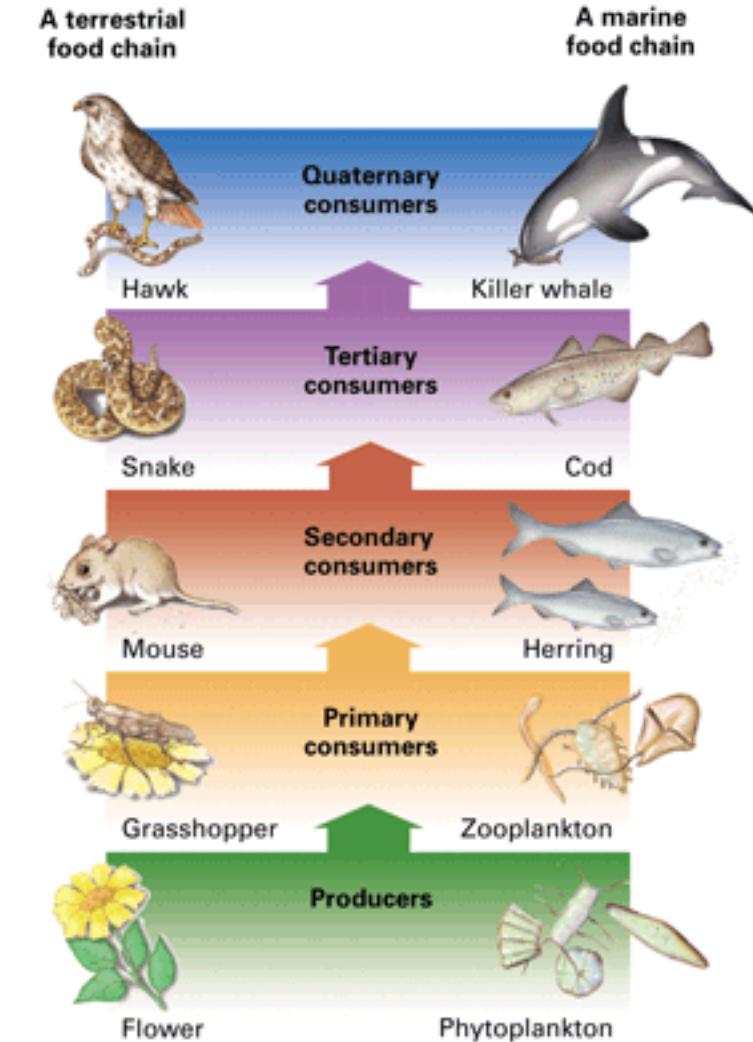
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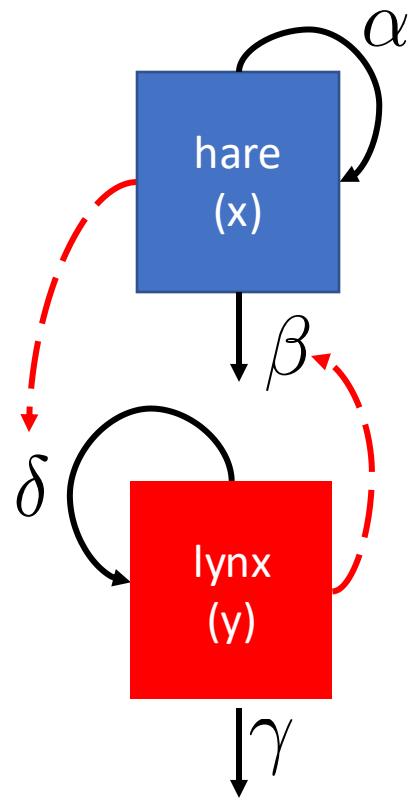
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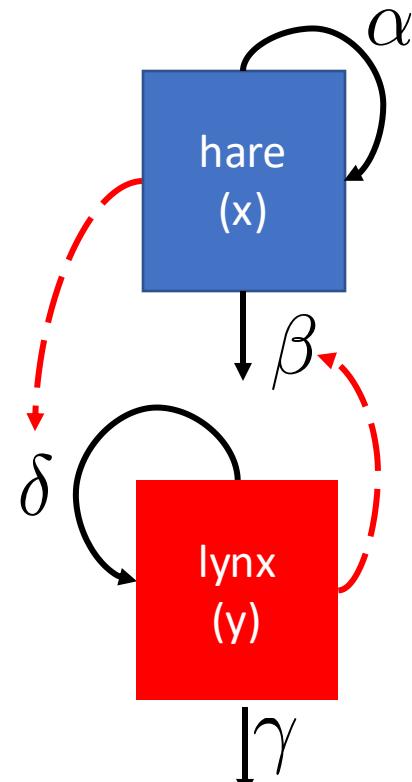
Lotka-Volterra predator-prey models with data



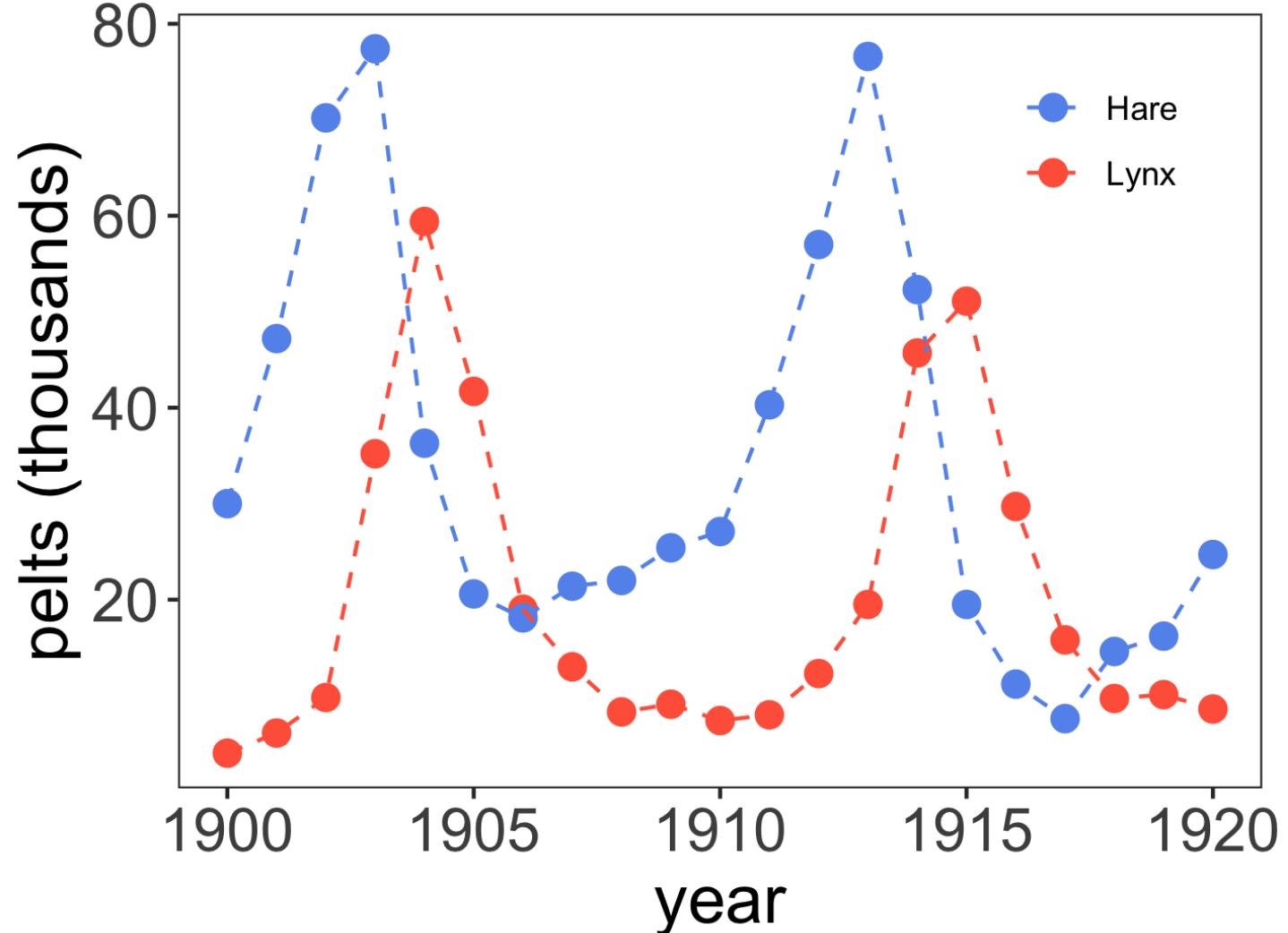
How does **hare** abundance **vary** with changes in **lynx** abundance?



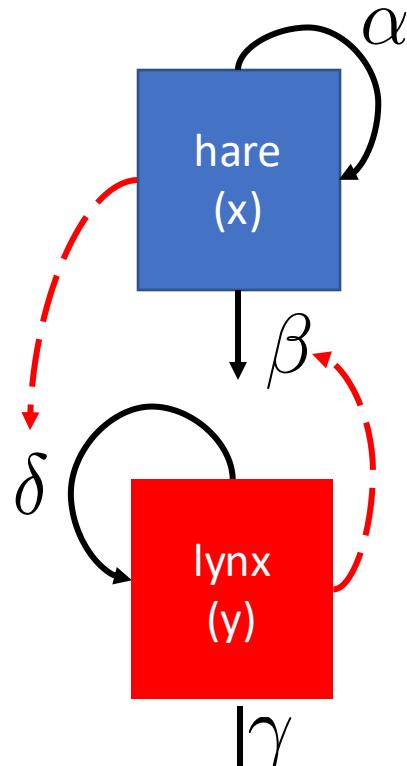
Lotka-Volterra predator-prey models with data



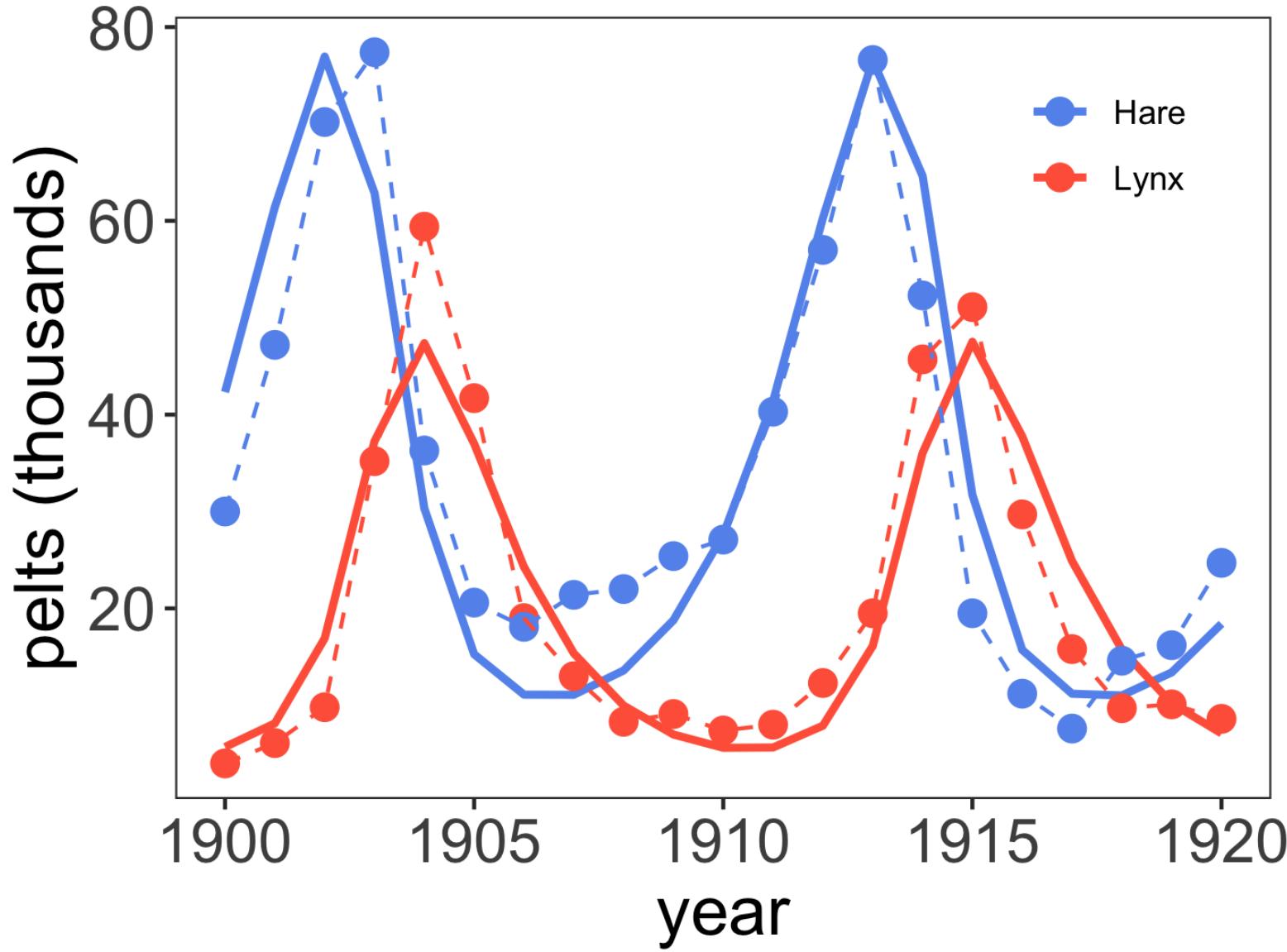
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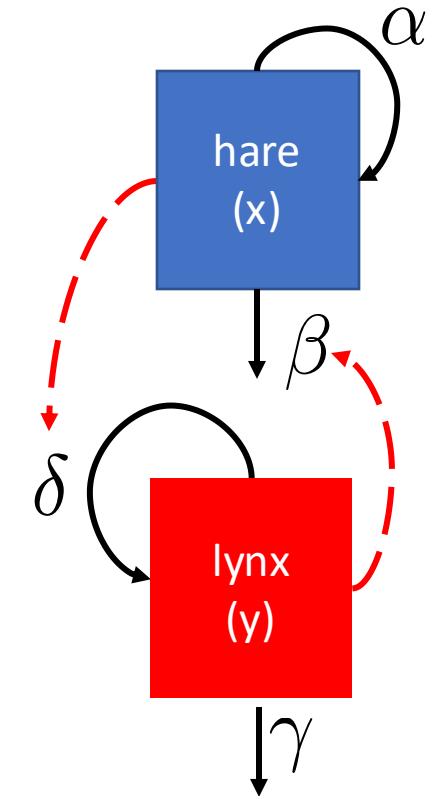
Lotka-Volterra predator-prey models with data



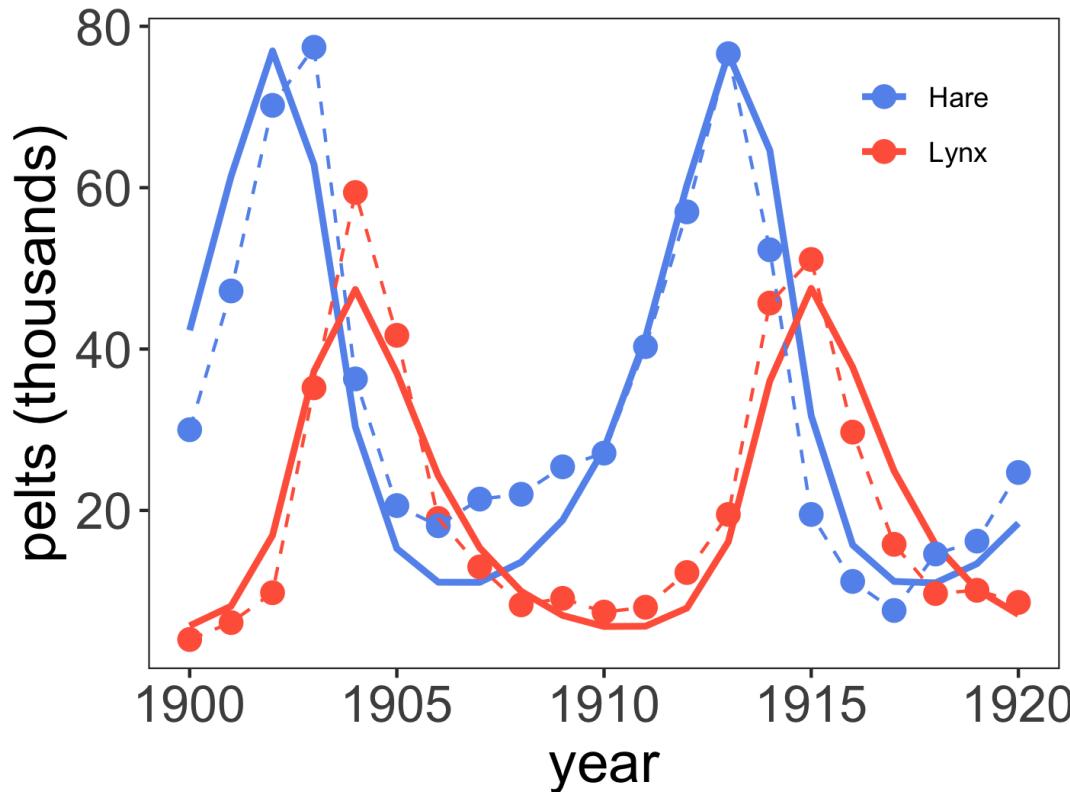
How does **hare** abundance **vary** with changes in **lynx** abundance?



Lotka-Volterra predator-prey models with data



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



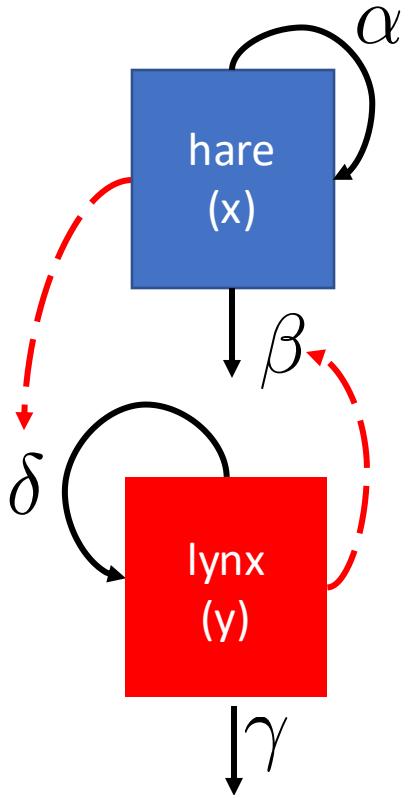
$$\frac{dx}{dt} = \alpha x - \beta xy$$

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

- Fitting a model to data allows us to estimate parameters – remember those growth rates from the human population models!
- Here, we can explore the growth rate of the prey under exponential growth (α), the efficiency of kill (β) and digestion (δ) by the predator, and the natural death rate of the predator (γ).

- $\alpha = .0897$ hare/year
- $\beta = .0000157$ hare/lynx/year
- $\delta = .0250$ lynx/hare/year
- $\gamma = .0174$ lynx /year

Lotka-Volterra predator-prey **isoclines**



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

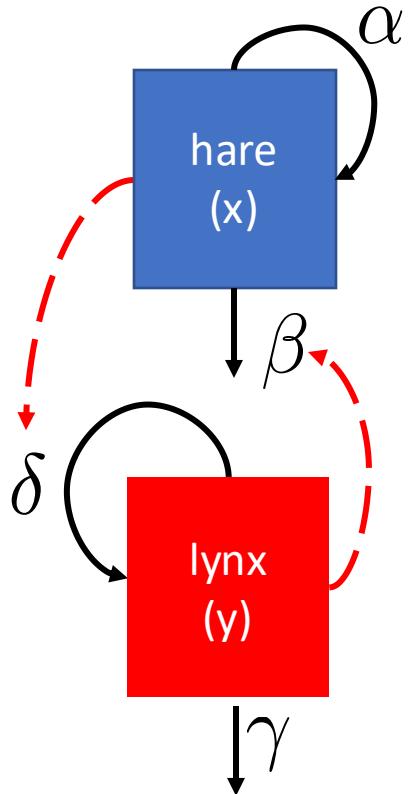
$$\frac{dx}{dt} = \alpha x - \beta xy$$

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

The **zero-growth isocline** (or **nullcline**) refers to the line at which the rate of change for **one population in a two-population interaction model is not changing**.

(e.g. one of the differential equations is set equal to zero)

Lotka-Volterra predator-prey **isoclines**



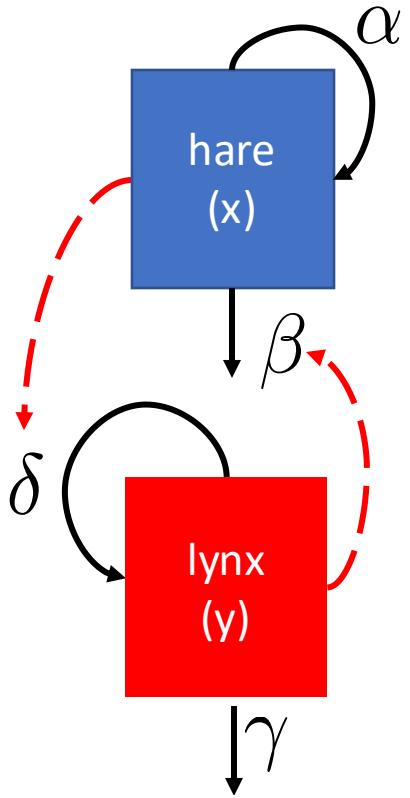
$$\frac{dx}{dt} = \alpha x - \beta xy$$

(hint: this means the prey population is not changing!)

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

What are the **prey** isoclines?

Lotka-Volterra predator-prey **isoclines**



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

$$\frac{dx}{dt} = \alpha x - \beta xy$$
$$\frac{dy}{dt} = \delta xy - \gamma y$$

What are the **prey** isoclines?

$$0 = \alpha x - \beta xy$$
$$0 = x(\alpha - \beta y)$$

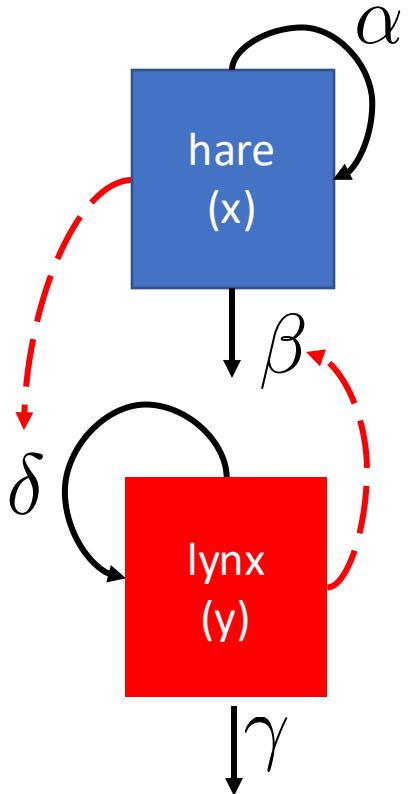
isoclines at:

$$x = 0$$
$$y = \frac{\alpha}{\beta}$$

This is the predator number that results in no change in the prey population!

(because prey are top-down regulated)

Lotka-Volterra predator-prey **isoclines**



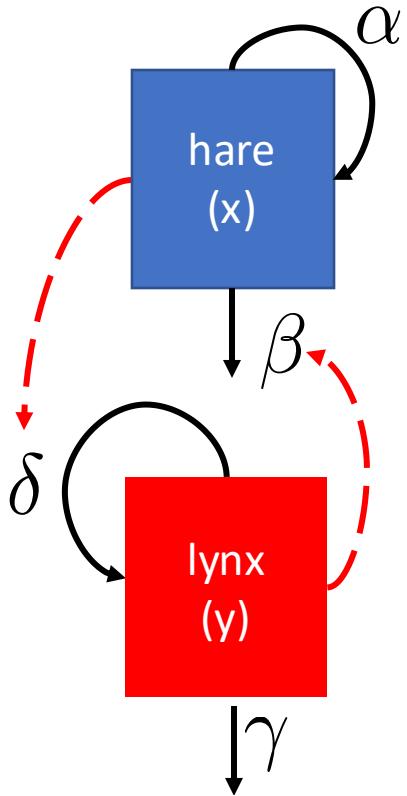
$$\frac{dx}{dt} = \alpha x - \beta xy$$

What are the **predator** isoclines?

(hint: this means the predator population is not changing!)

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

Lotka-Volterra predator-prey **isoclines**



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

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

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

What are the **predator** isoclines?

$$0 = \delta xy - \gamma y$$

$$0 = y(\delta x - \gamma)$$

isoclines at:

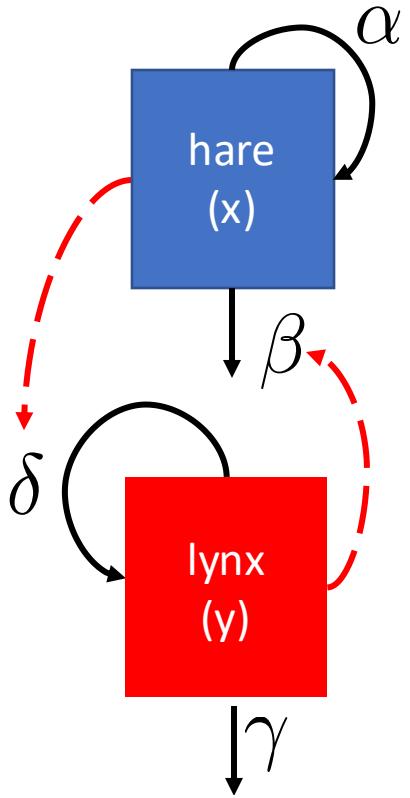
$$y = 0$$

$$x = \frac{\gamma}{\delta}$$

This is the prey number that results in no change in the predator population!

(because predators are bottom-up regulated)

Lotka-Volterra predator-prey **isoclines**



$$\frac{dx}{dt} = \alpha x - \beta xy$$
$$\frac{dy}{dt} = \delta xy - \gamma y$$

prey isoclines:

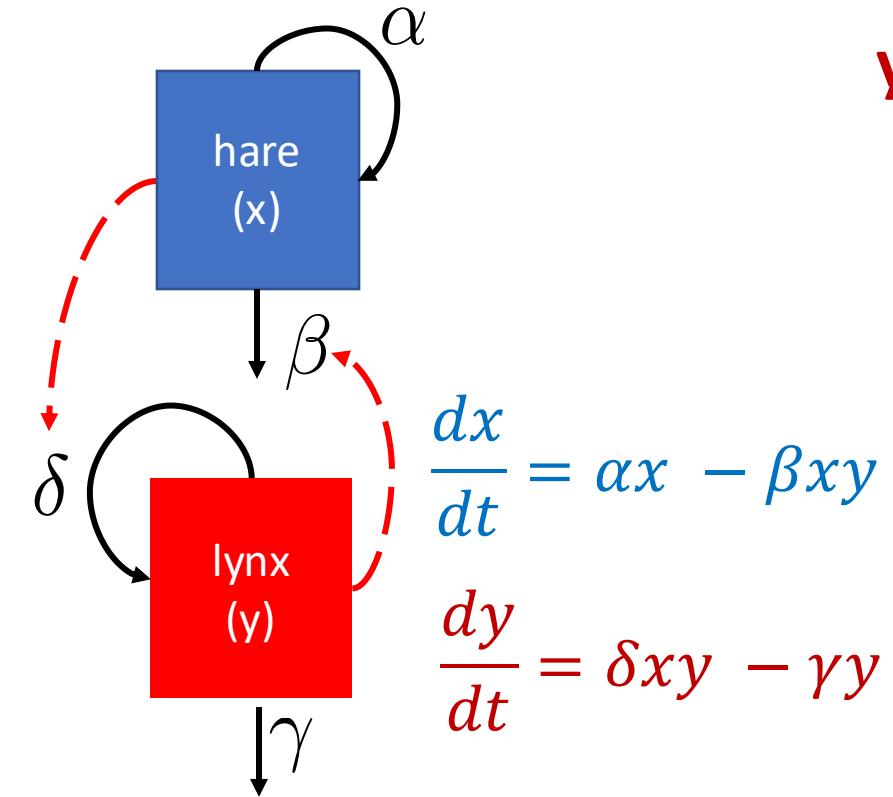
$$x = 0$$
$$y = \frac{\alpha}{\beta}$$

predator isoclines:

$$y = 0$$
$$x = \frac{\gamma}{\delta}$$

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

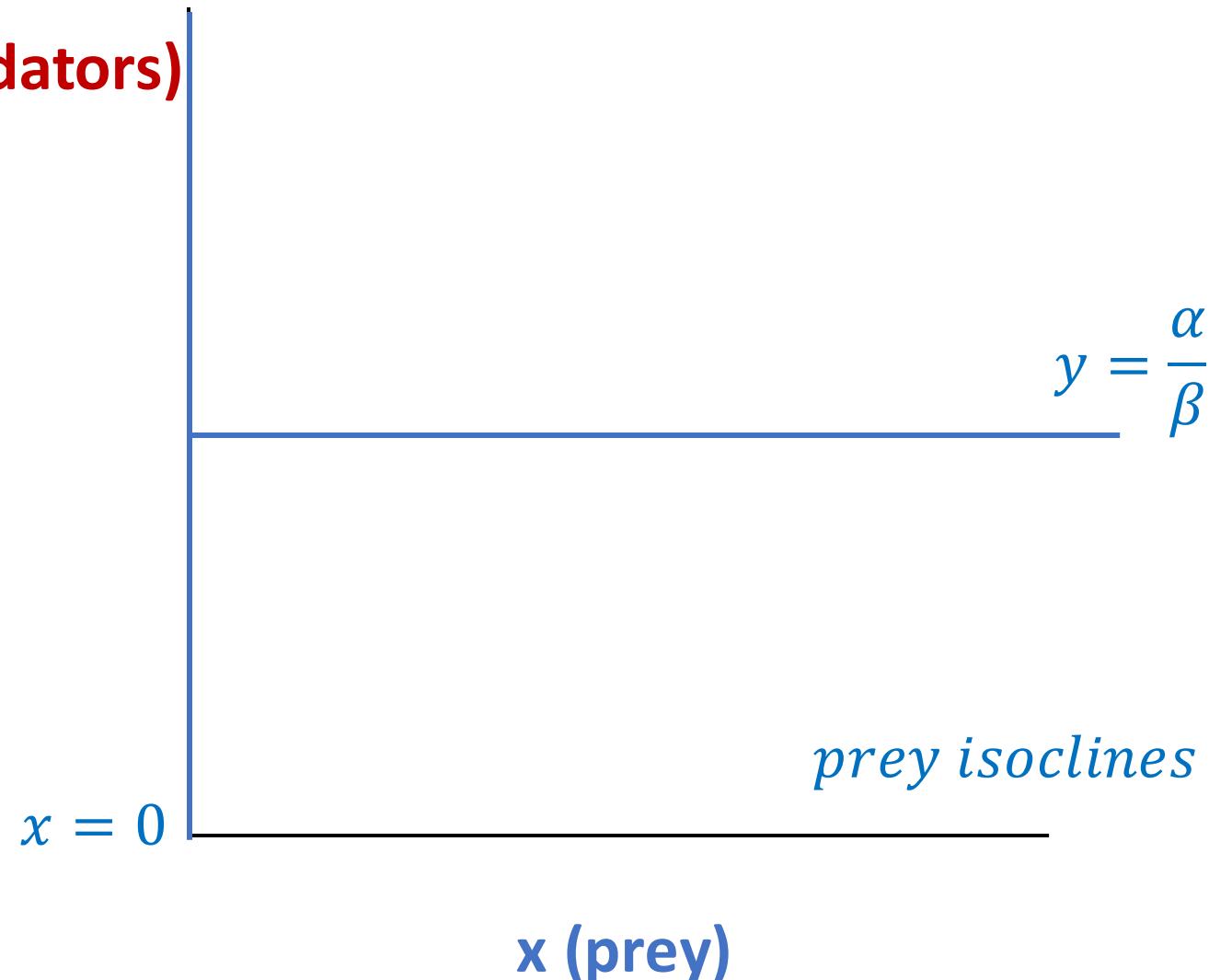
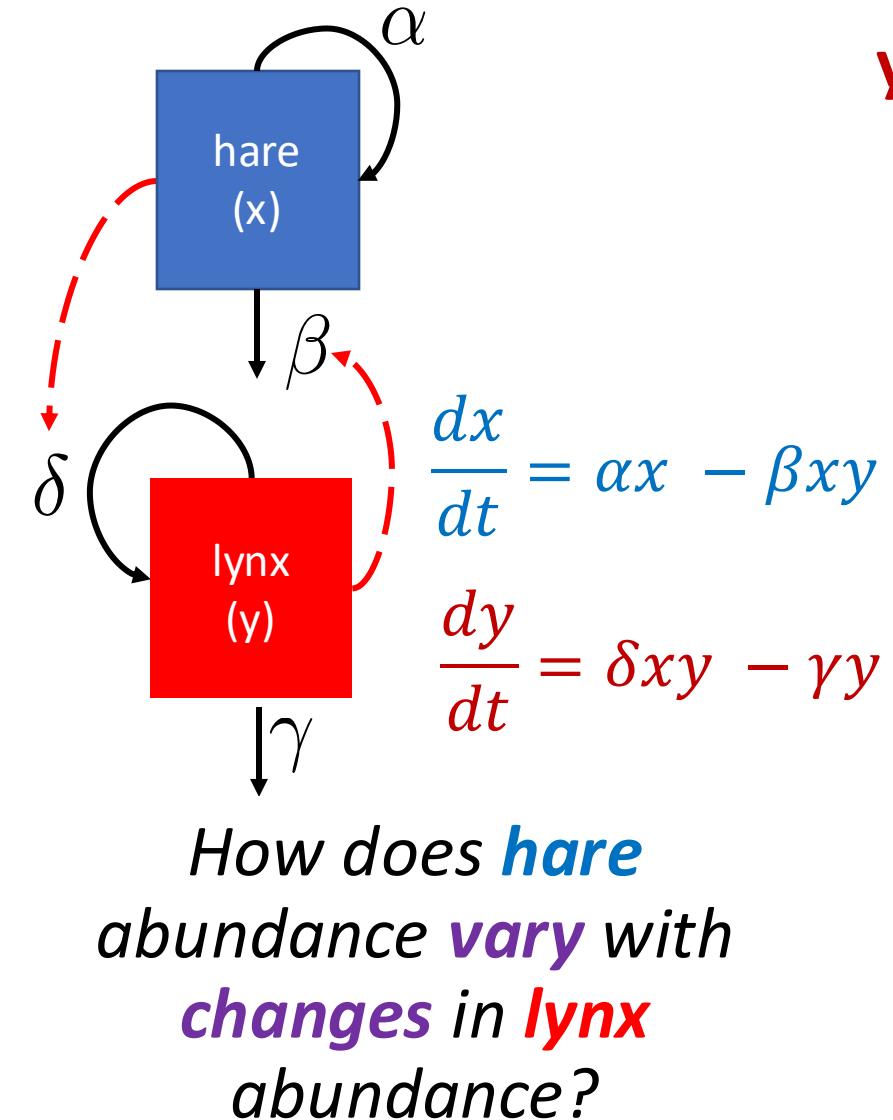
Lotka-Volterra predator-prey isoclines



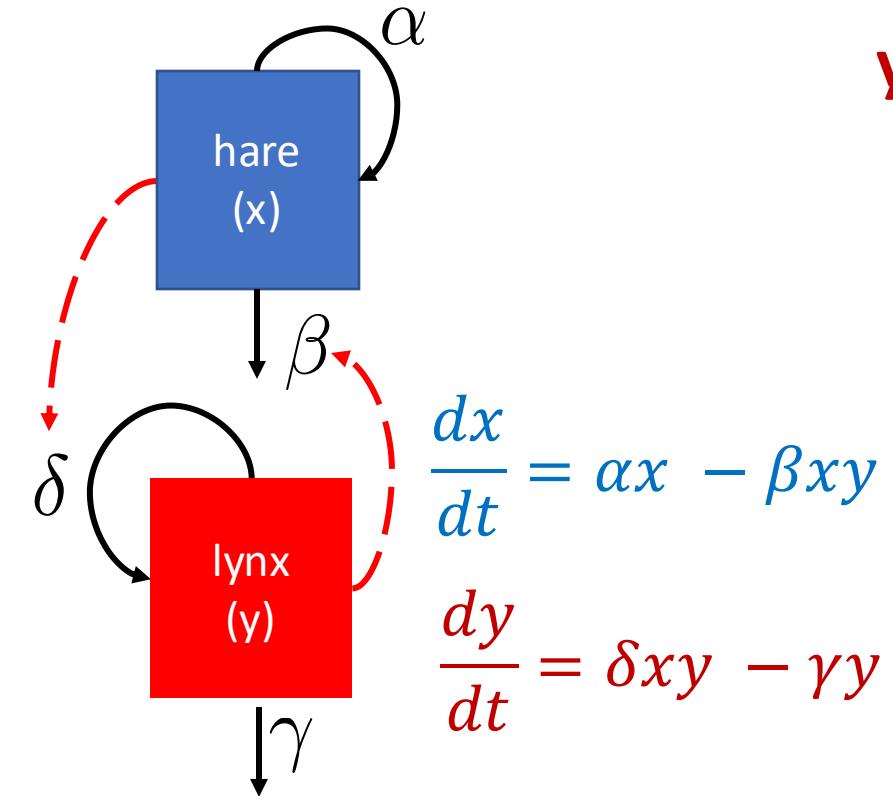
*How does **hare** abundance **vary** with changes in **lynx** abundance?*



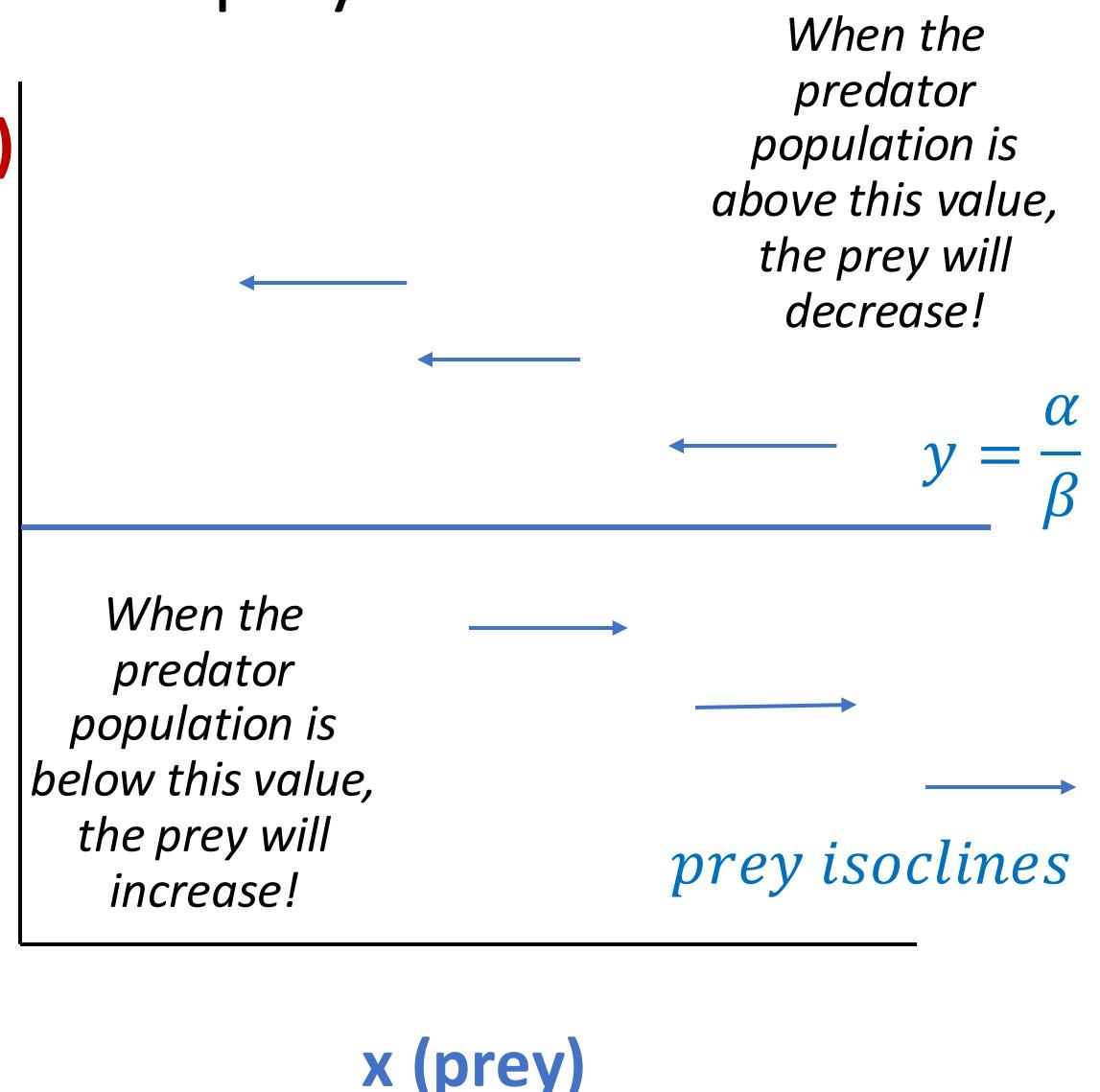
Lotka-Volterra predator-prey isoclines



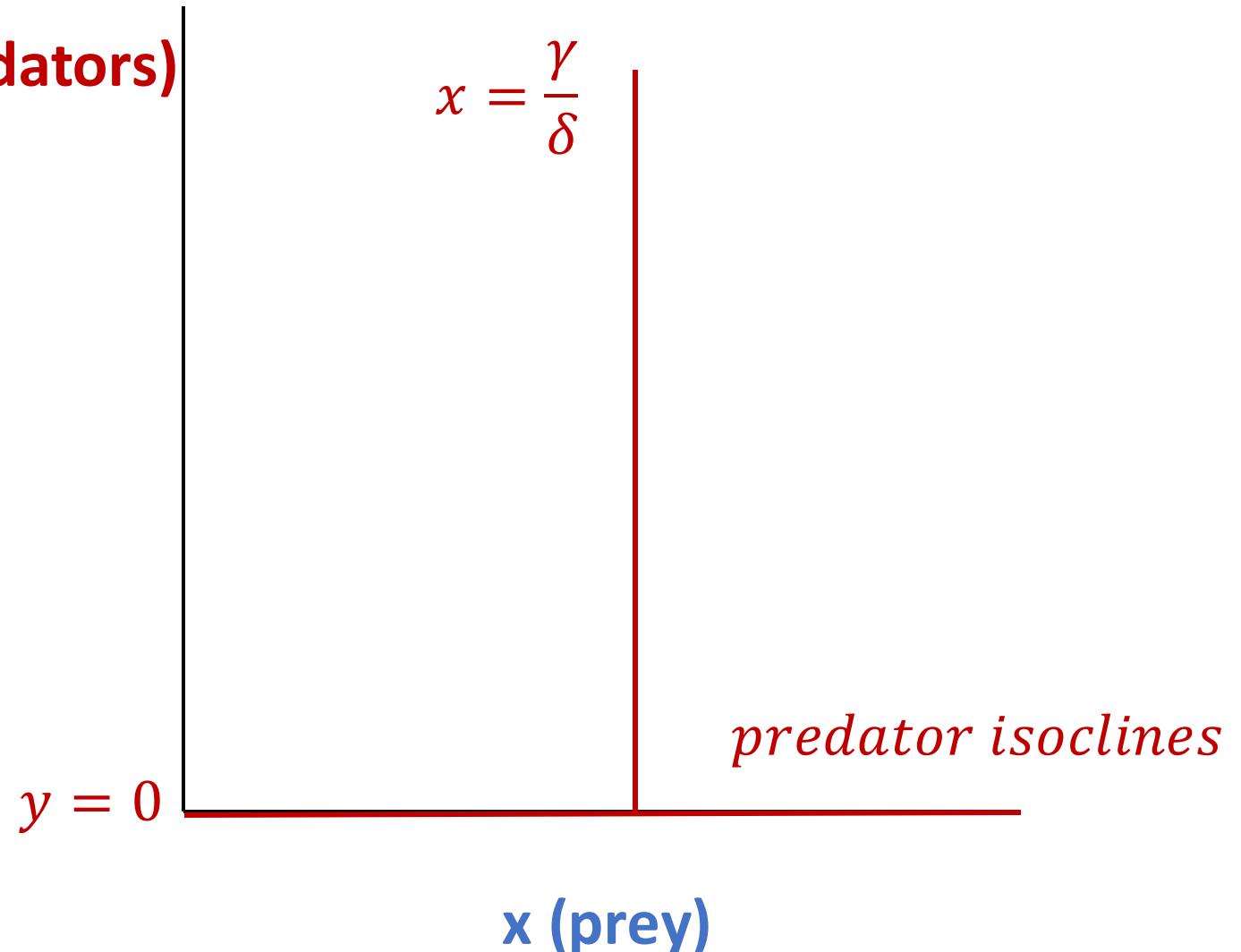
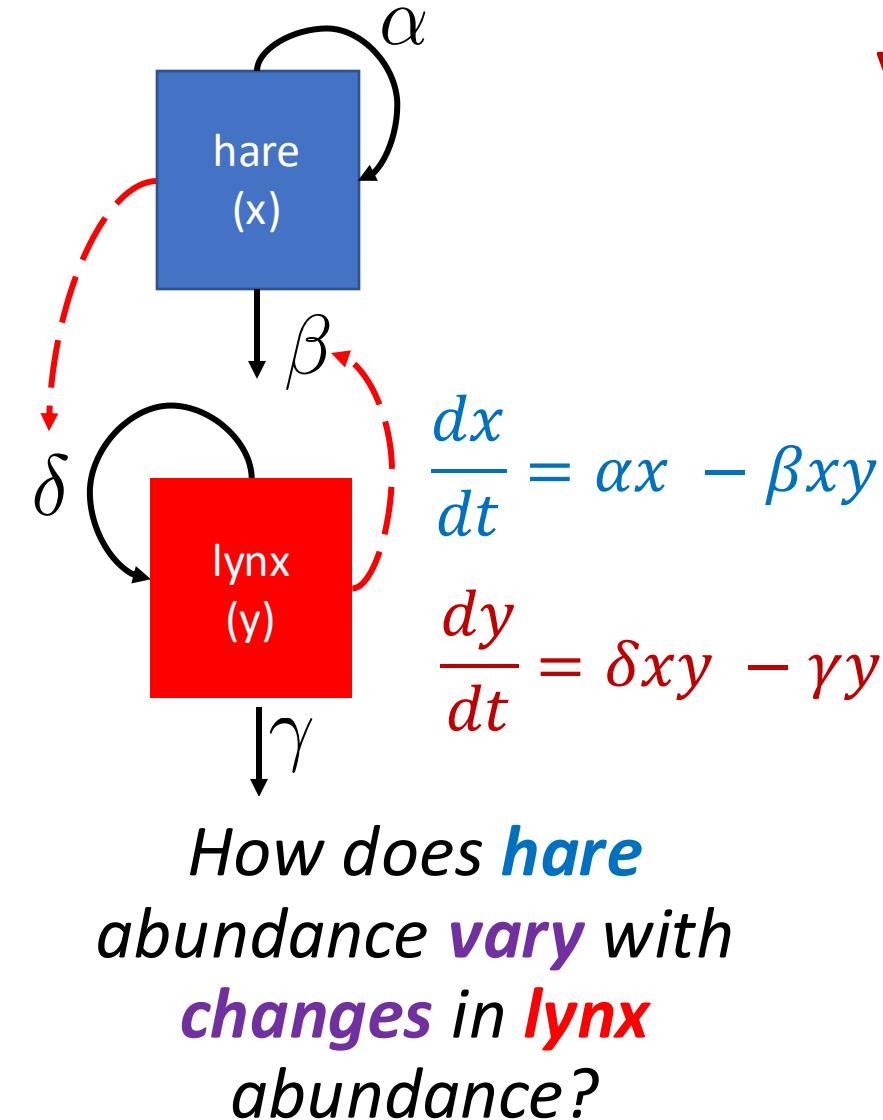
Lotka-Volterra predator-prey isoclines



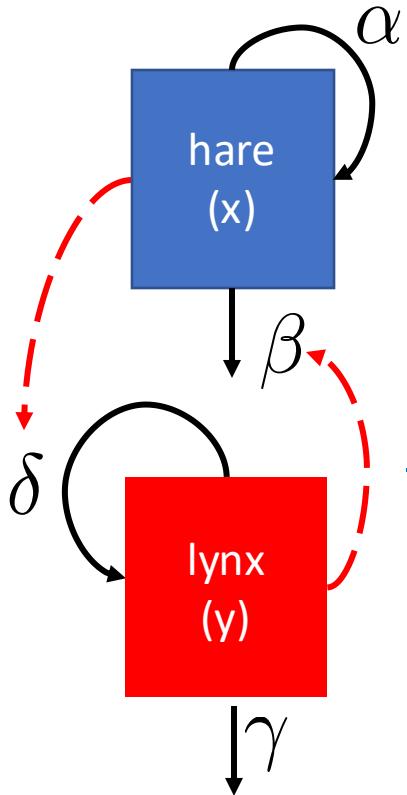
How does **hare** abundance **vary** with changes in **lynx** abundance?



Lotka-Volterra predator-prey isoclines



Lotka-Volterra predator-prey isoclines



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

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

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

y (predators)

$$x = \frac{\gamma}{\delta}$$

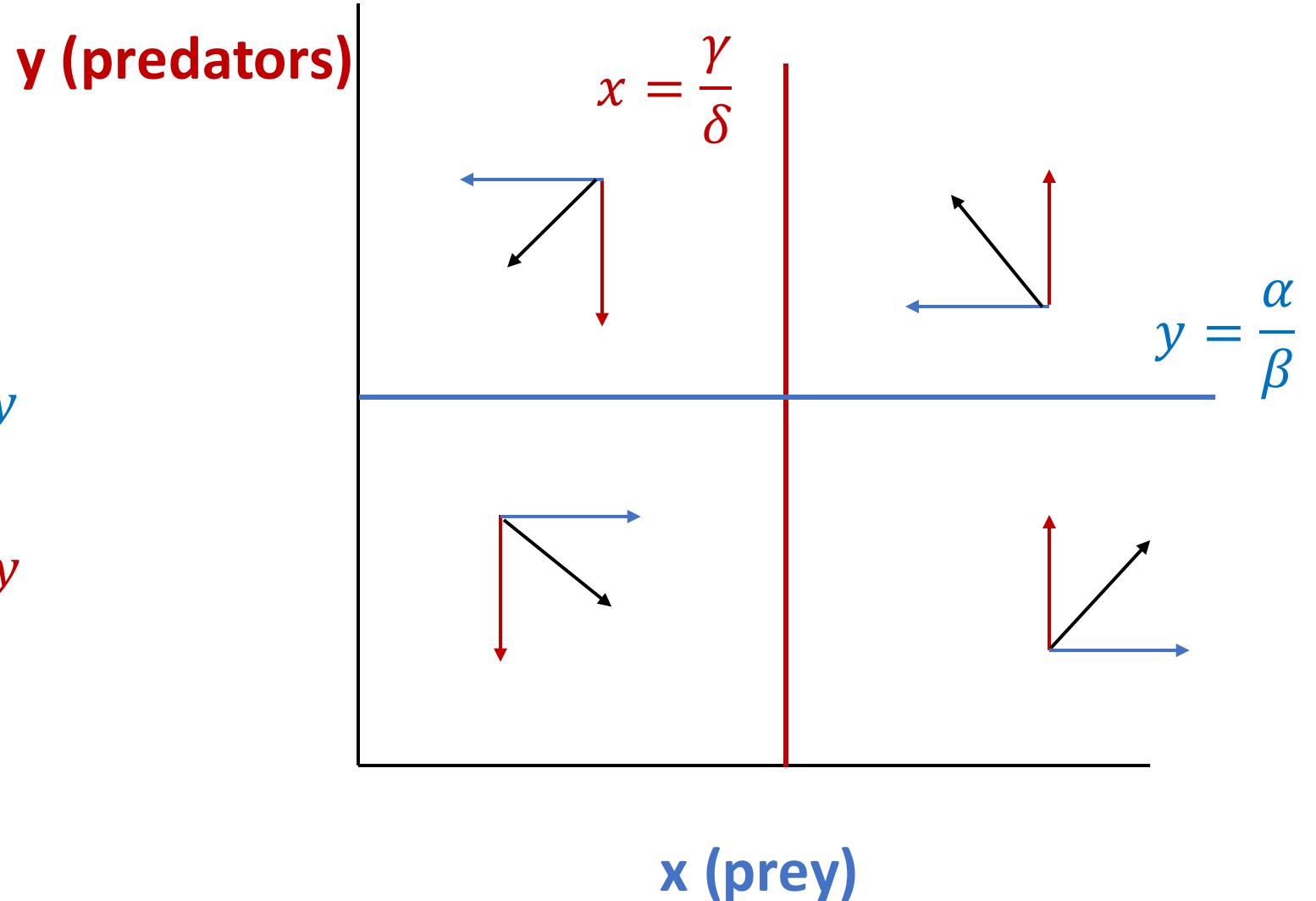
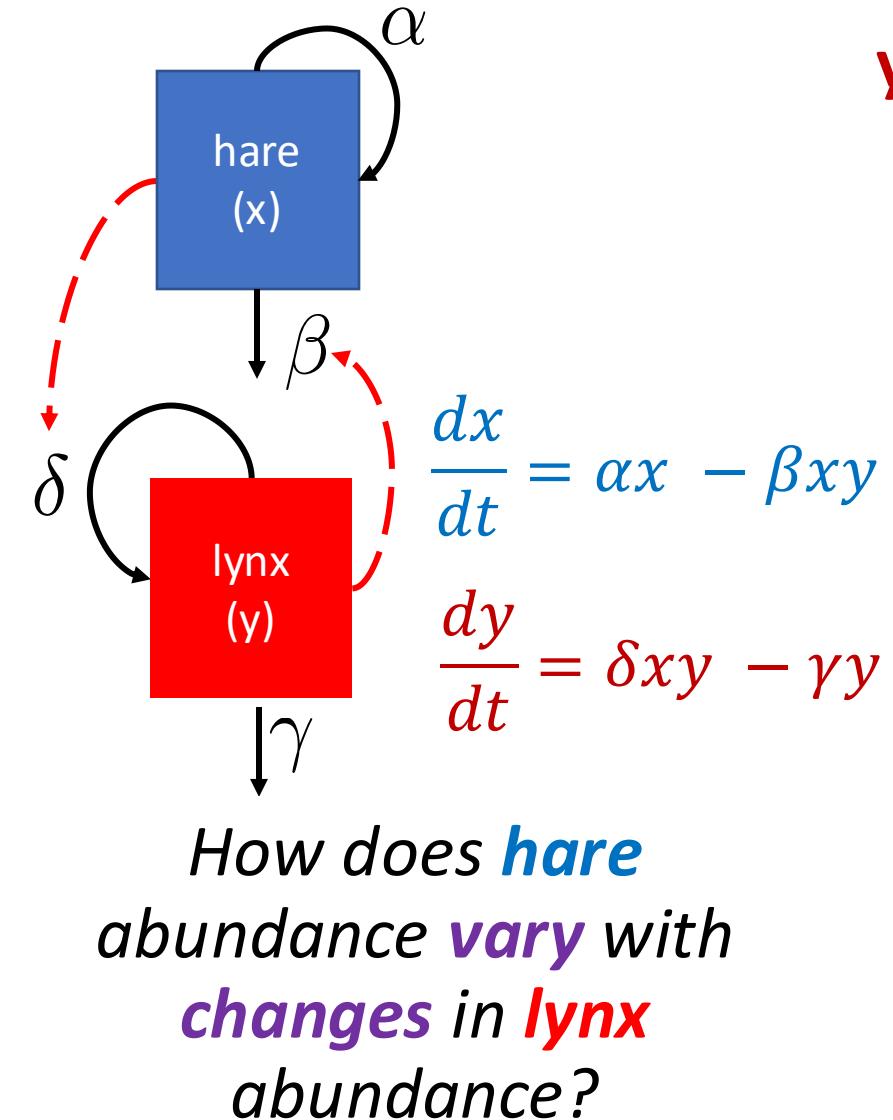
When the prey population is below this value, the predators will decrease!

x (prey)

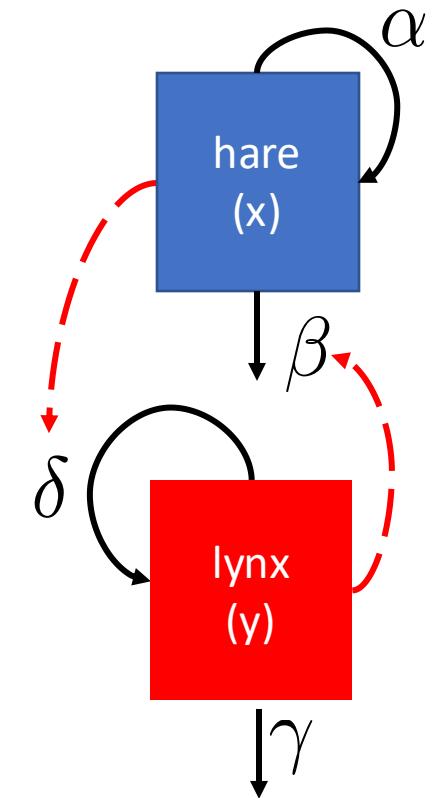
When the prey population is above this value, the predators will increase!

predator isoclines

Lotka-Volterra predator-prey isoclines



Lotka-Volterra predator-prey **isoclines**

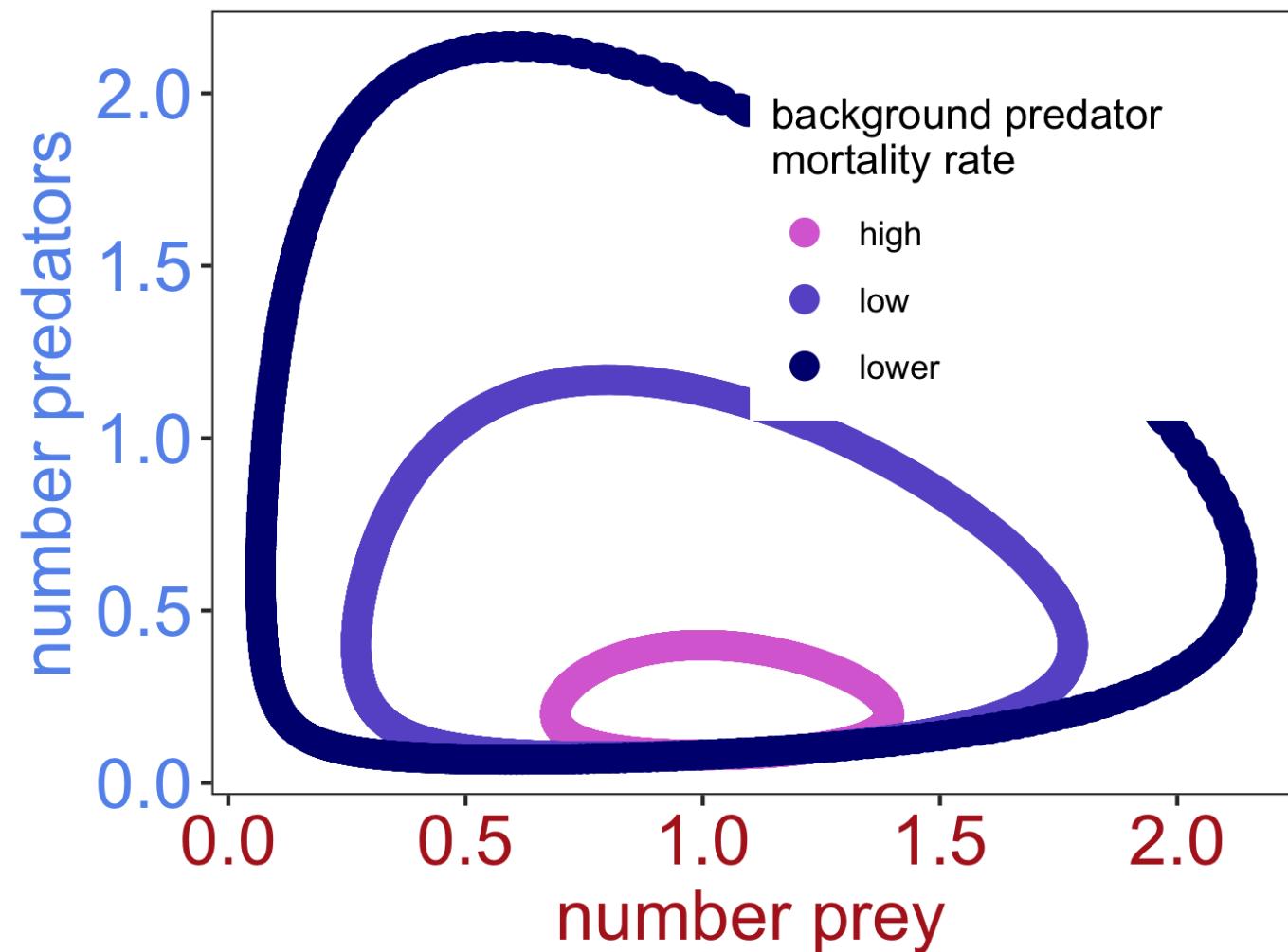


How does **hare** abundance **vary** with changes in **lynx** abundance?

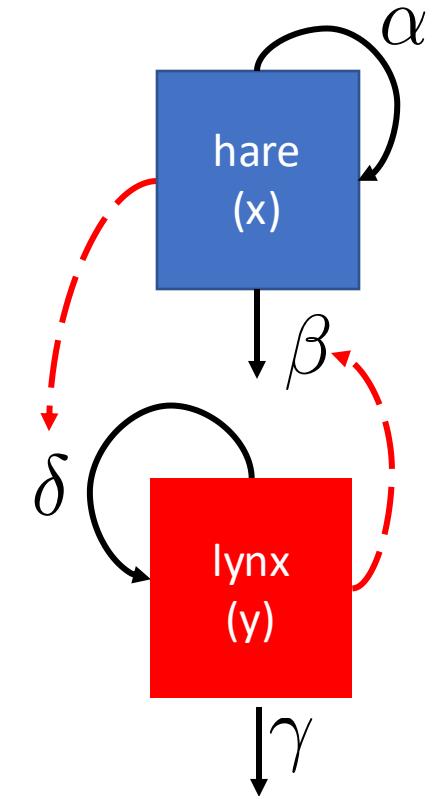
$$\frac{dx}{dt} = \alpha x - \beta xy$$

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

Predator-prey cycles can be visualized as oscillations.



Lotka-Volterra predator-prey **isoclines**

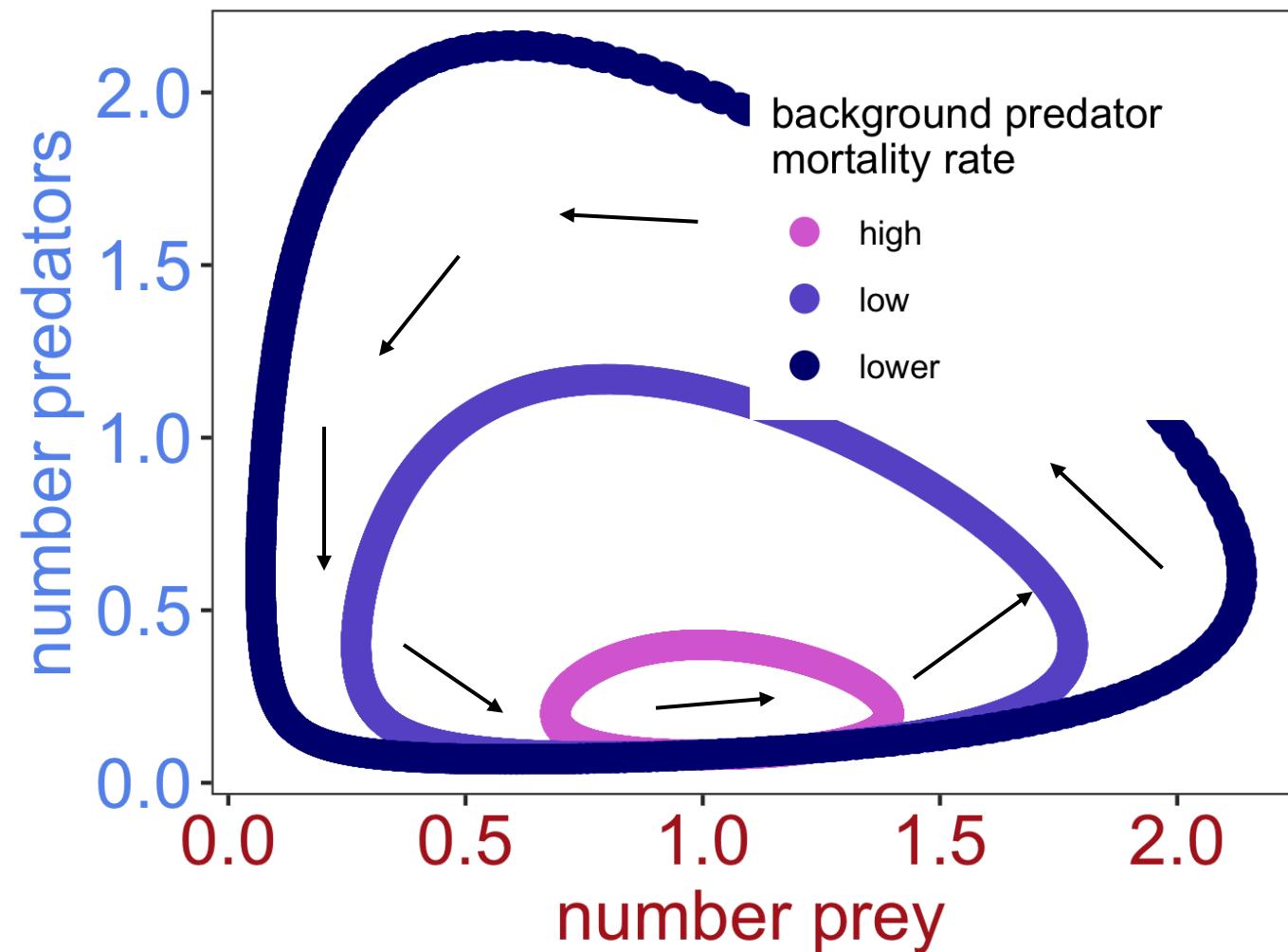


How does **hare** abundance **vary** with changes in **lynx** abundance?

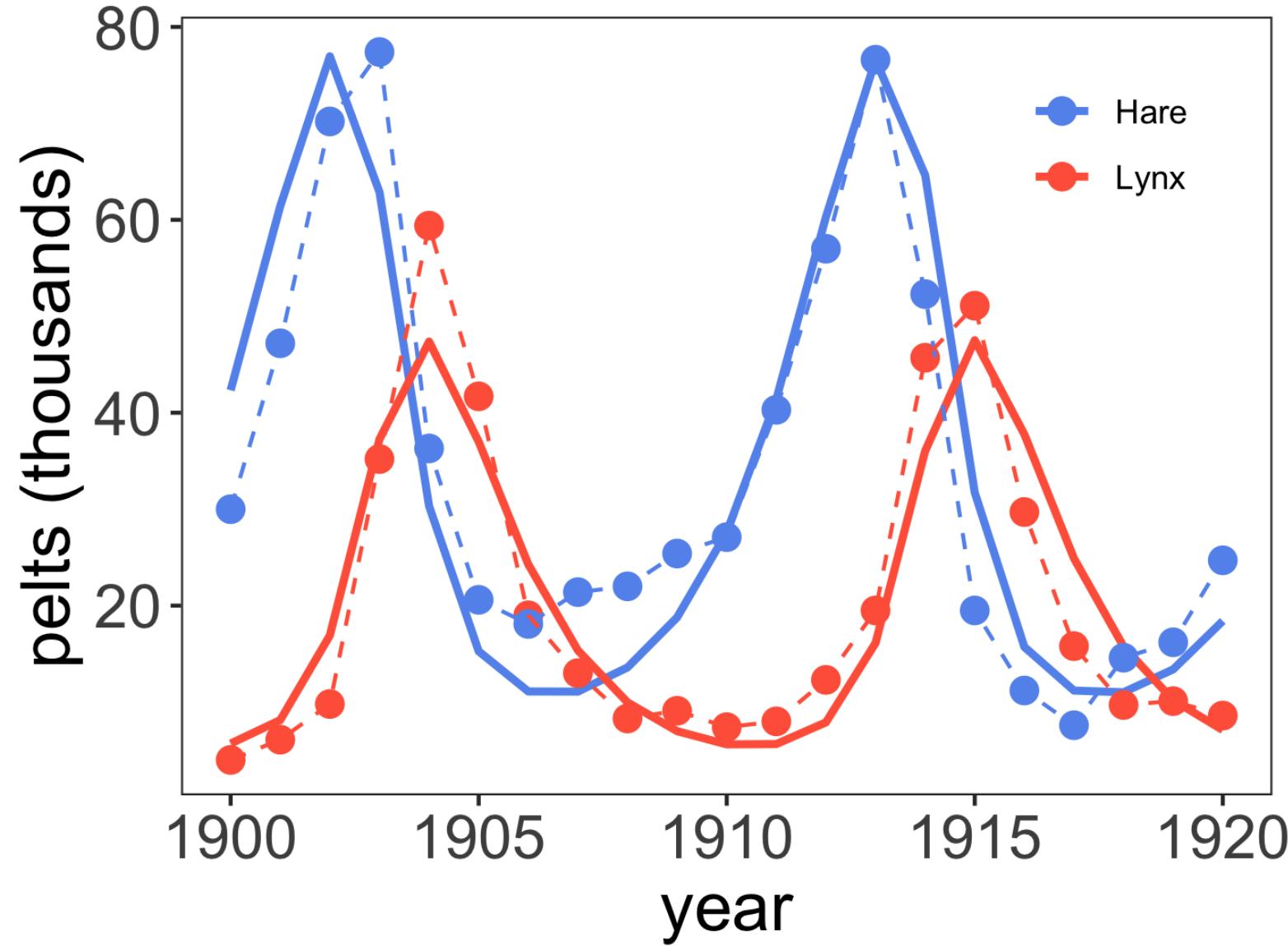
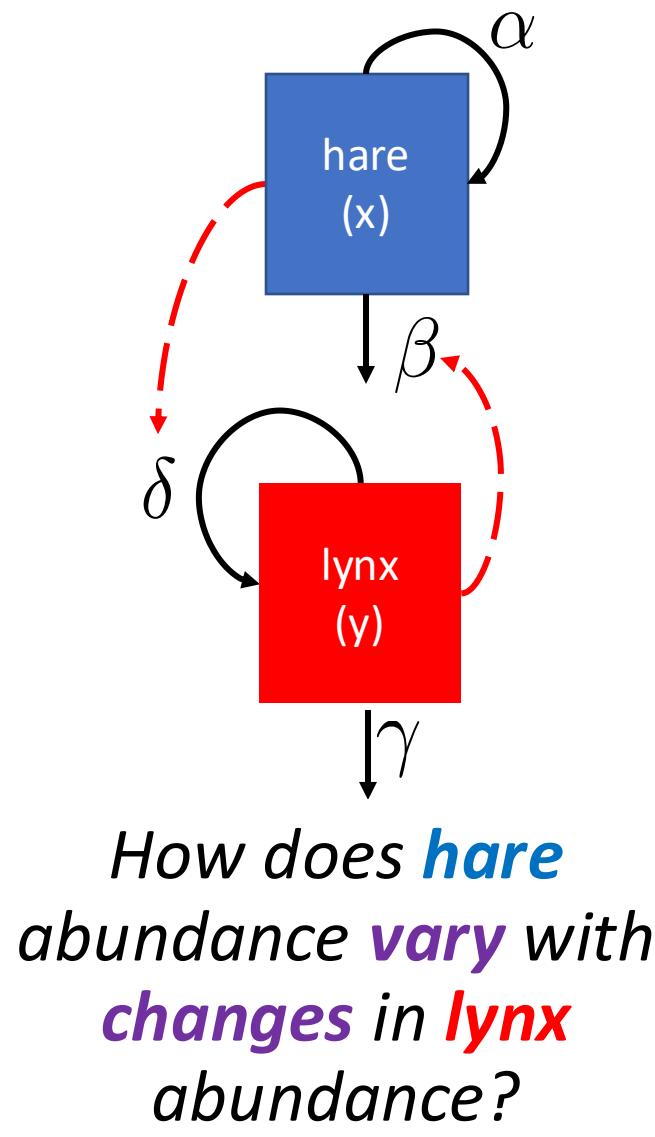
$$\frac{dx}{dt} = \alpha x - \beta xy$$

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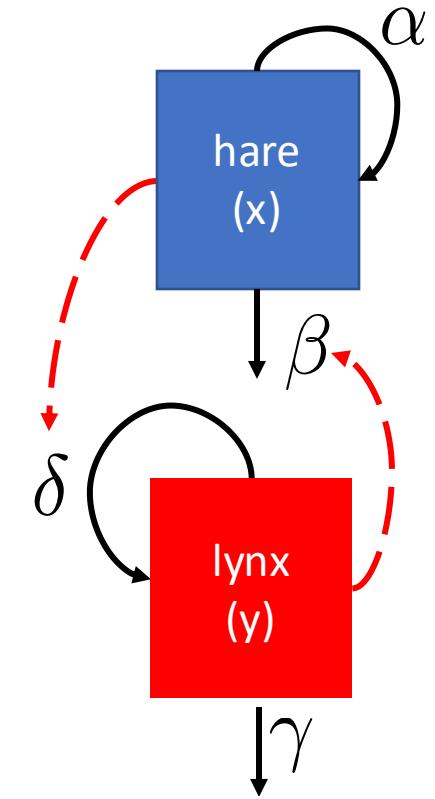
Predator-prey cycles can be visualized as oscillations.



These oscillations are just another way of visualizing the time series!

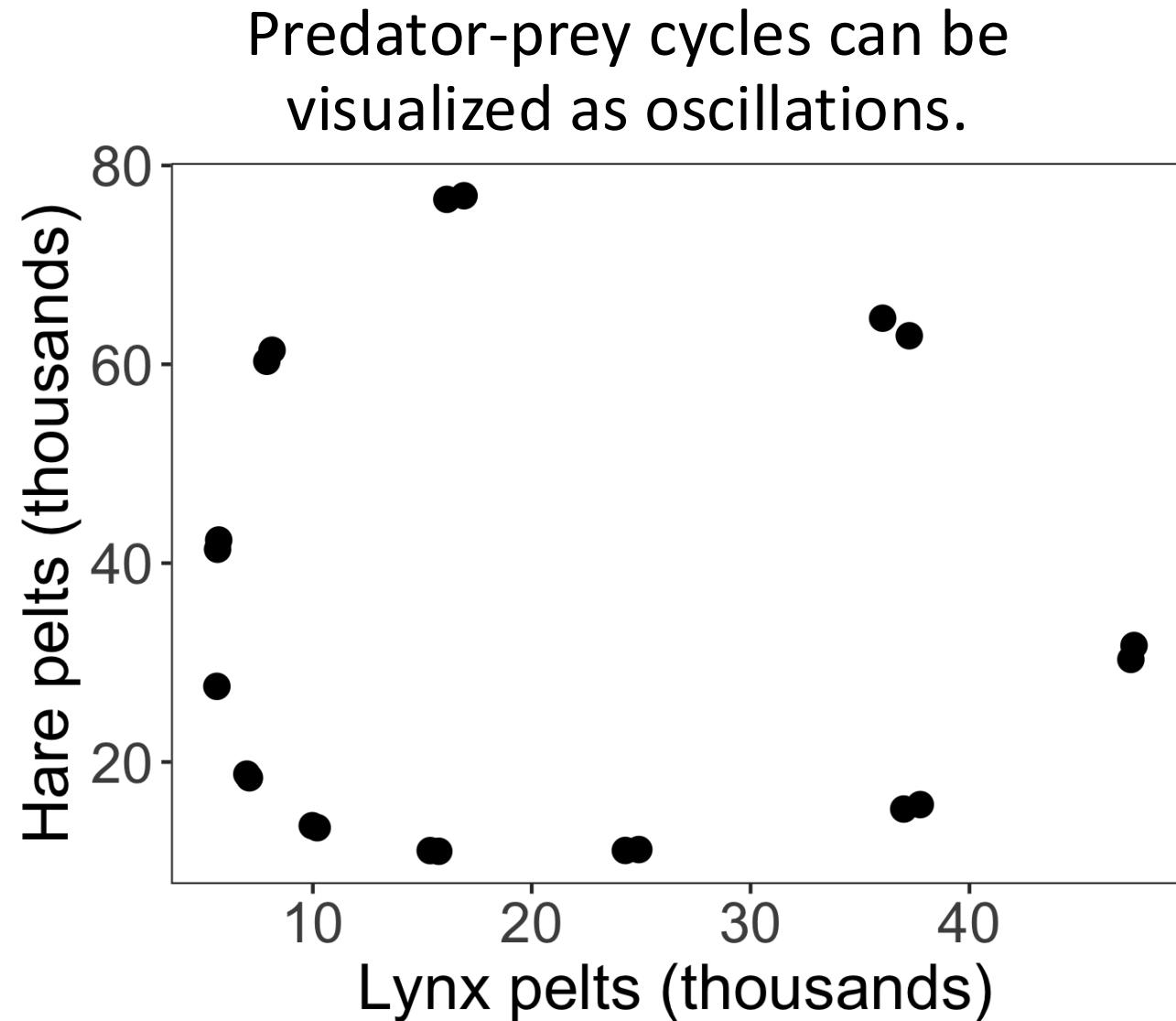


Lotka-Volterra predator-prey **isoclines** with data

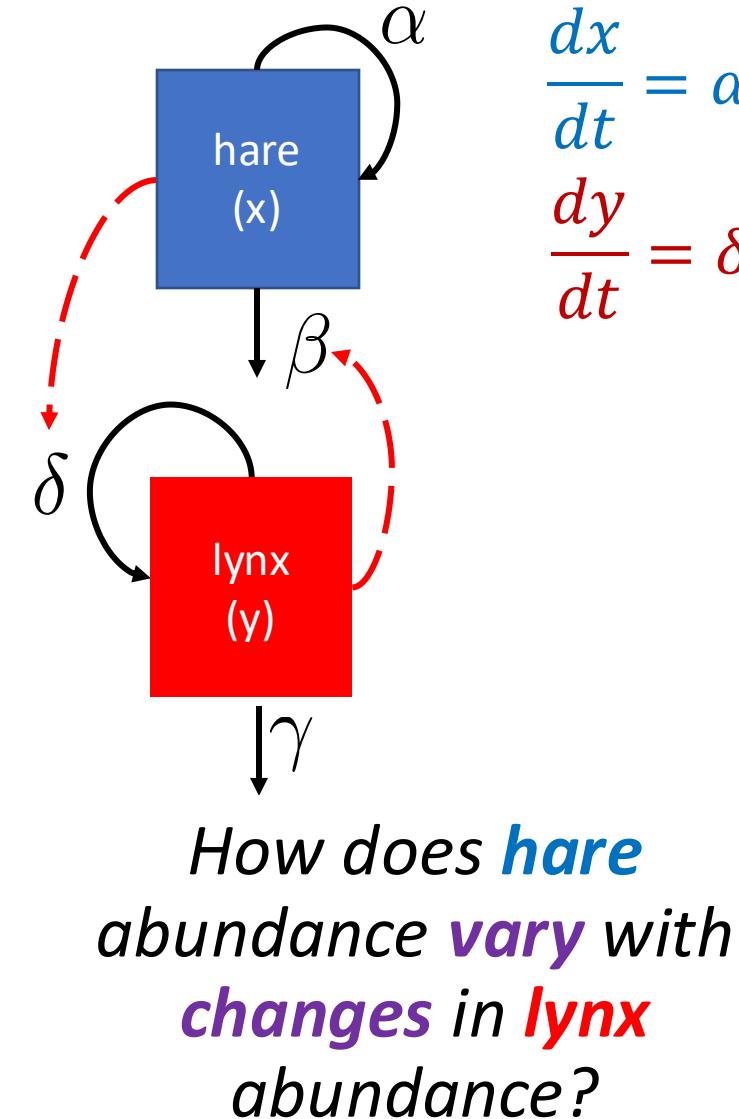


How does **hare** abundance **vary** with changes in **lynx** abundance?

$$\frac{dx}{dt} = \alpha x - \beta xy$$
$$\frac{dy}{dt} = \delta xy - \gamma y$$



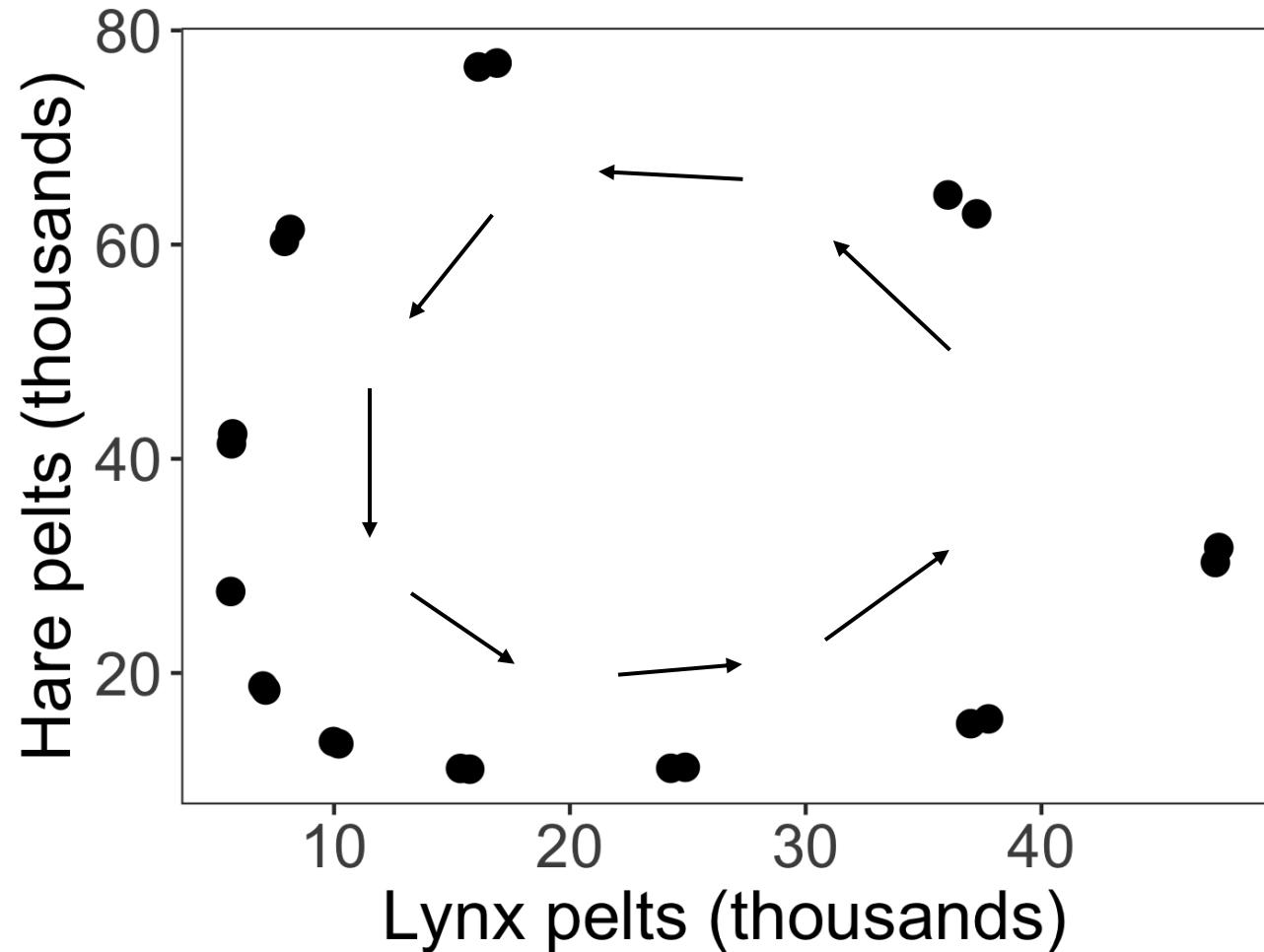
Lotka-Volterra predator-prey **isoclines** with data



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

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

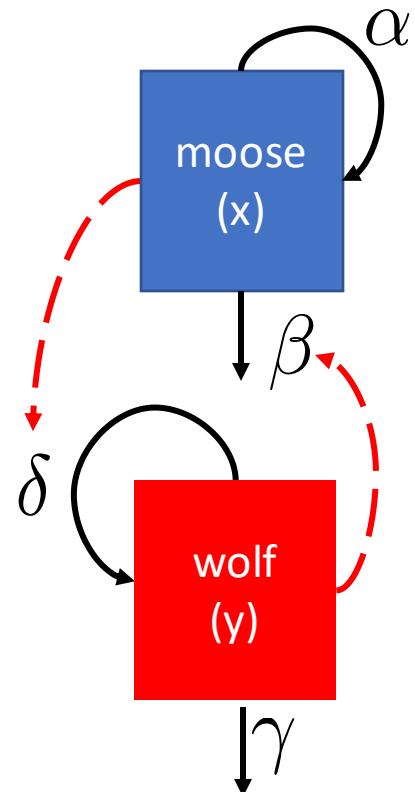
Predator-prey cycles can be visualized as oscillations.



Another famous example: Wolf-Moose on Isle Royale

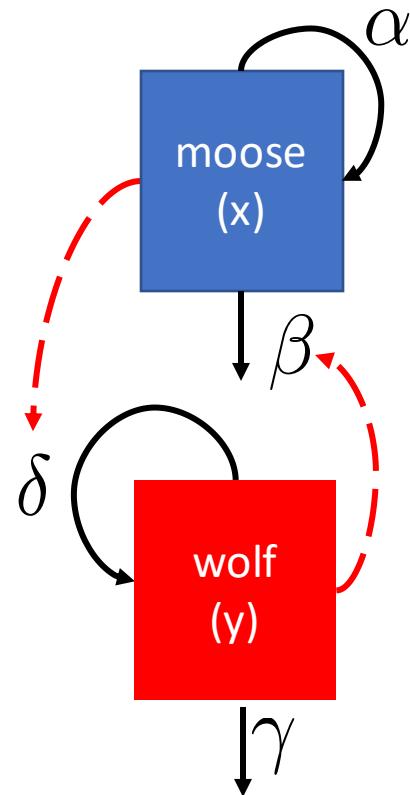


isleroyalewolf.org

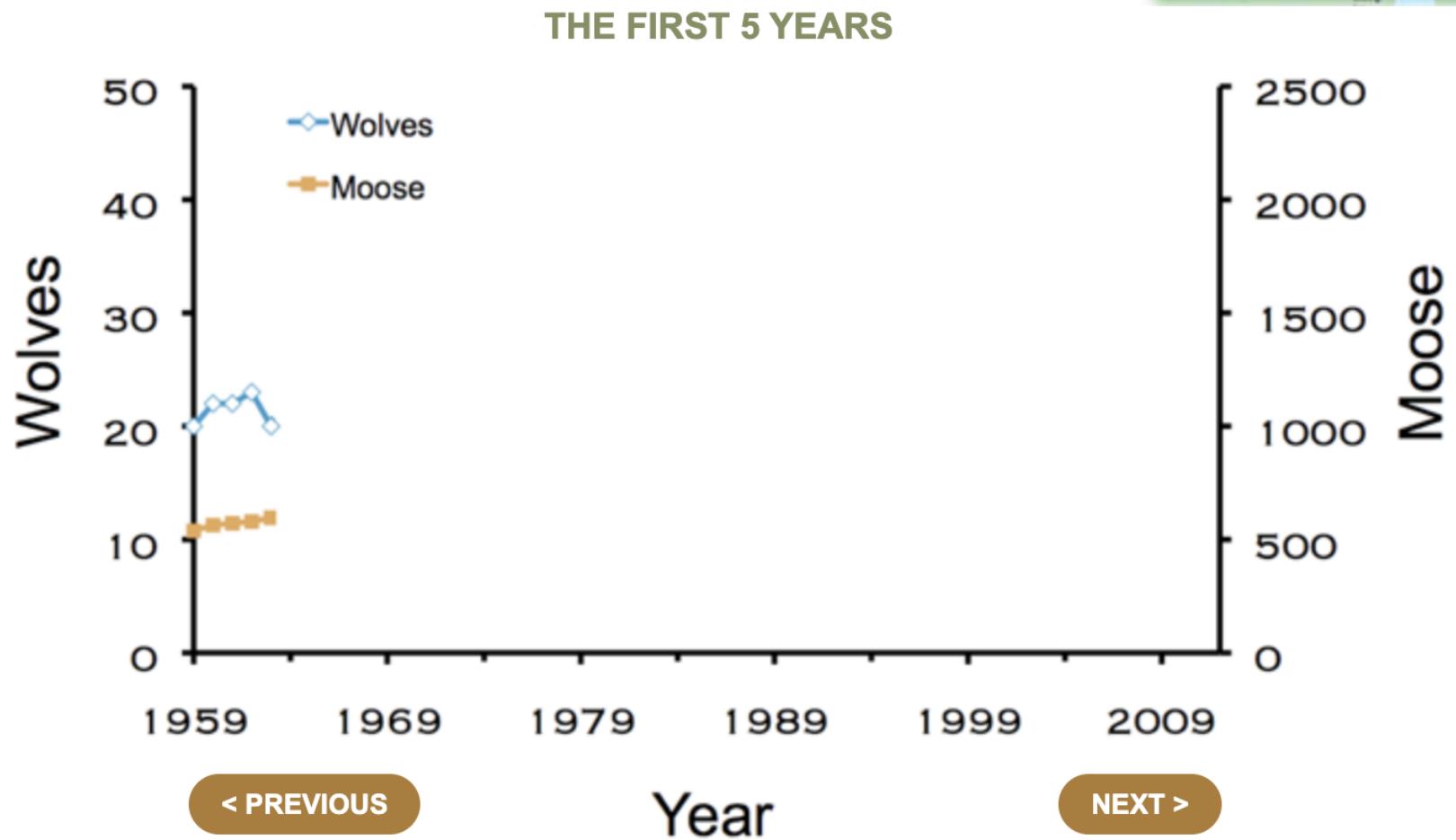


*How does **moose** abundance **vary** with changes in **wolf** abundance?*

Another famous example: Wolf-Moose on Isle Royale

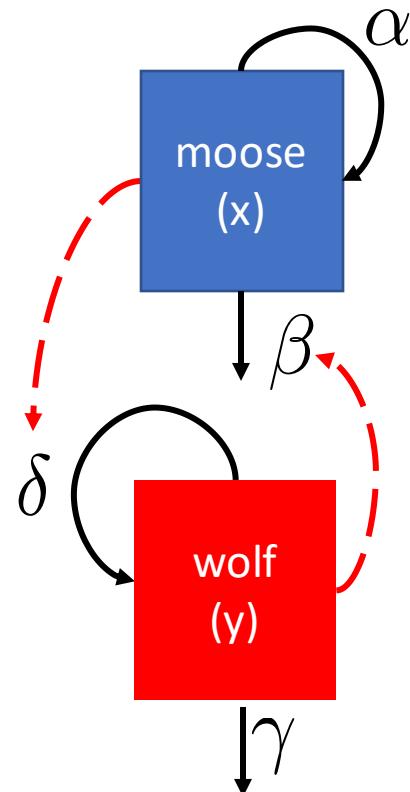


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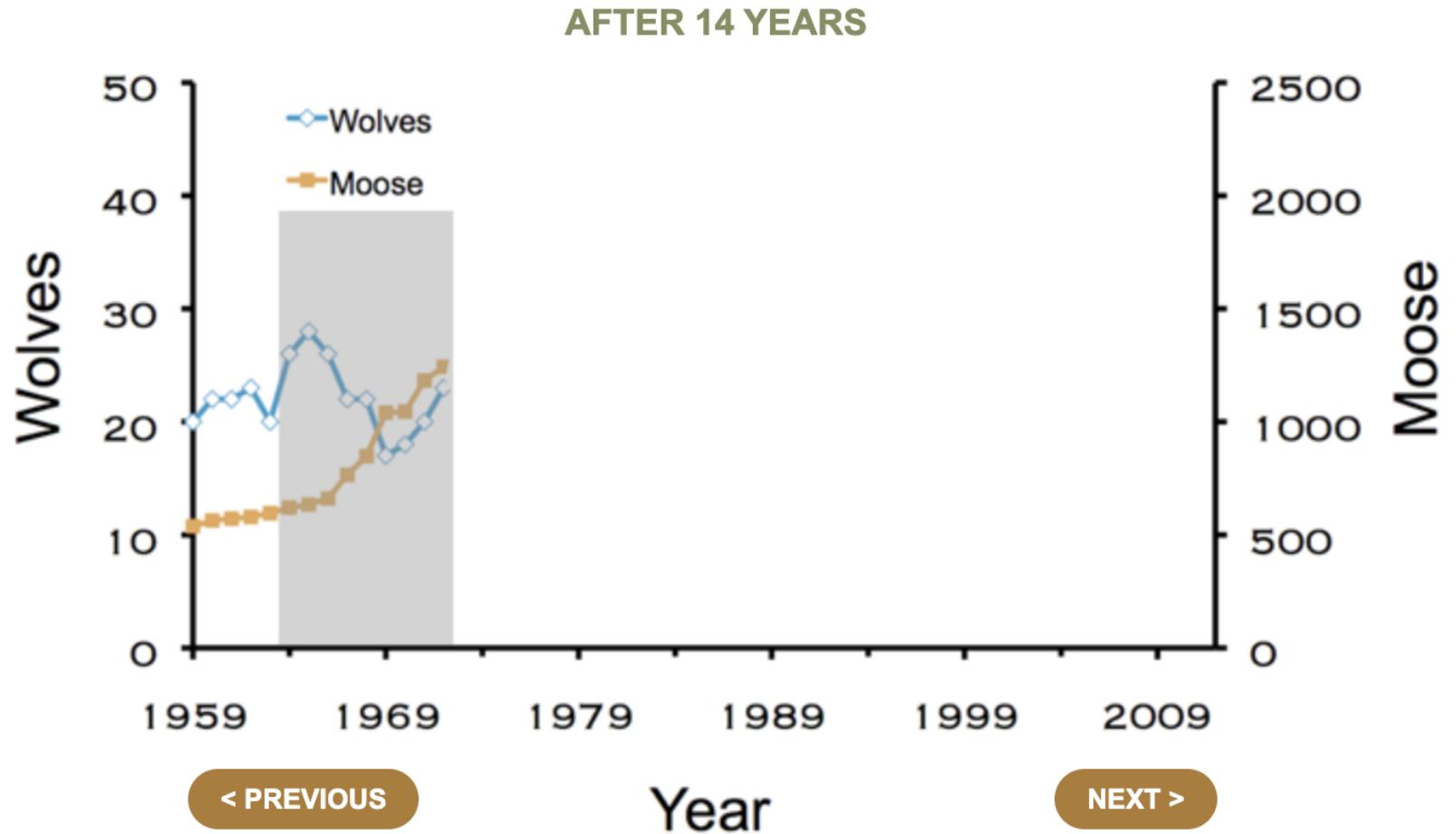


After observing relatively constant abundances for five years, it seemed that the wolves and moose of Isle Royale had struck some kind of a balance of nature.

Another famous example: Wolf-Moose on Isle Royale

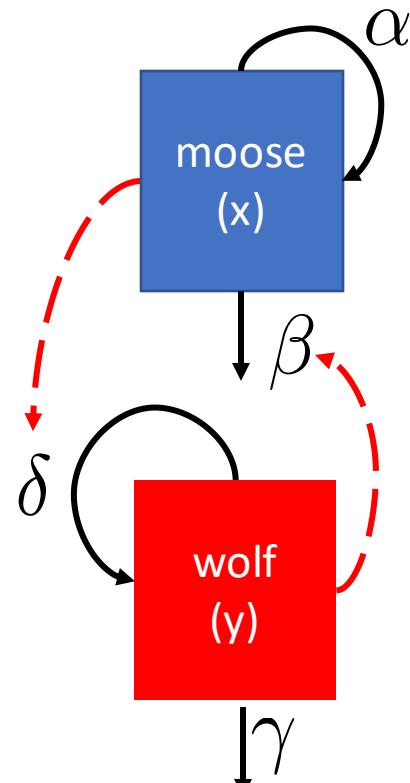


How does **moose** abundance **vary** with changes in **wolf** abundance?

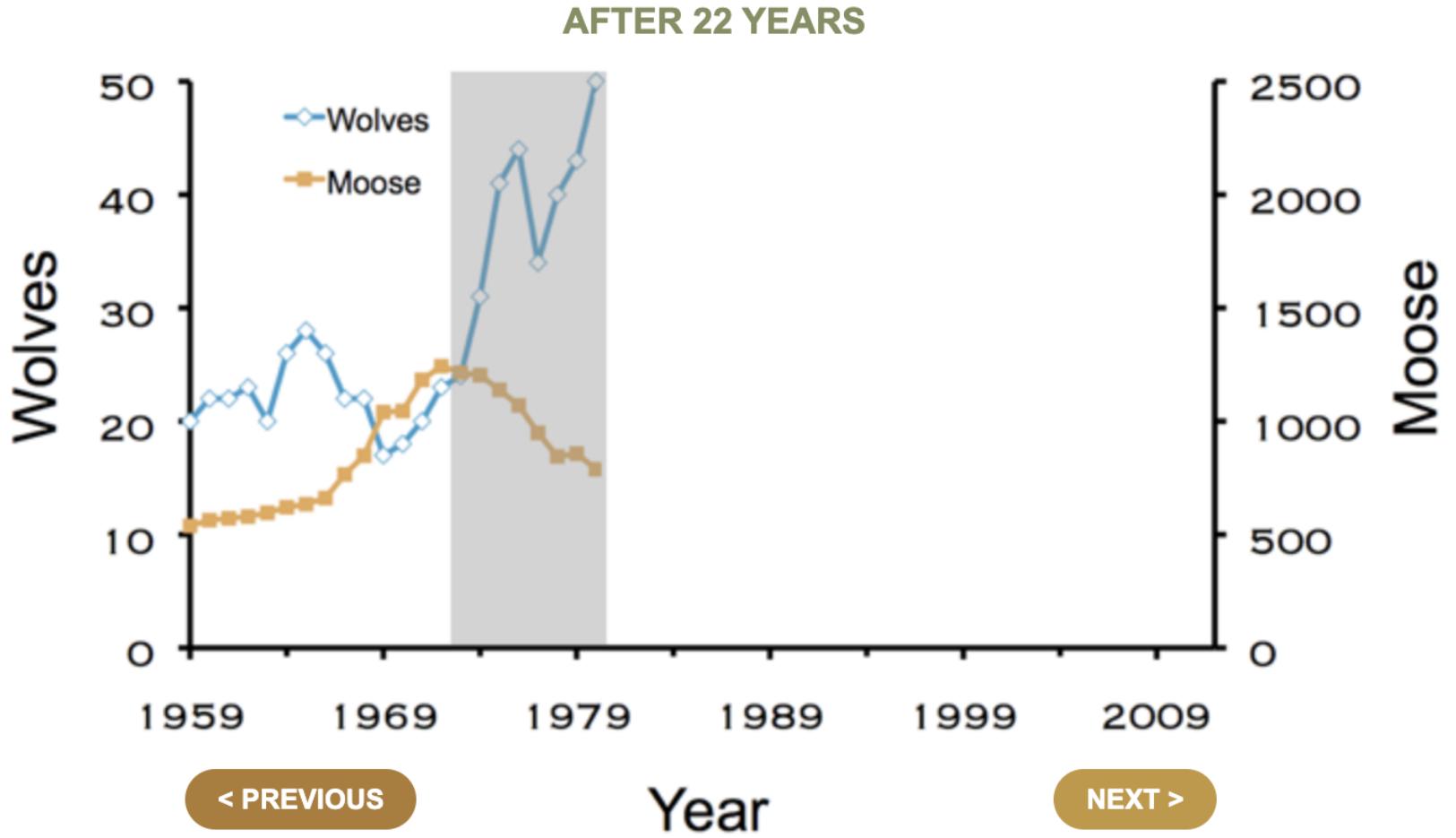


Over time wolf abundance fluctuated a bit. But, after a series of mild winters moose abundance doubled. There'd been a major shift in the balance.

Another famous example: Wolf-Moose on Isle Royale

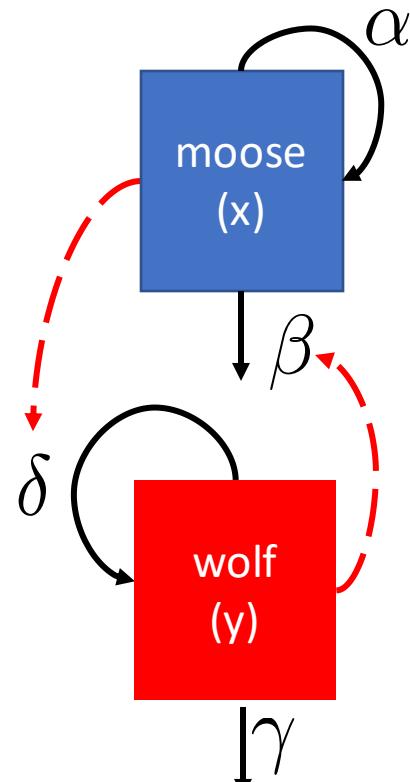


How does **moose** abundance **vary** with changes in **wolf** abundance?

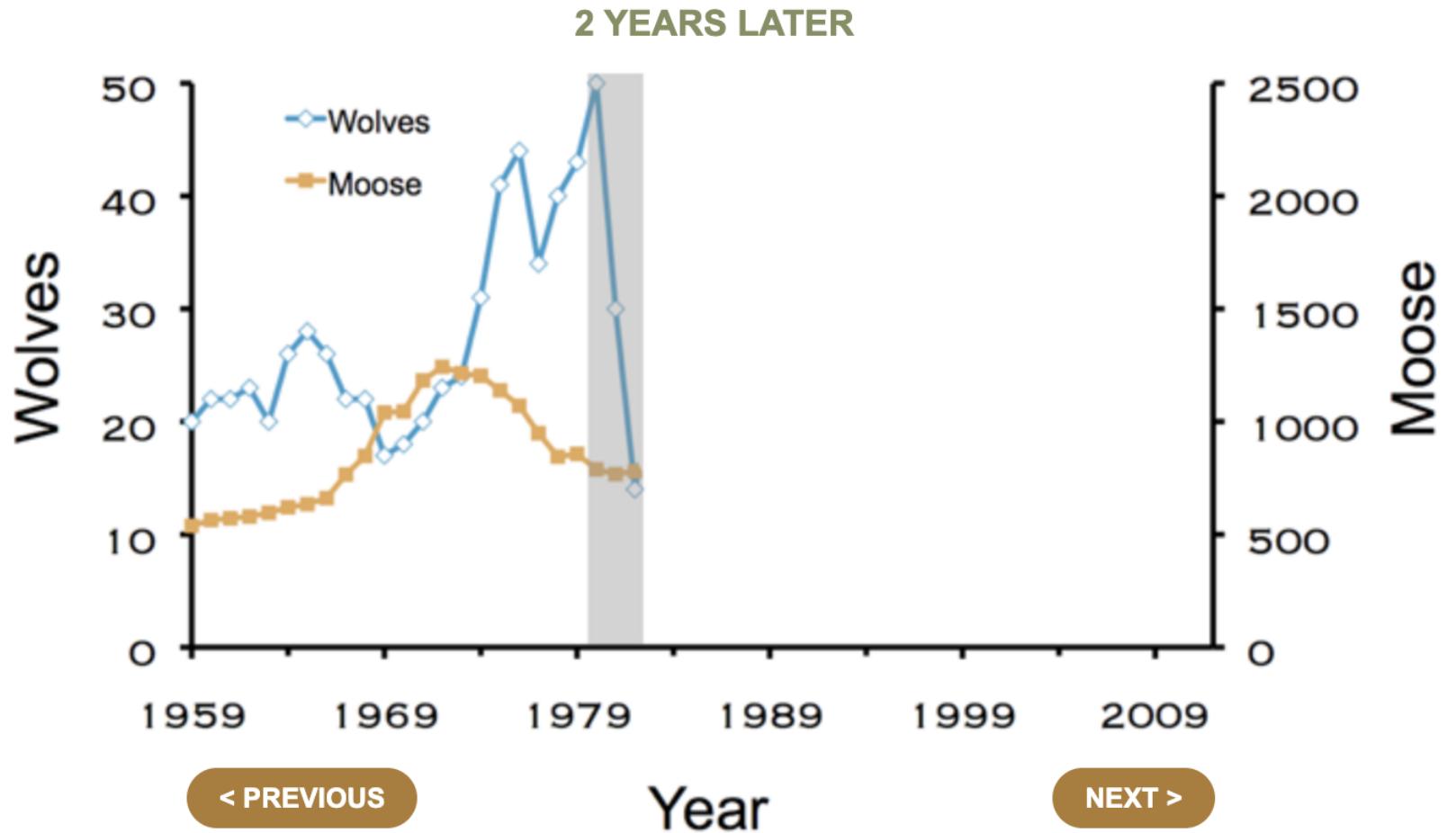


Then a series of severe winters, increased wolf predation, and moose abundance was cut in half. Wolves soared to 50 individuals.

Another famous example: Wolf-Moose on Isle Royale

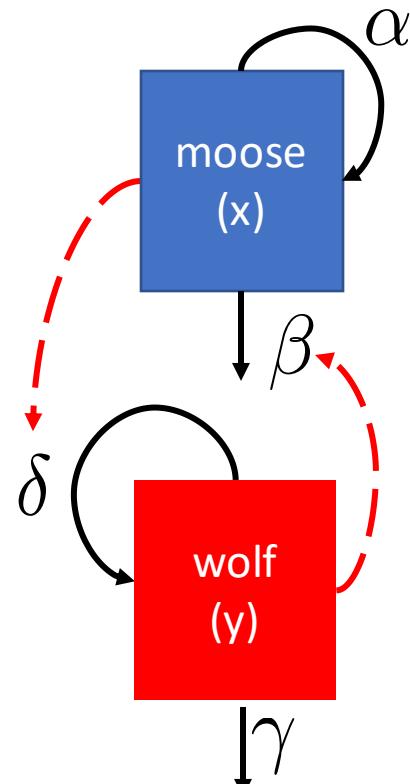


How does **moose** abundance **vary** with changes in **wolf** abundance?

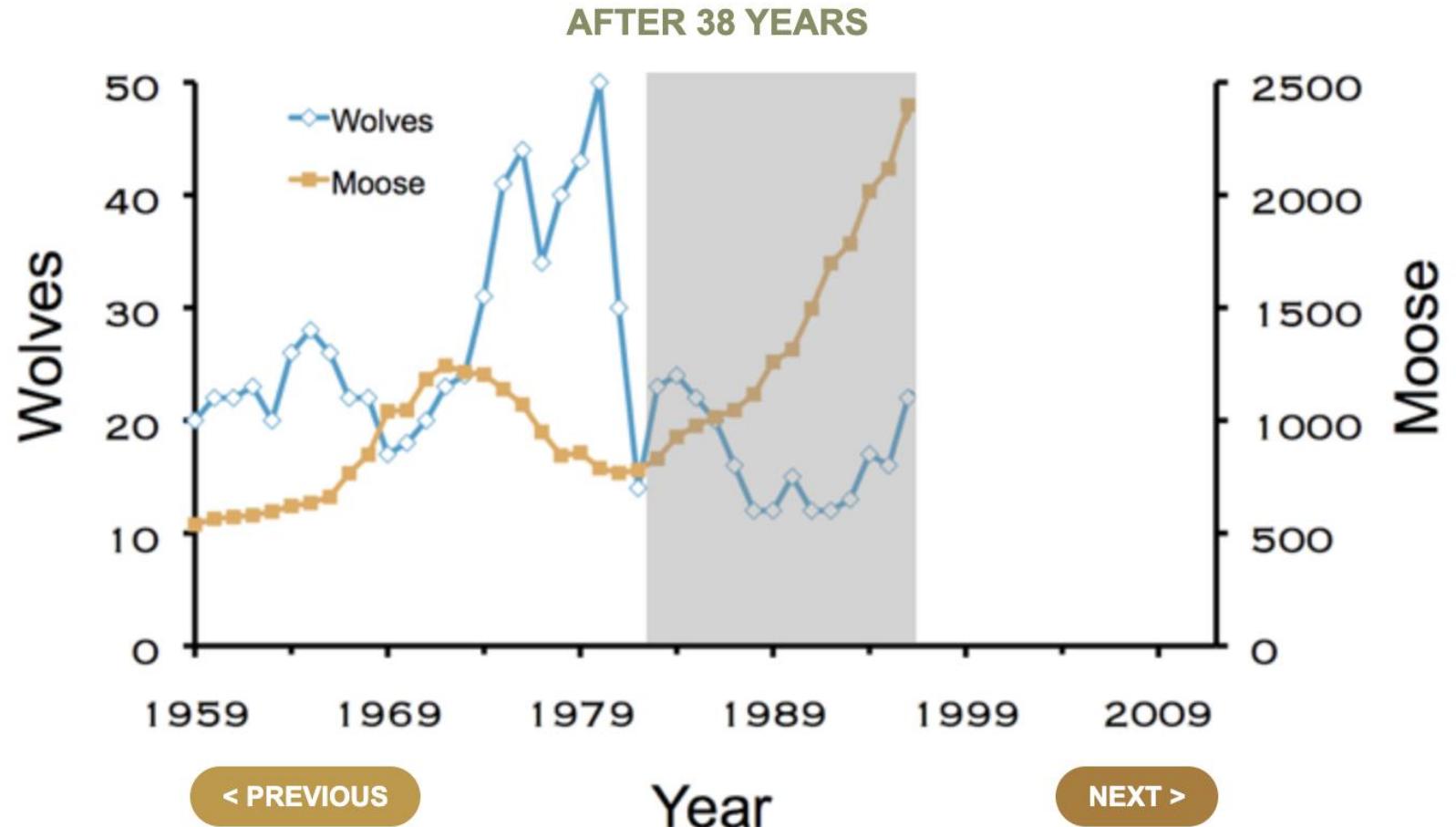


Humans inadvertently introduce canine parvovirus, a wolf disease. The wolf population crashes.

Another famous example: Wolf-Moose on Isle Royale



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



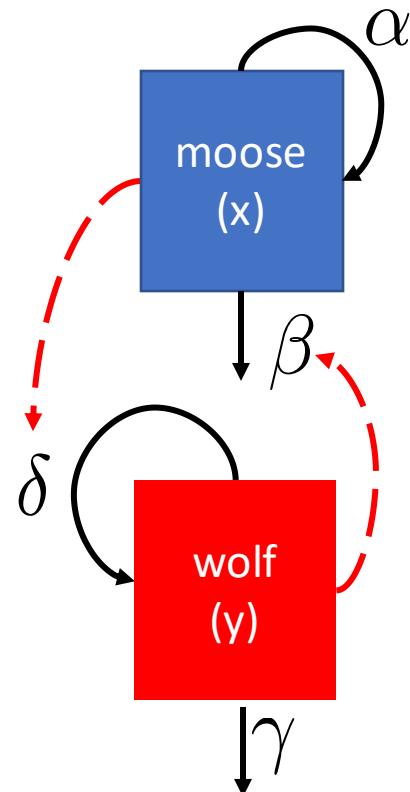
< PREVIOUS

Year

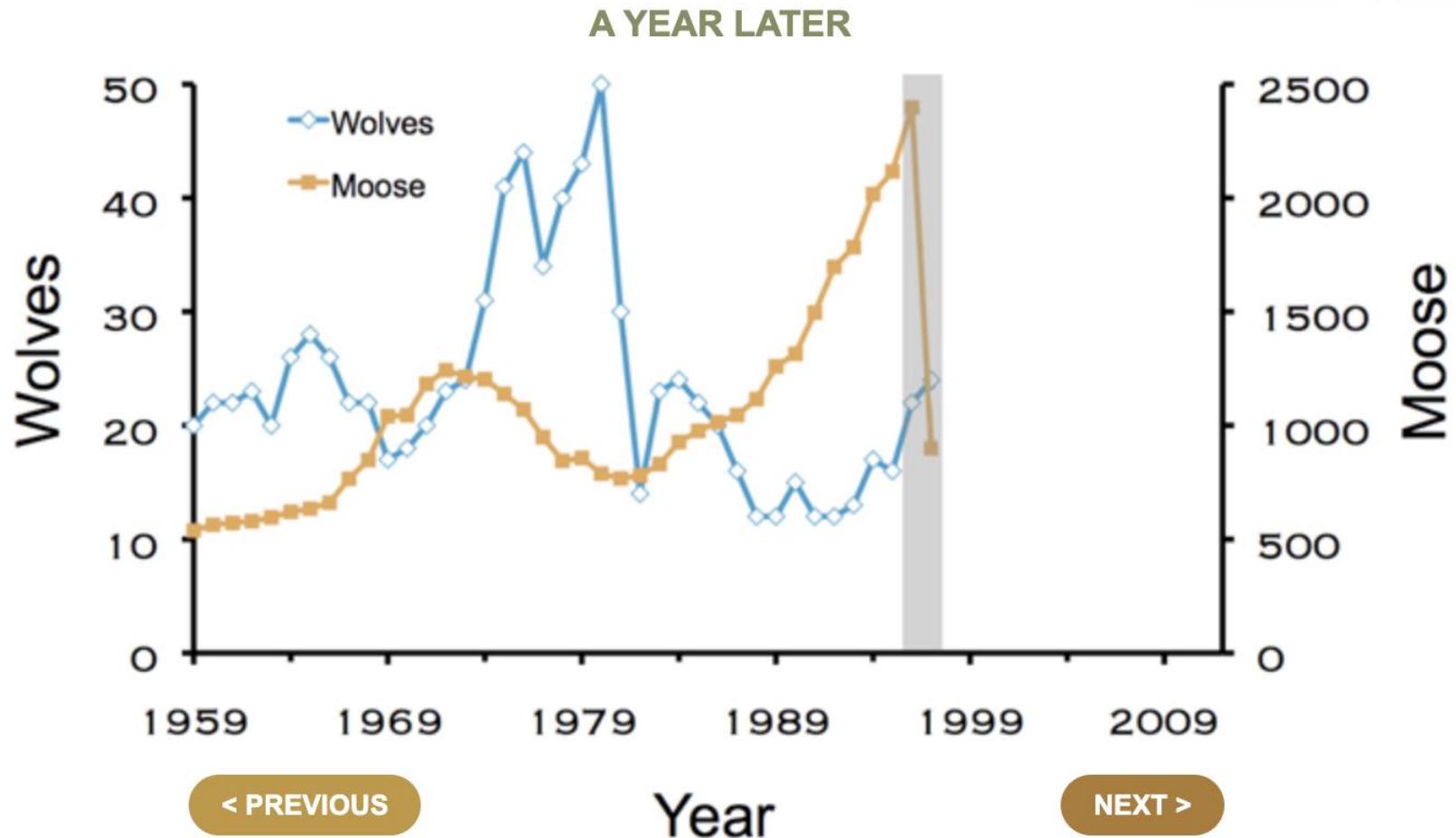
NEXT >

With a reprieve from wolf predation, the moose population explodes. We begin to think, but cannot yet prove, that inbreeding among wolves explains why they languish in low abundance for over a decade.

Another famous example: Wolf-Moose on Isle Royale

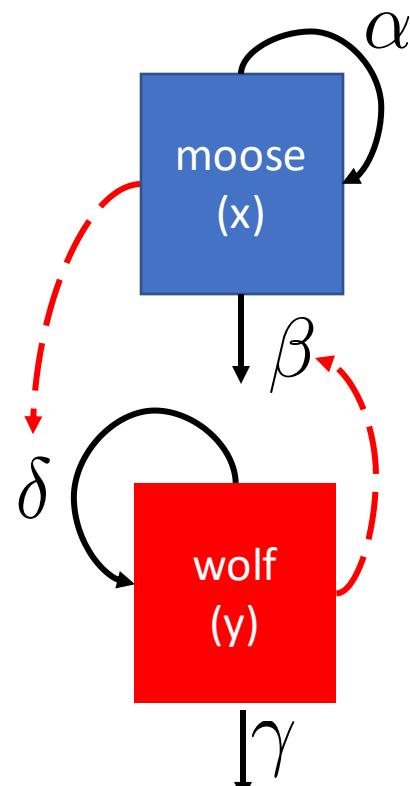


How does **moose** abundance **vary** with changes in **wolf** abundance?

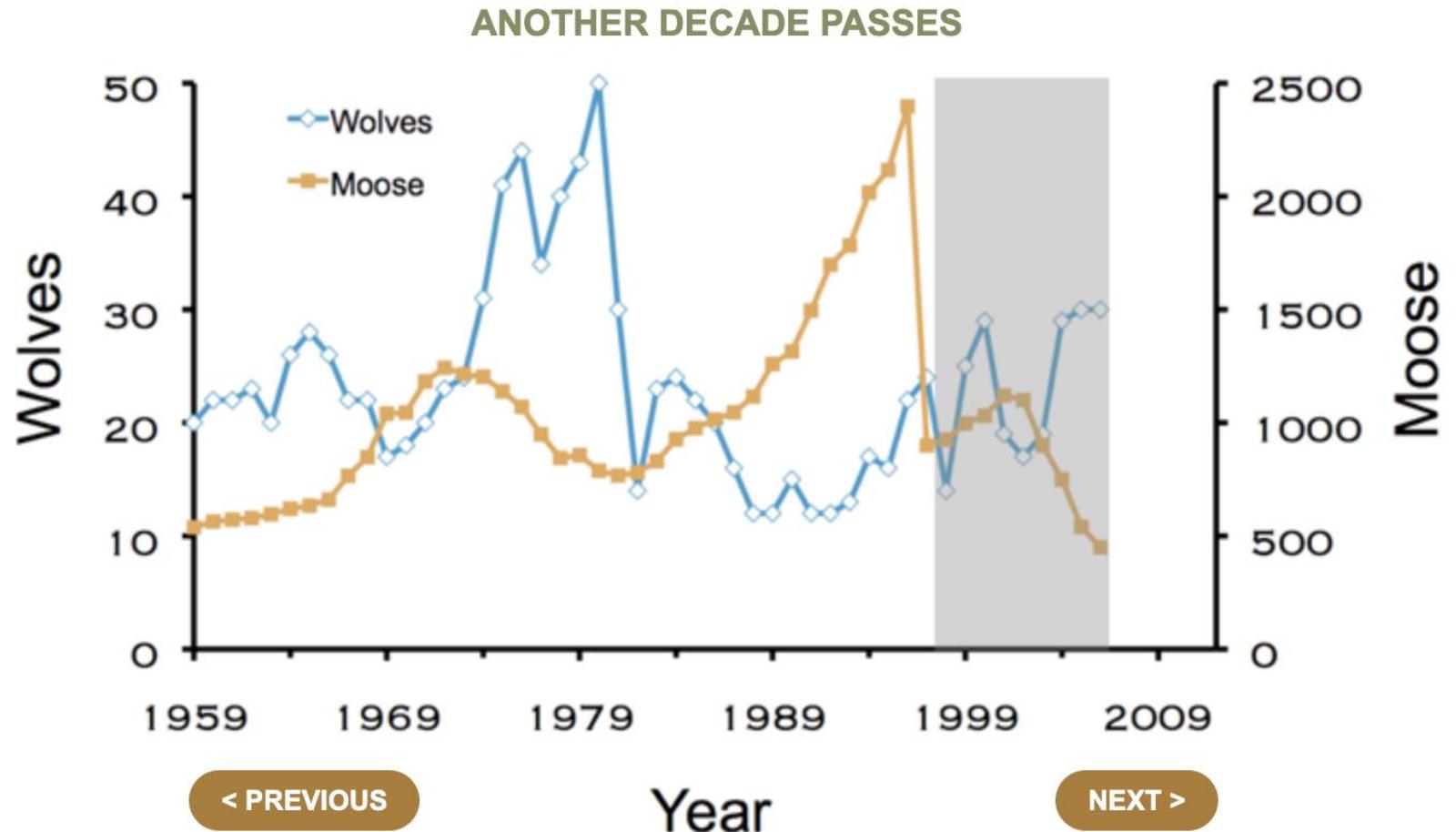


Intense competition for a declining forage, an outbreak of winter ticks, and the severe winter. They all conspired against the moose population which collapsed in 1996.

Another famous example: Wolf-Moose on Isle Royale

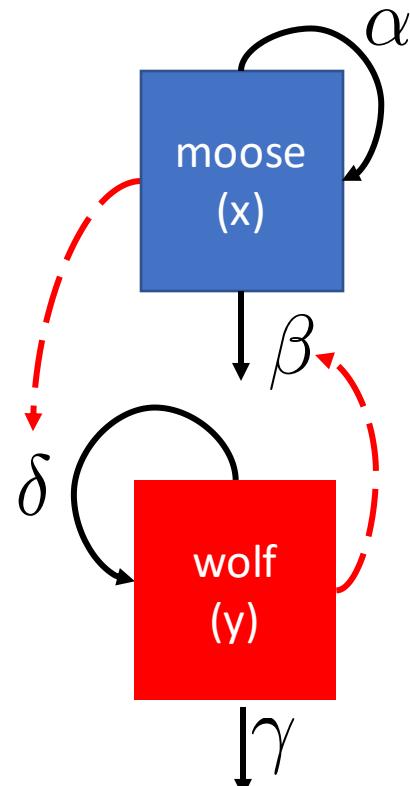


*How does moose abundance **vary** with changes in wolf abundance?*

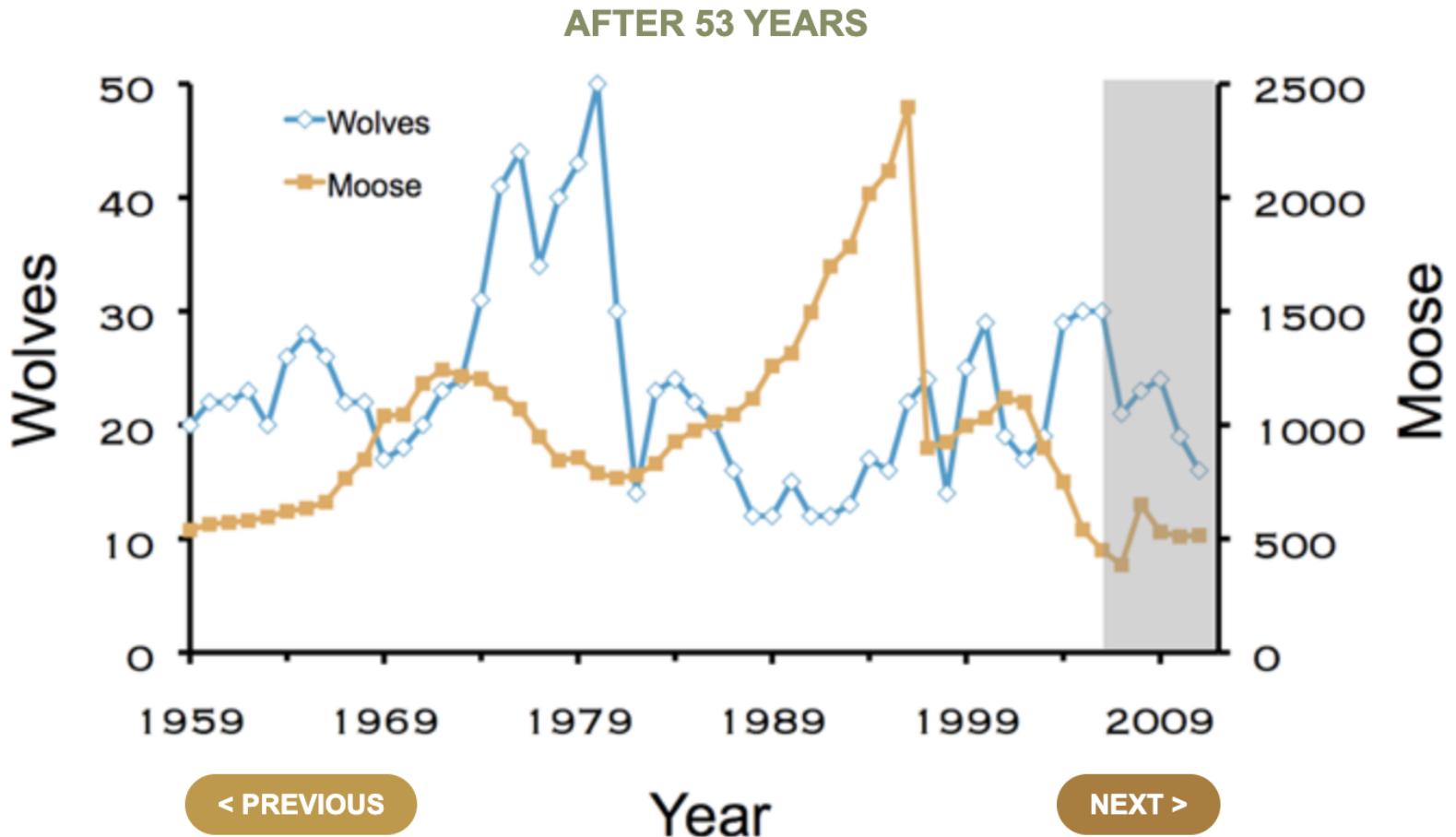


Moose continue to dwindle. In 1997, a wolf immigrates from Canada, bringing an infusion of new genes. The wolves increase erratically.

Another famous example: Wolf-Moose on Isle Royale



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



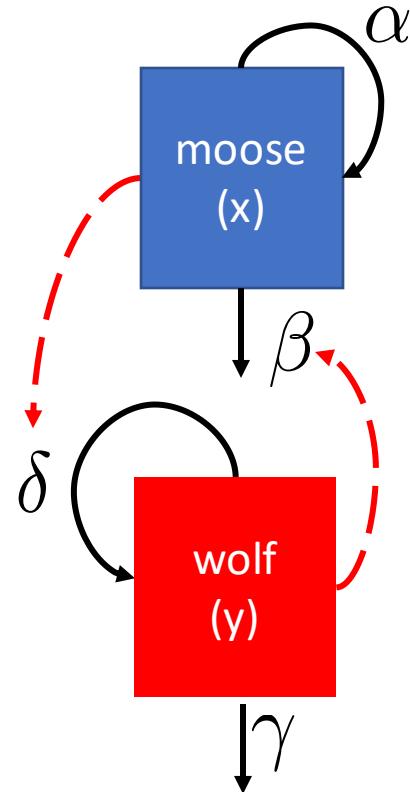
< PREVIOUS

Year

NEXT >

The wolf population eventually stumbles as the moose continue to be kept low by high rates of predation, ticks, and hot summers.

Another famous example: Wolf-Moose on Isle Royale



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

Field Work Opportunity for College Students



This could
be you!

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.

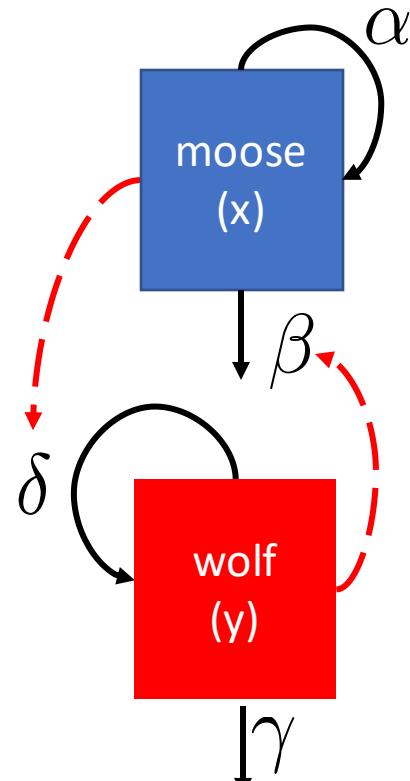


Duration: Approximately 4-5 weeks between early-May and mid-June.

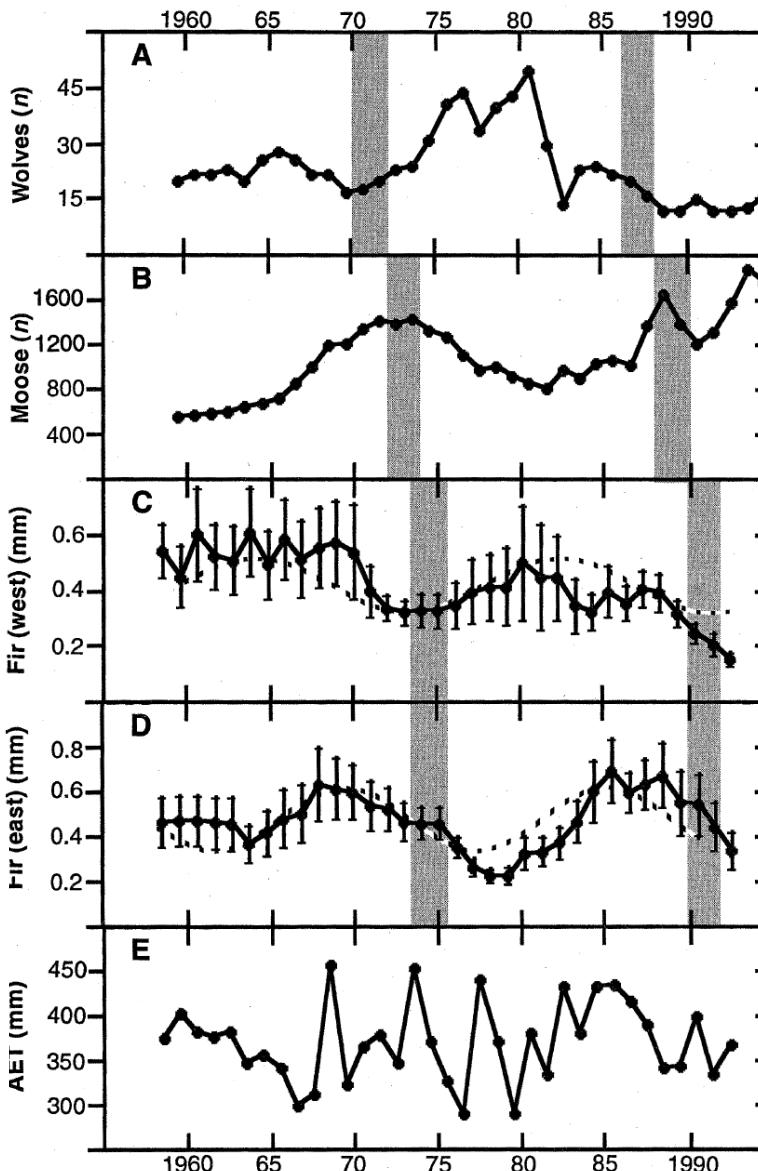
Work Environment: Work is conducted on-trail and off-trail throughout Isle Royale. This is a physically demanding position; the climate, insects (mosquitoes and black flies), and terrain are often difficult. Volunteers may be required to carry up to 60 lbs. for varying distances (up to 10 miles per day) 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.

Another famous example: Wolf-Moose on Isle Royale



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



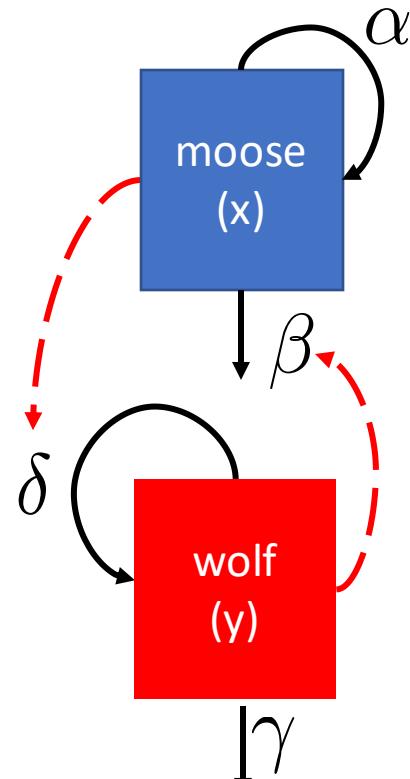
Wolf-moose dynamics on Isle Royale are **more complex than simple predator-prey**.

Wolves, Moose, and Tree Rings on Isle Royale

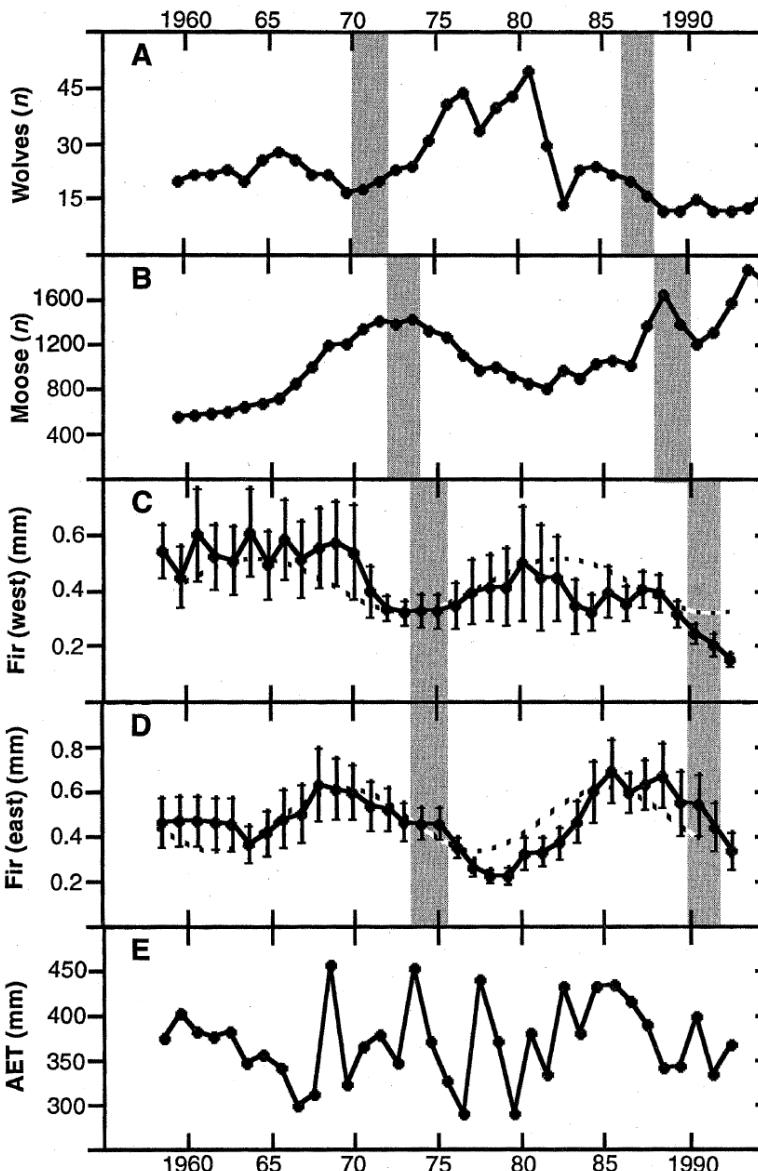
B. E. McLaren* and R. O. Peterson

SCIENCE • VOL. 266 • 2 DECEMBER 1994

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**.

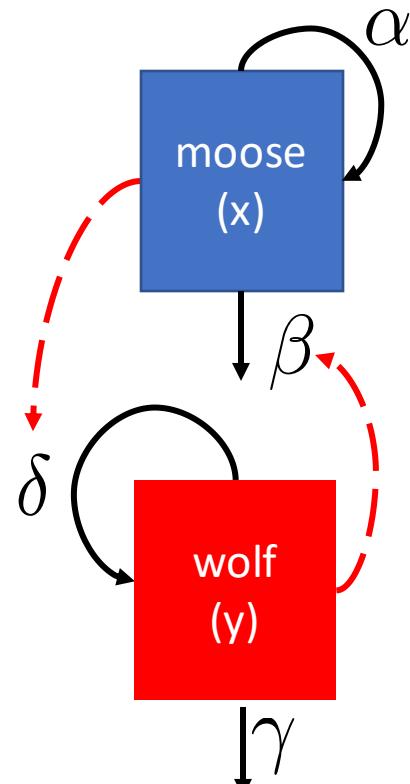
This 3-way interaction is an example of a **trophic cascade**.

Wolves, Moose, and Tree Rings on Isle Royale

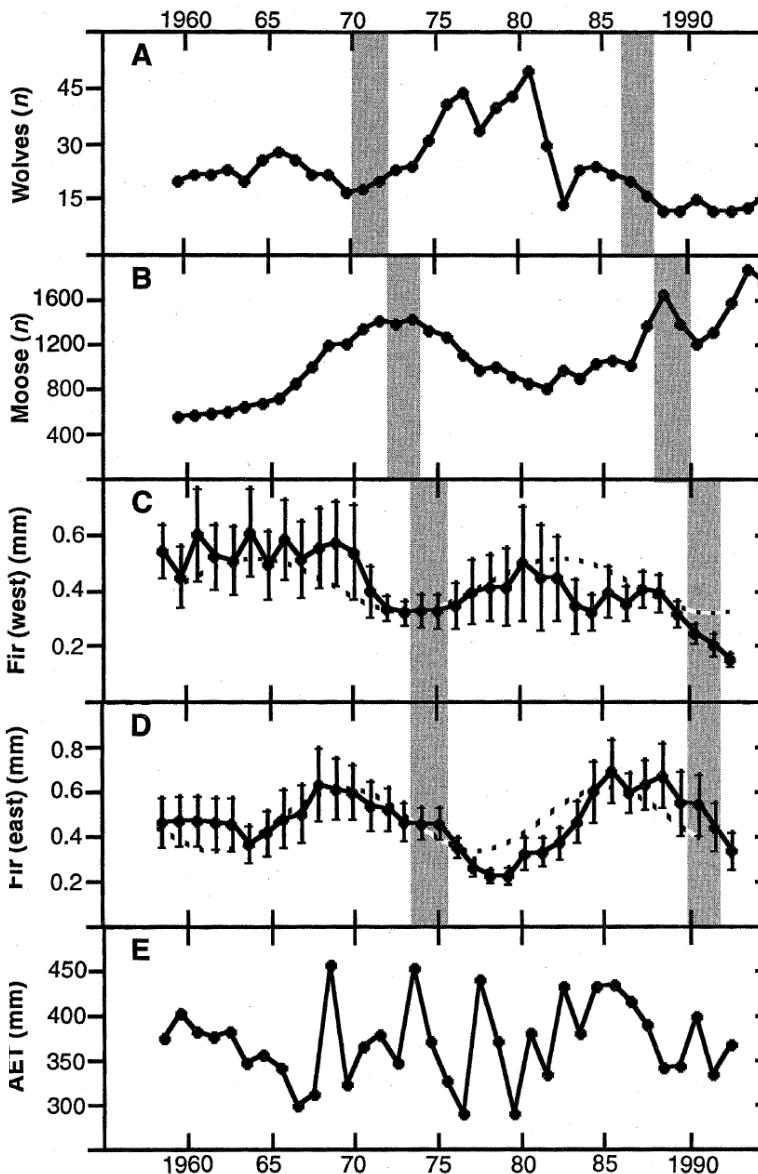
B. E. McLaren* and R. O. Peterson

SCIENCE • VOL. 266 • 2 DECEMBER 1994

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**.

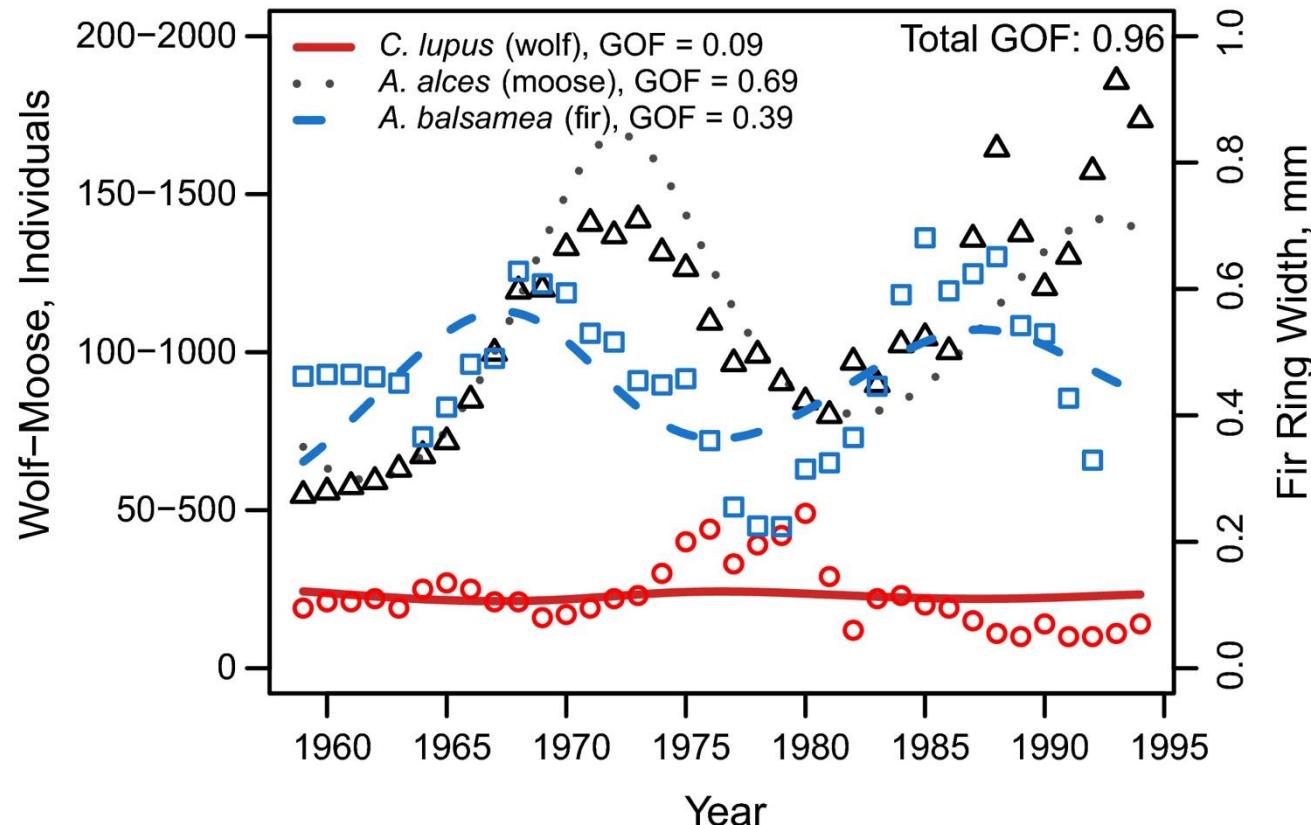
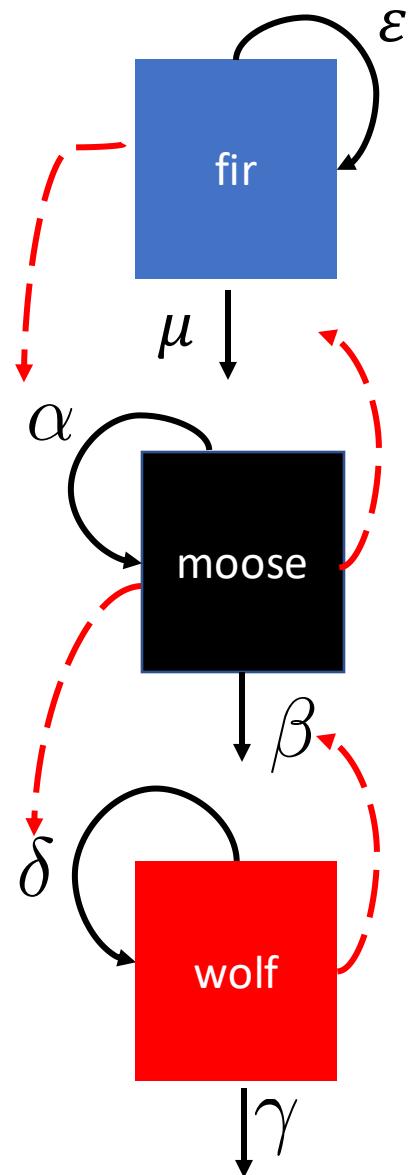
By definition, **trophic cascades span at least 3 trophic levels**, highlighting the process of **top-down** ecosystem control.

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.

Another famous example: Wolf-Moose on Isle Royale



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

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

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

Vol. XCIV, No. 879

The American Naturalist

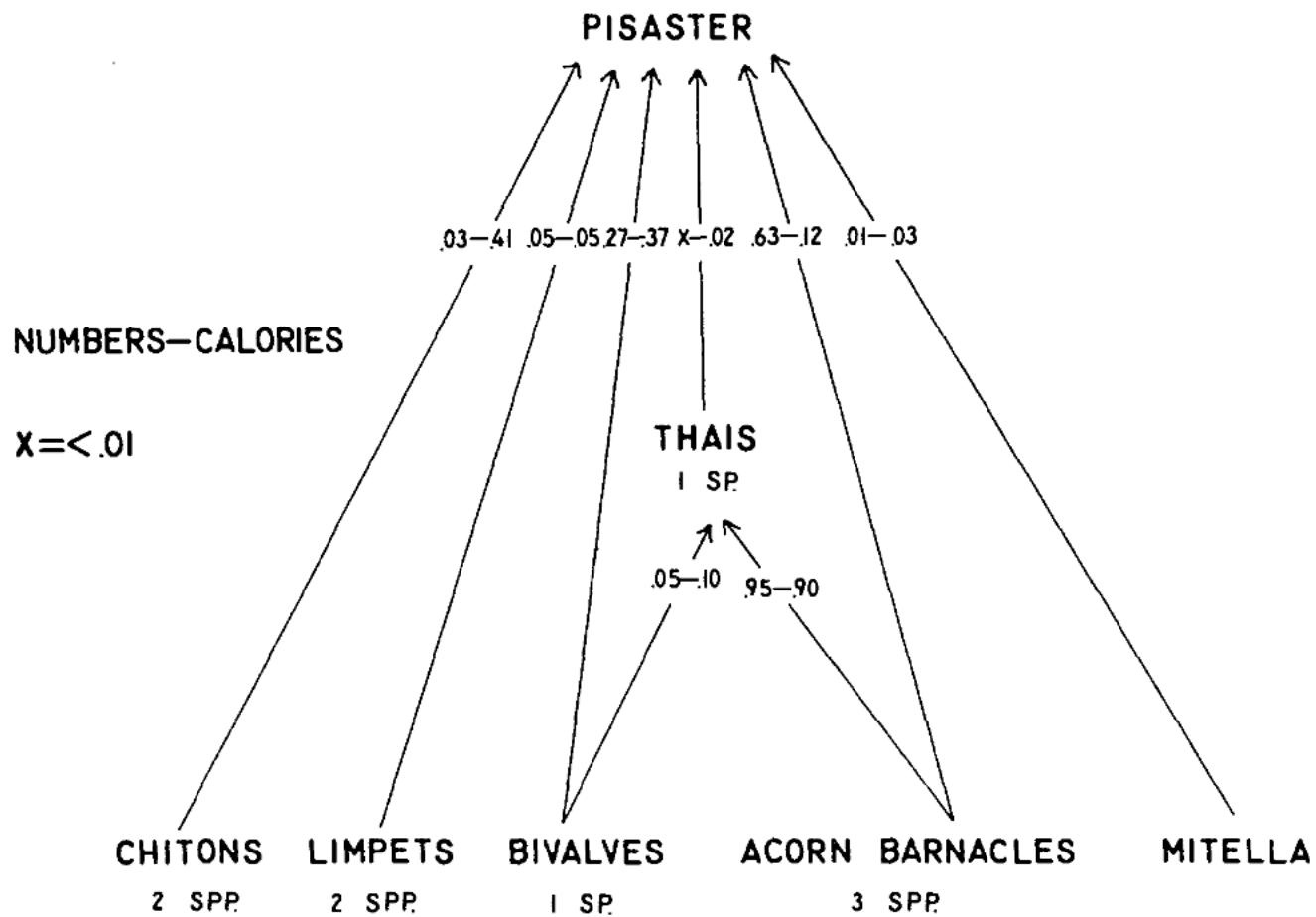
November–December, 1960

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** (and, as a result, ‘the world is green’)

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





0:0



Which of the following is an example of a trophic cascade?

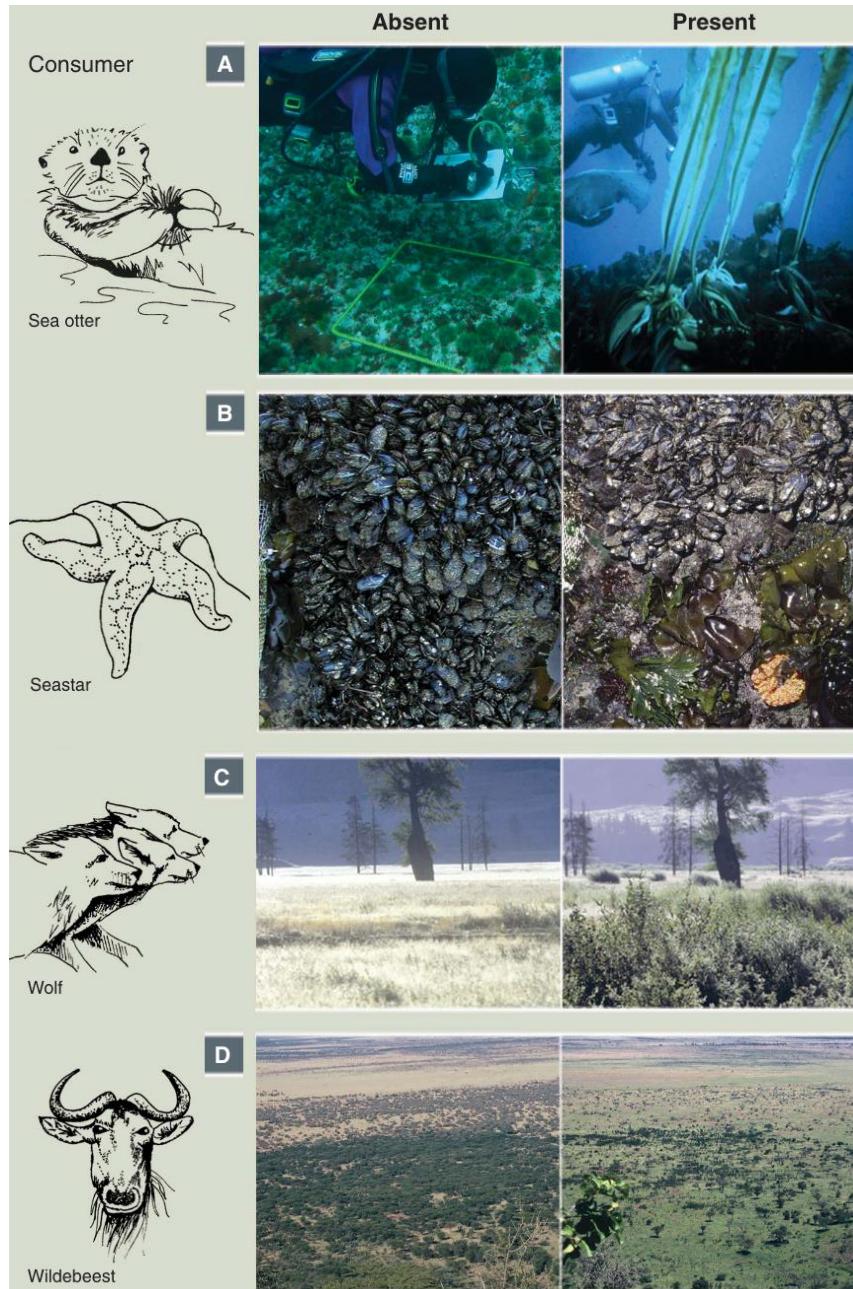
- A. Lion and zebra populations cyclically track one another in population booms and busts in the...

0%

- B. Consumption of fish SEE MORE by DDT after

Other famous **trophic cascades**:

Estes et al. 2011. *Science*.

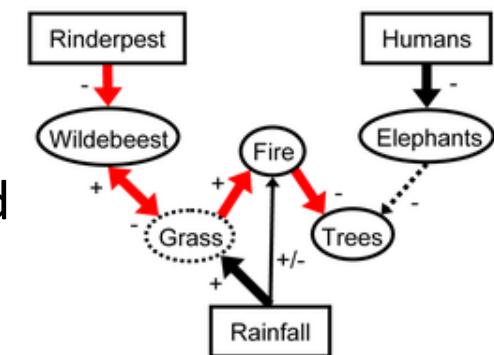


CA sea otters maintain kelp forest diversity by consuming herbivorous sea urchins. (Estes & Duggins 1995. *Ecological Monographs*)

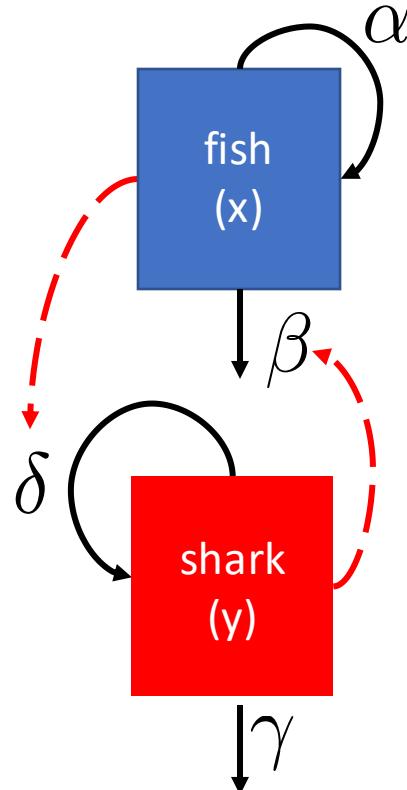
Starfish maintain diversity in Pacific intertidal by consuming space-dominating mussels. (Paine 1966 *The American Naturalist*)

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

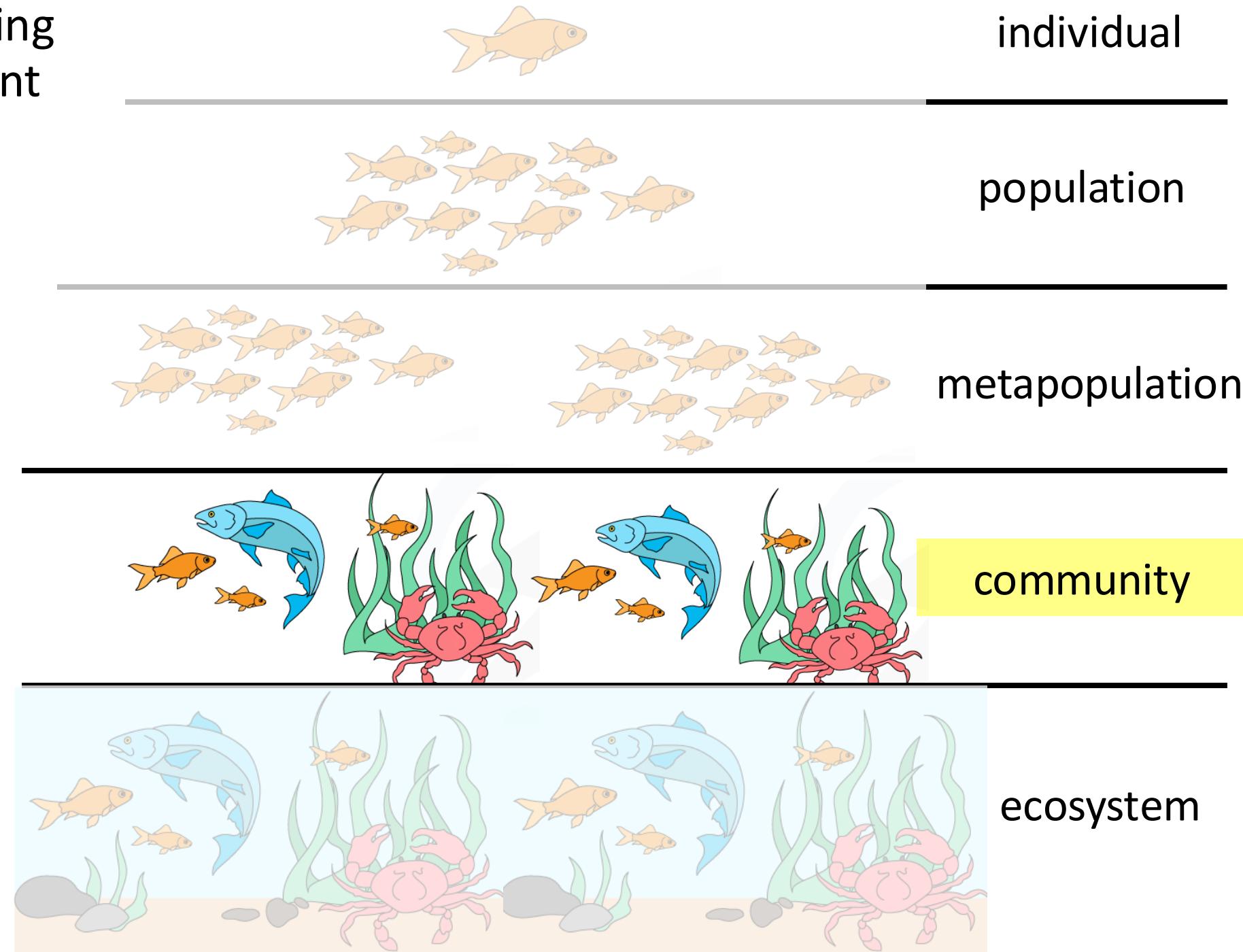
Rinderpest eradication releases wildebeest populations that control savanna, limit fire, and promote tree regrowth (Holdo et al. 2009. *PLoS Biology*)



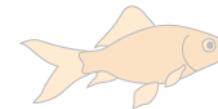
Community = interacting populations of different species



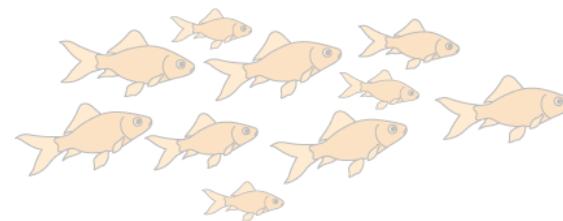
How does fish abundance **vary** with changes in shark abundance?



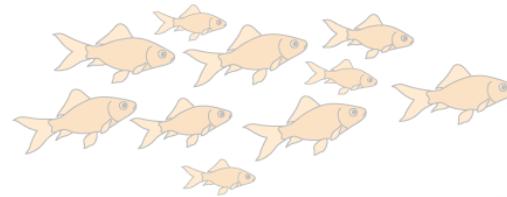
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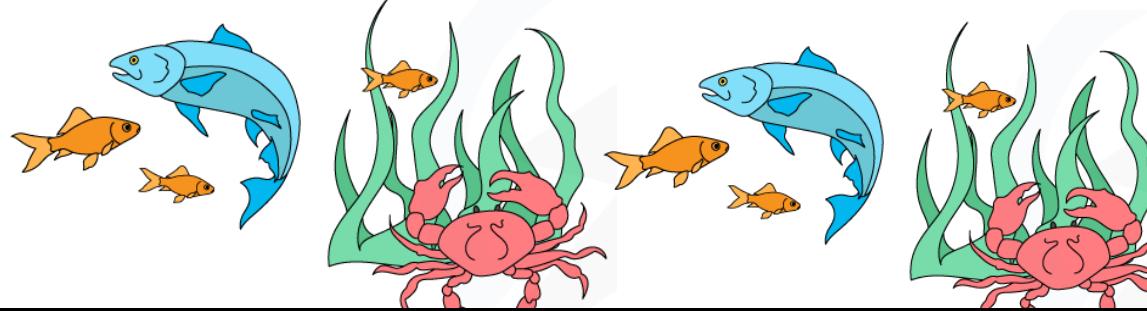
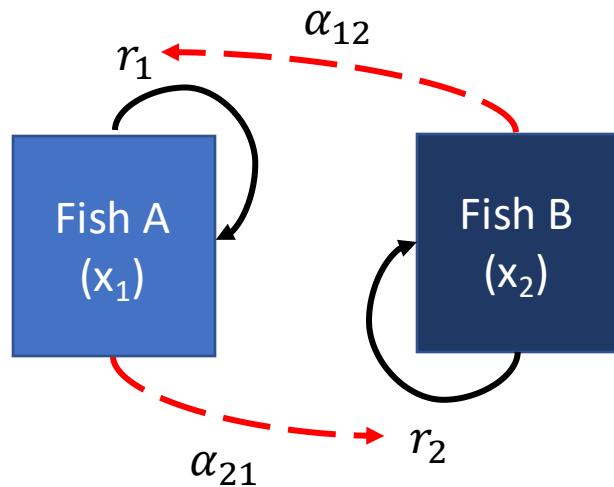
individual



population

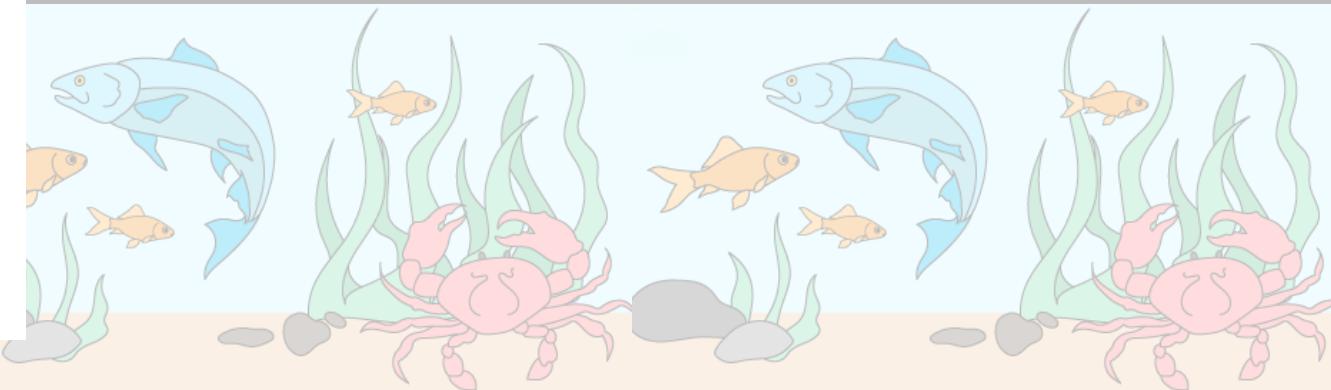


metapopulation



community

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



ecosystem

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

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

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

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intraspecies competition
of species 1 (akin to
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intraspecies competition
of species 2

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

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intraspecies competition
of species 2

interspecies
competition with
species 2

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).

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

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α_{12} = effect of species 2 on
the population of species 1

α_{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!

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Four equilibria at:

$$x_1^* = 0 ; x_2^* = 0 \quad \text{Trivial.}$$

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Four equilibria at:

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

$$x_1^* = 0 ; x_2^* = K_2 \quad \text{Species 1 extinct. Species 2 at carrying capacity.}$$

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Four equilibria at:

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

Coexistence.



00

G

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

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

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

- A) Specie... 0%
- B) Specie... 0%
- C) Specie... 0%
- D) Specie... 0%

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

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

big

*x*₂

0

*x*₁

big

big

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big

x_2

0

x_1

big

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.

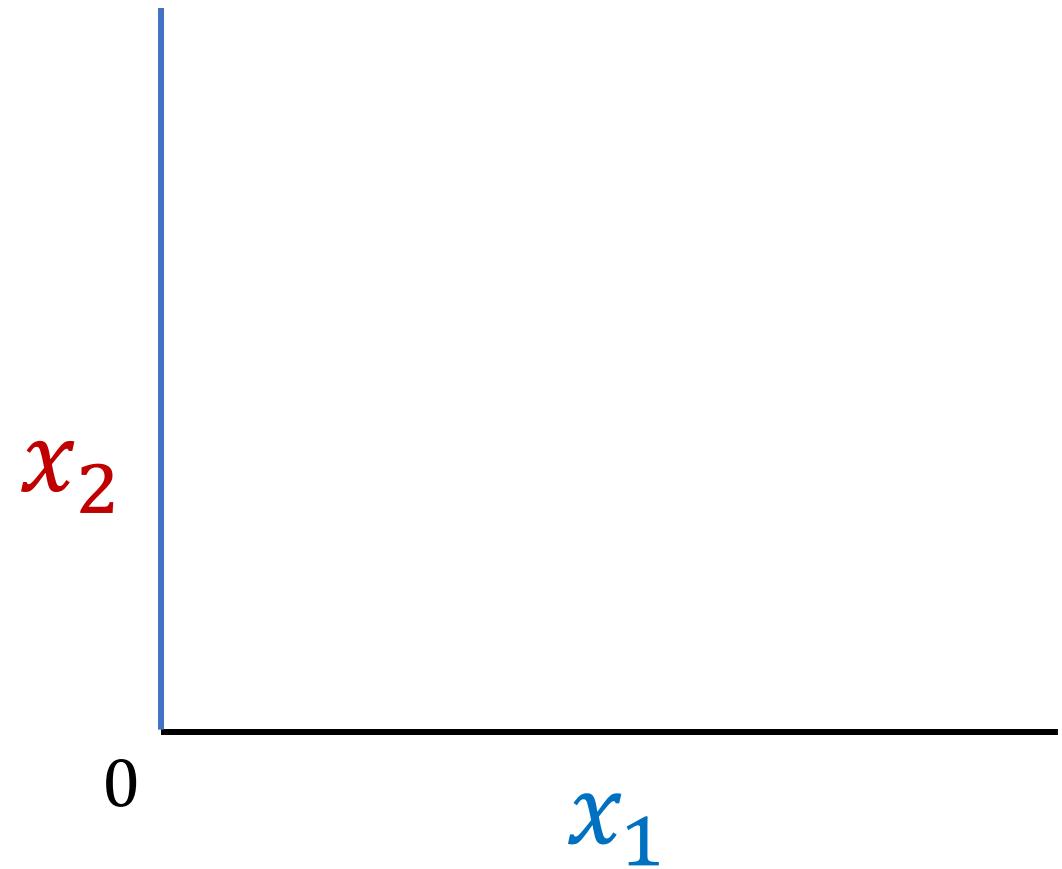
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first nullcline at $x_1 = 0$



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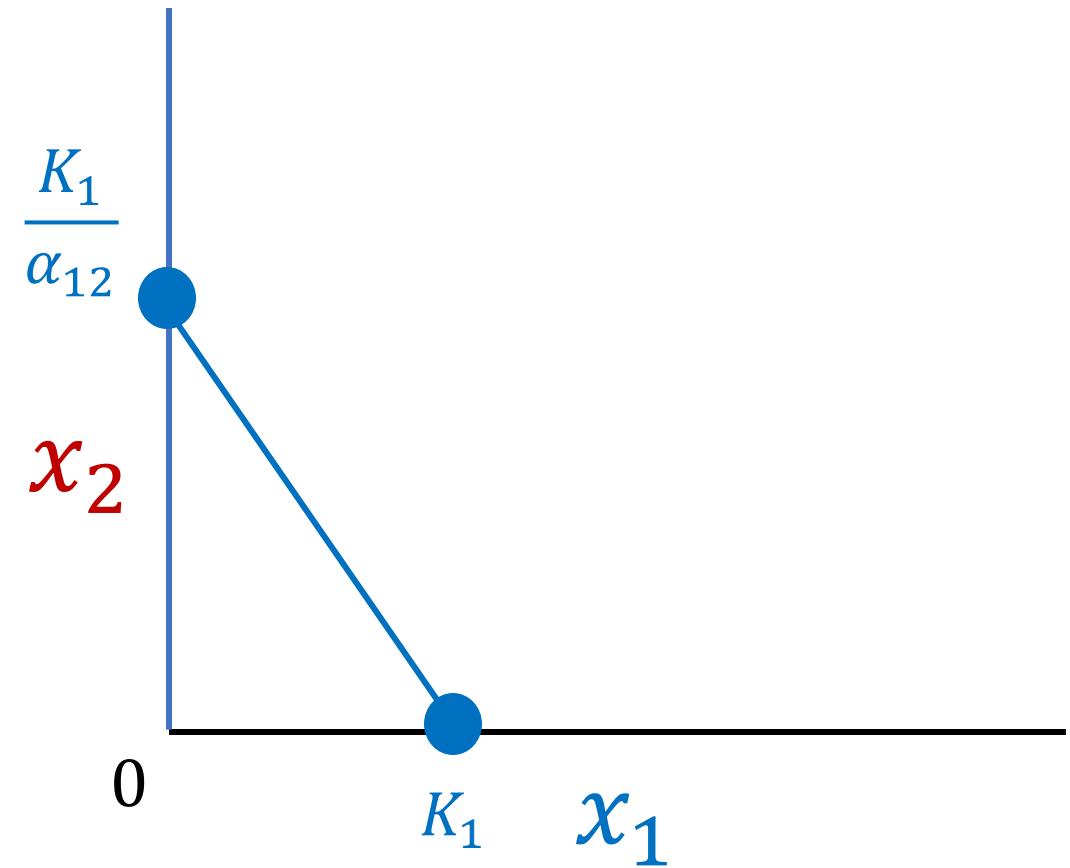
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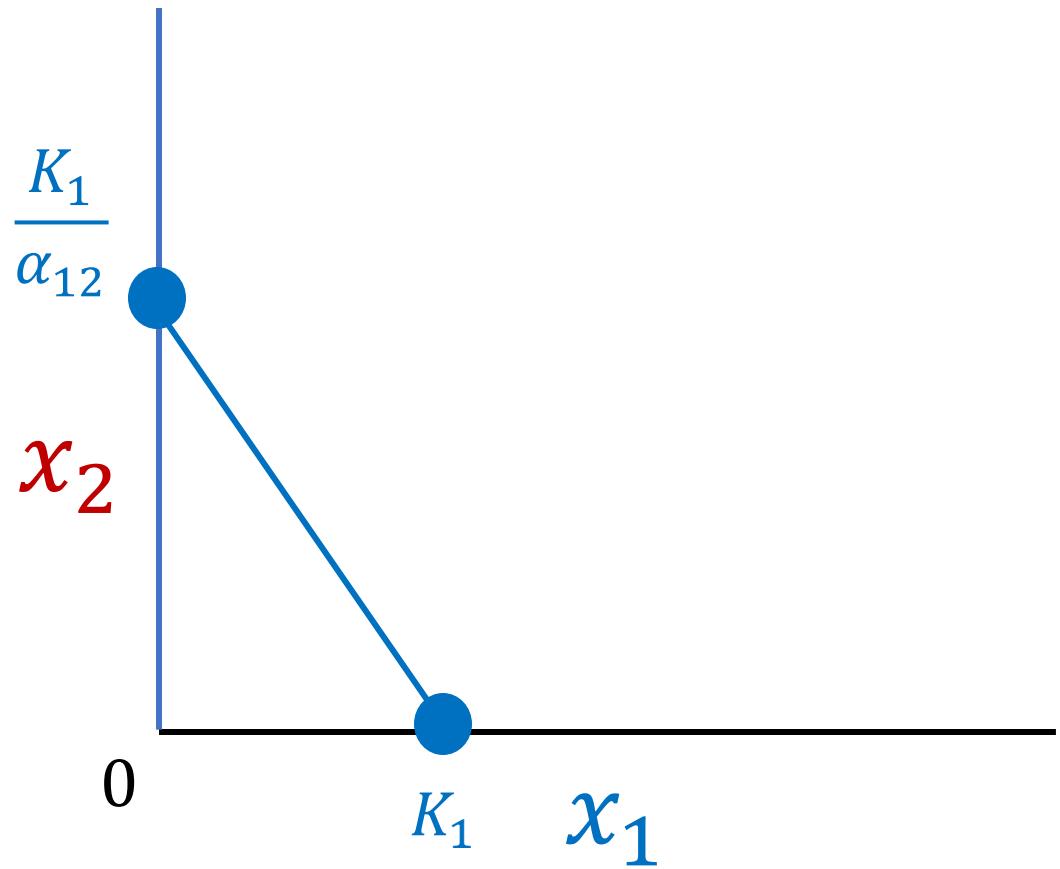
first nullcline at $x_1 = 0$

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



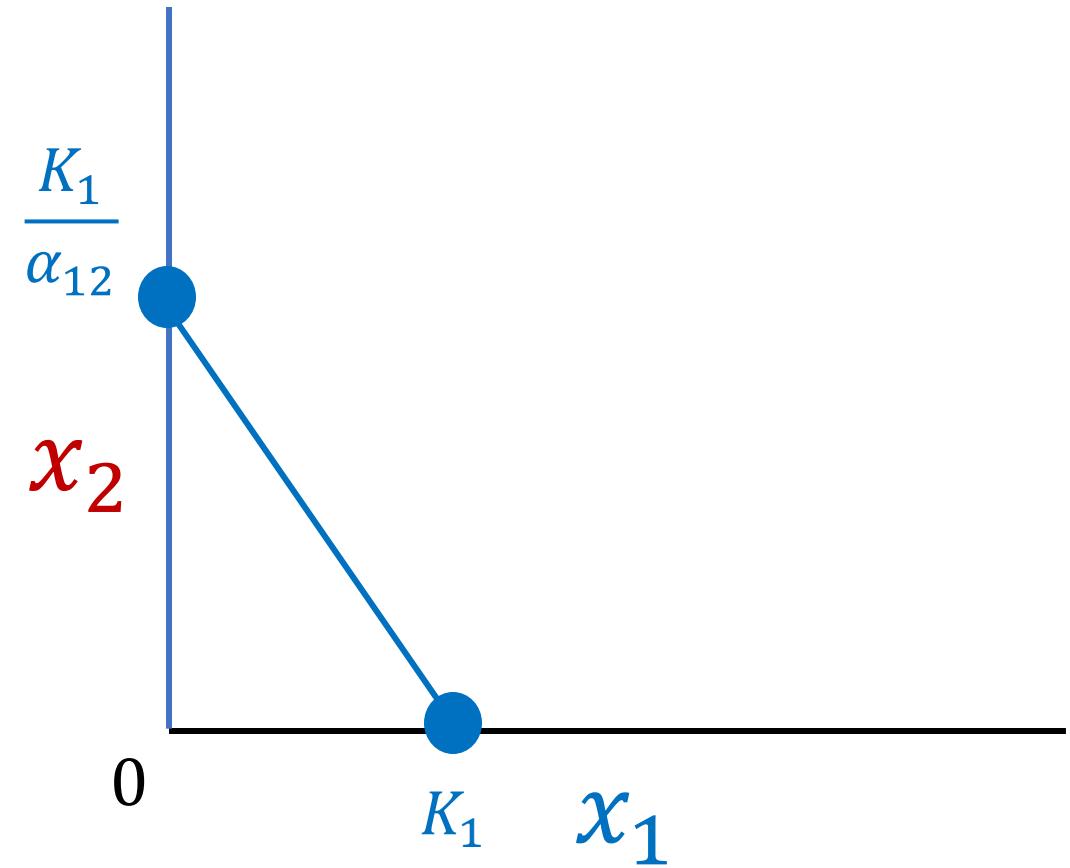
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- Following a perturbation, the population should return to equilibrium!



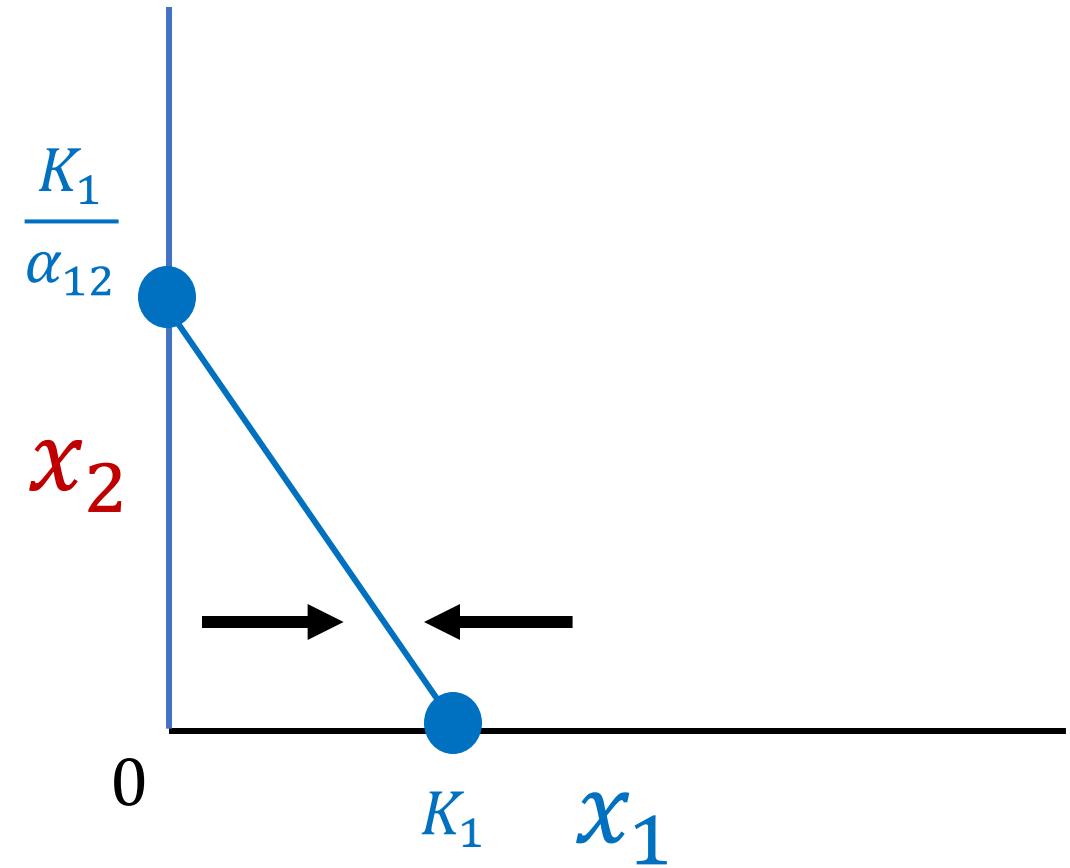
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Nullclines (or isoclines) of the Lotka-Volterra competition model

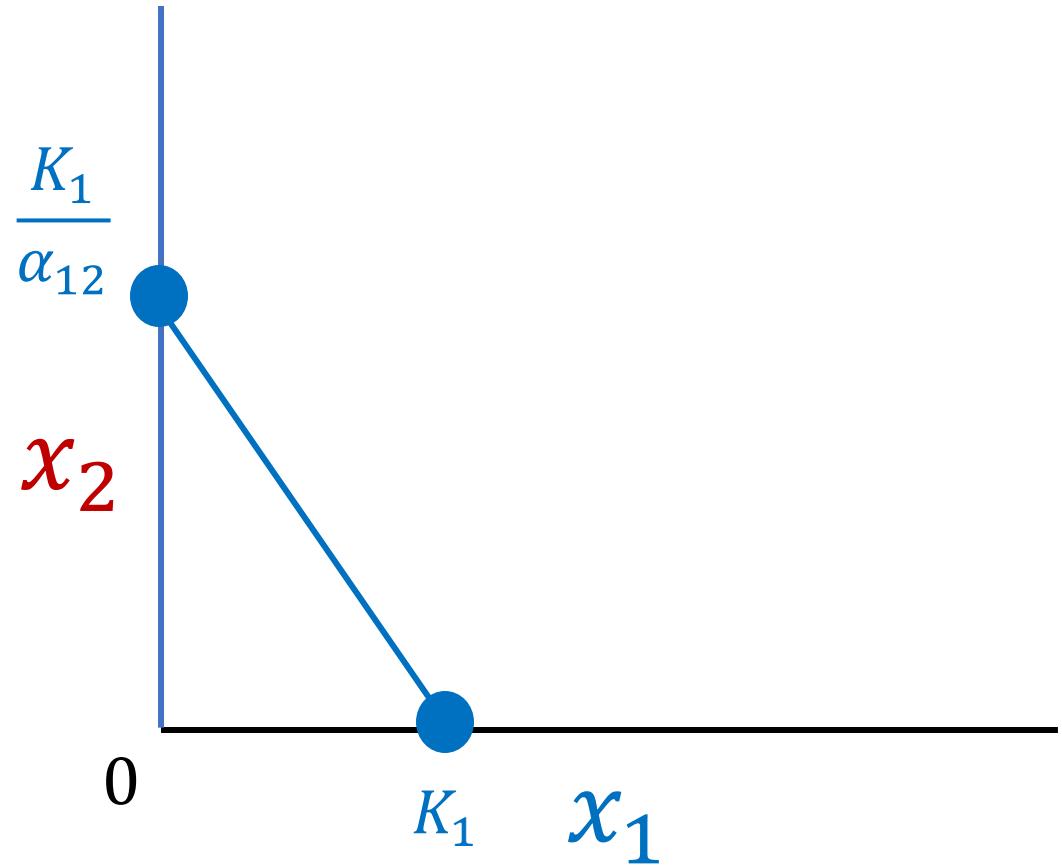
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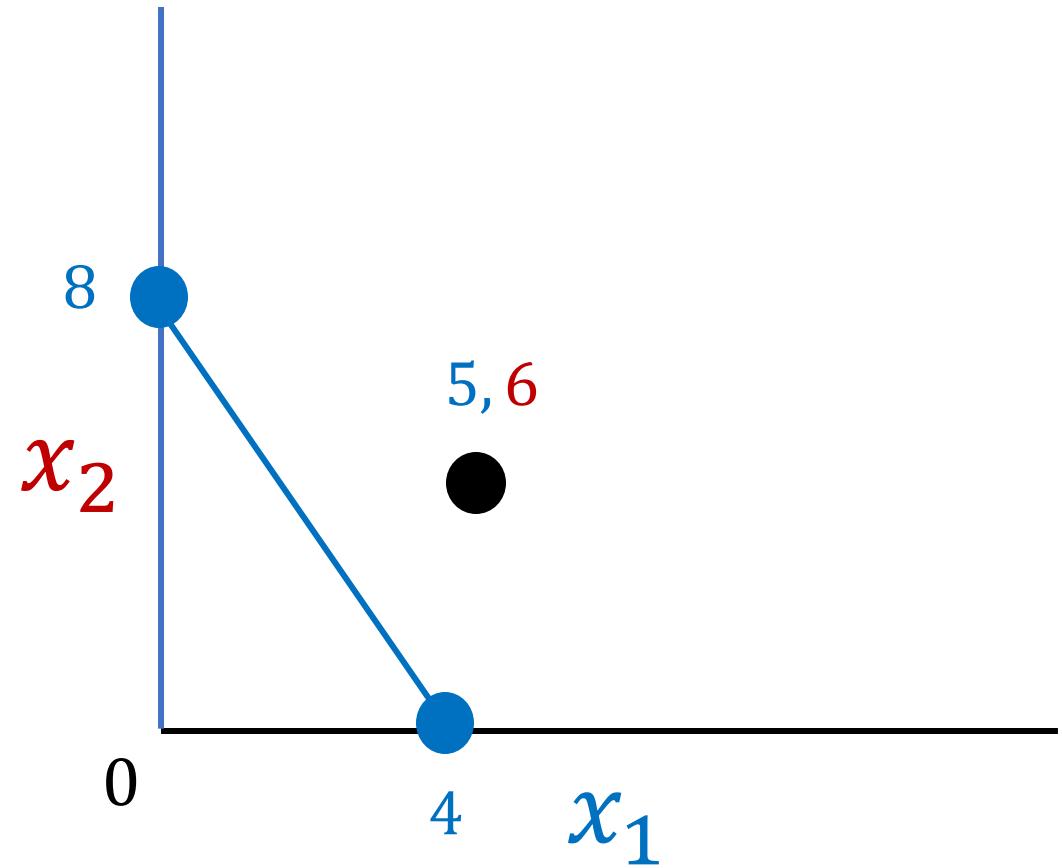
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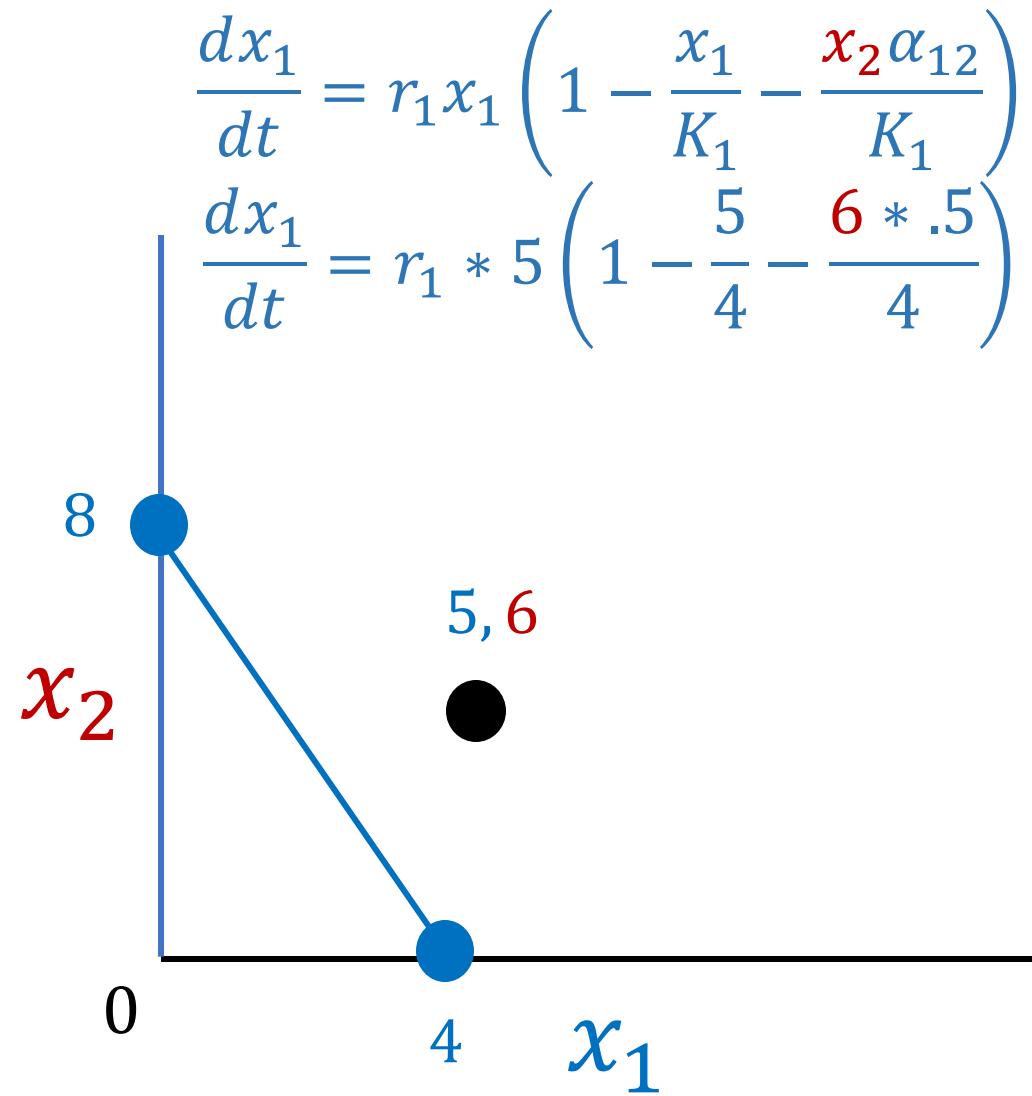
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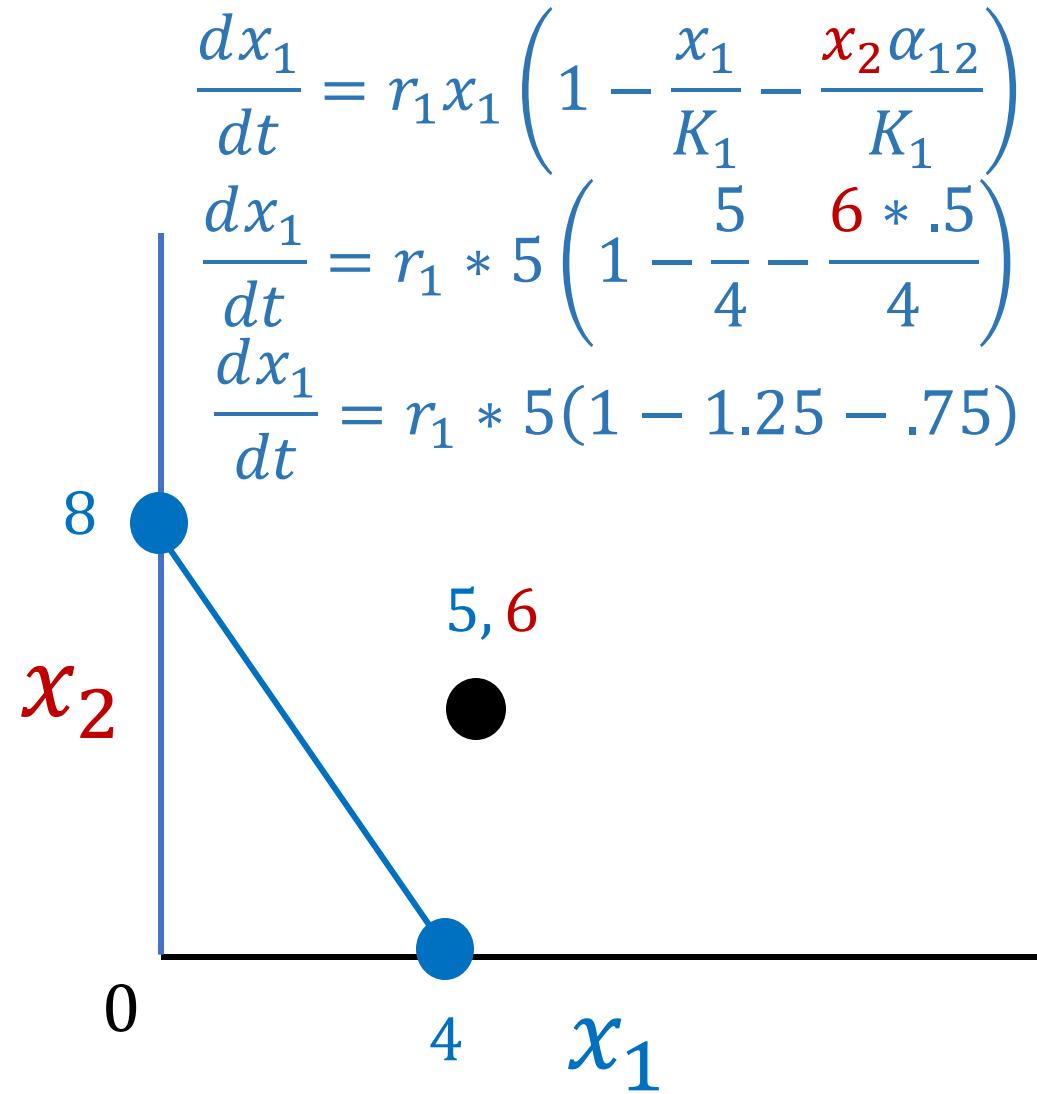
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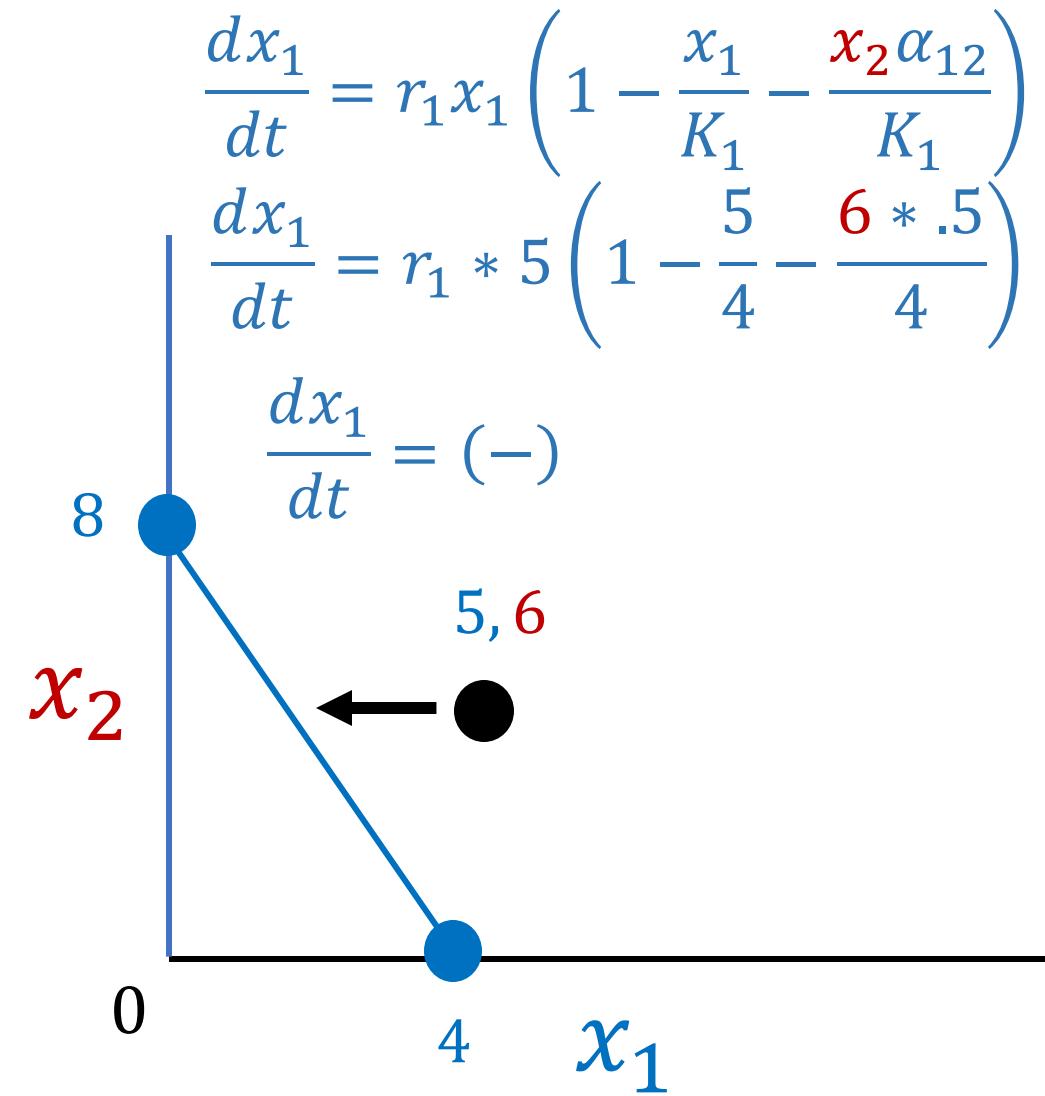
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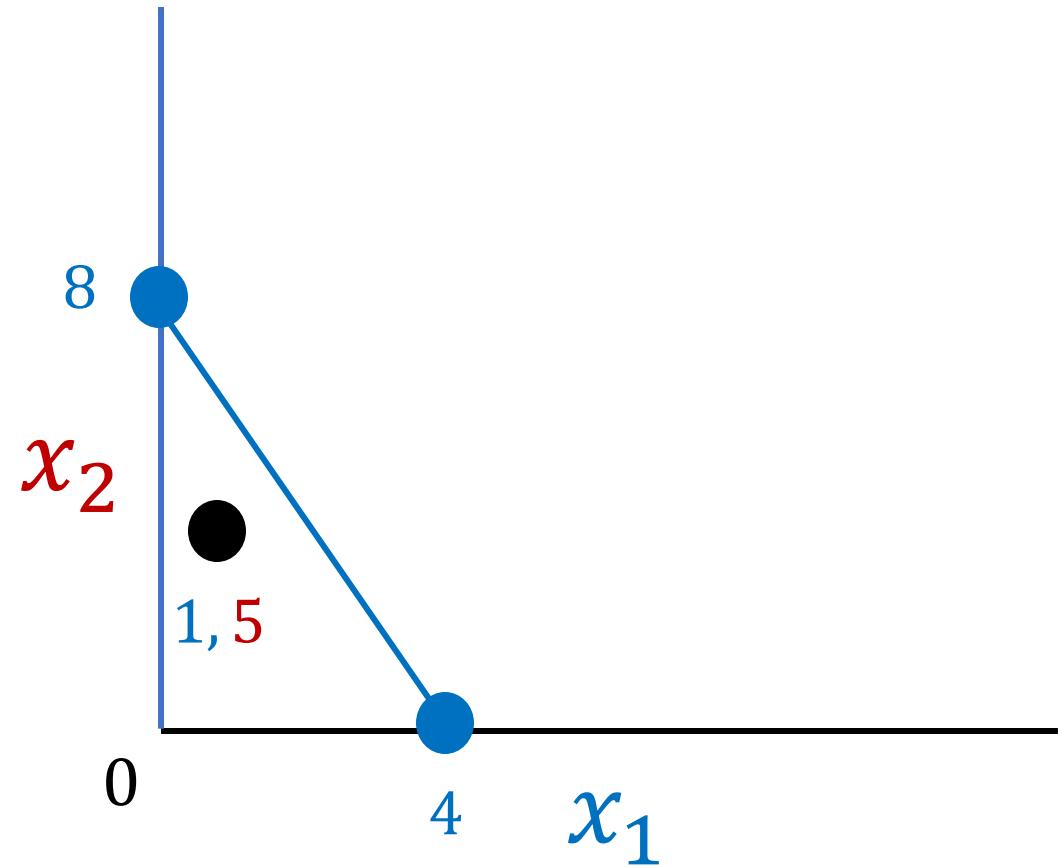
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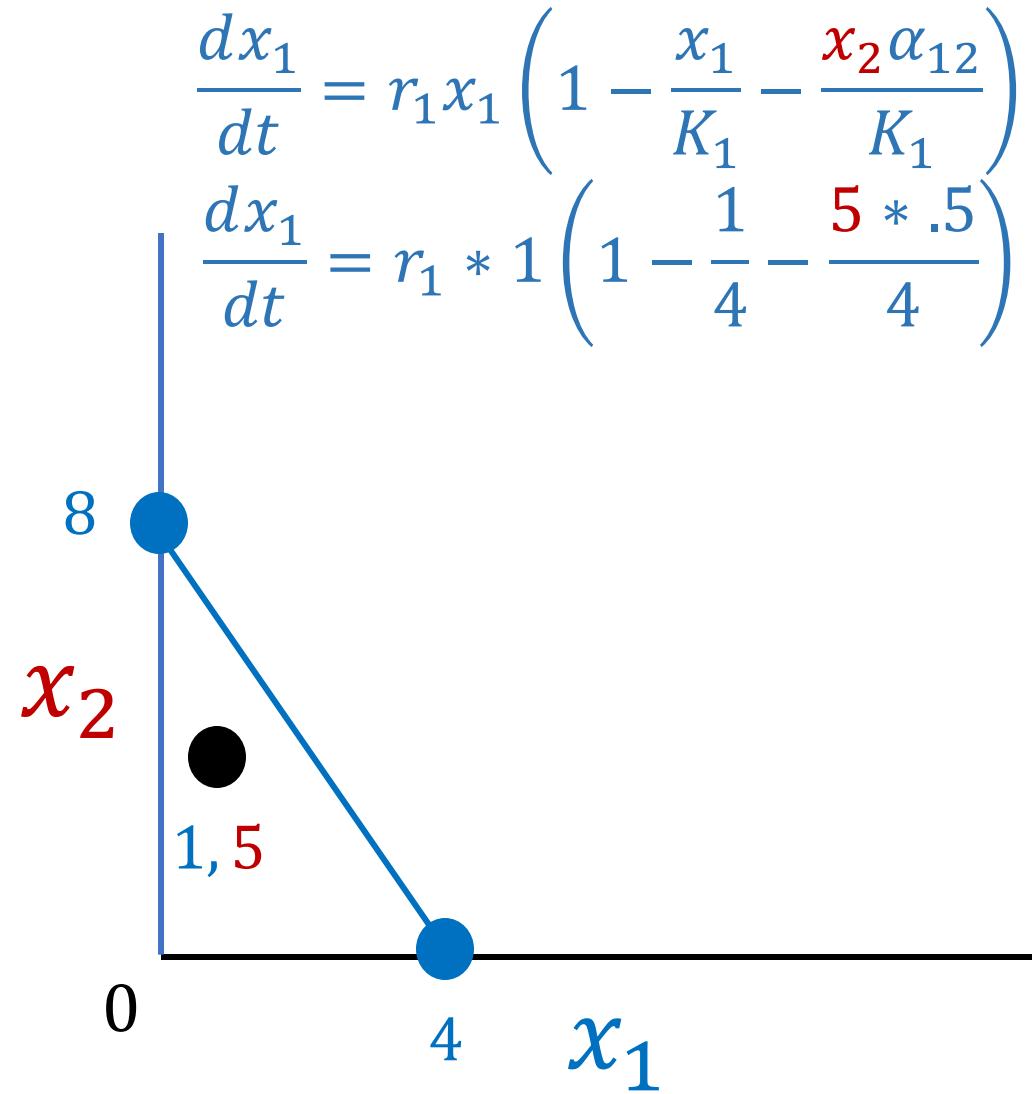
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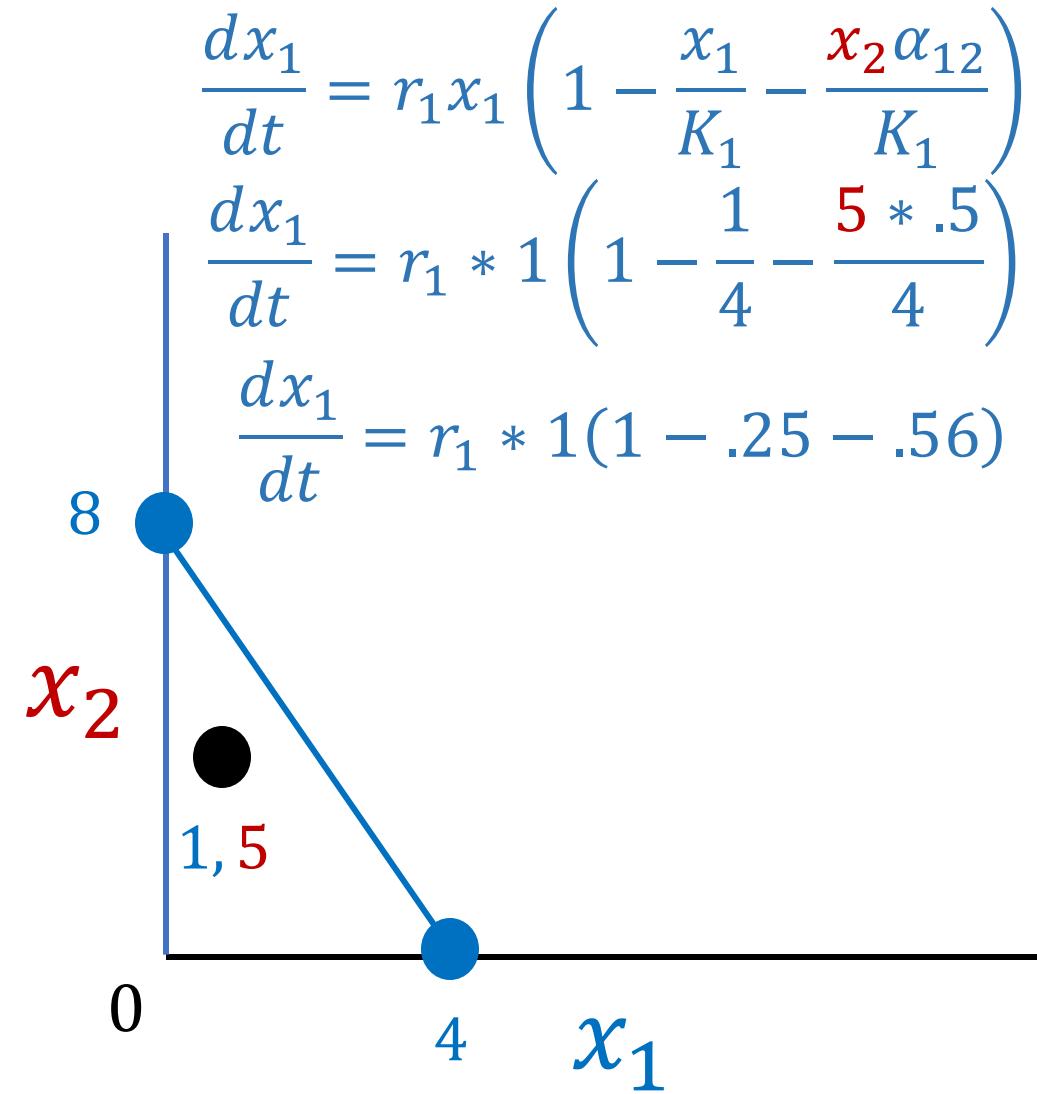
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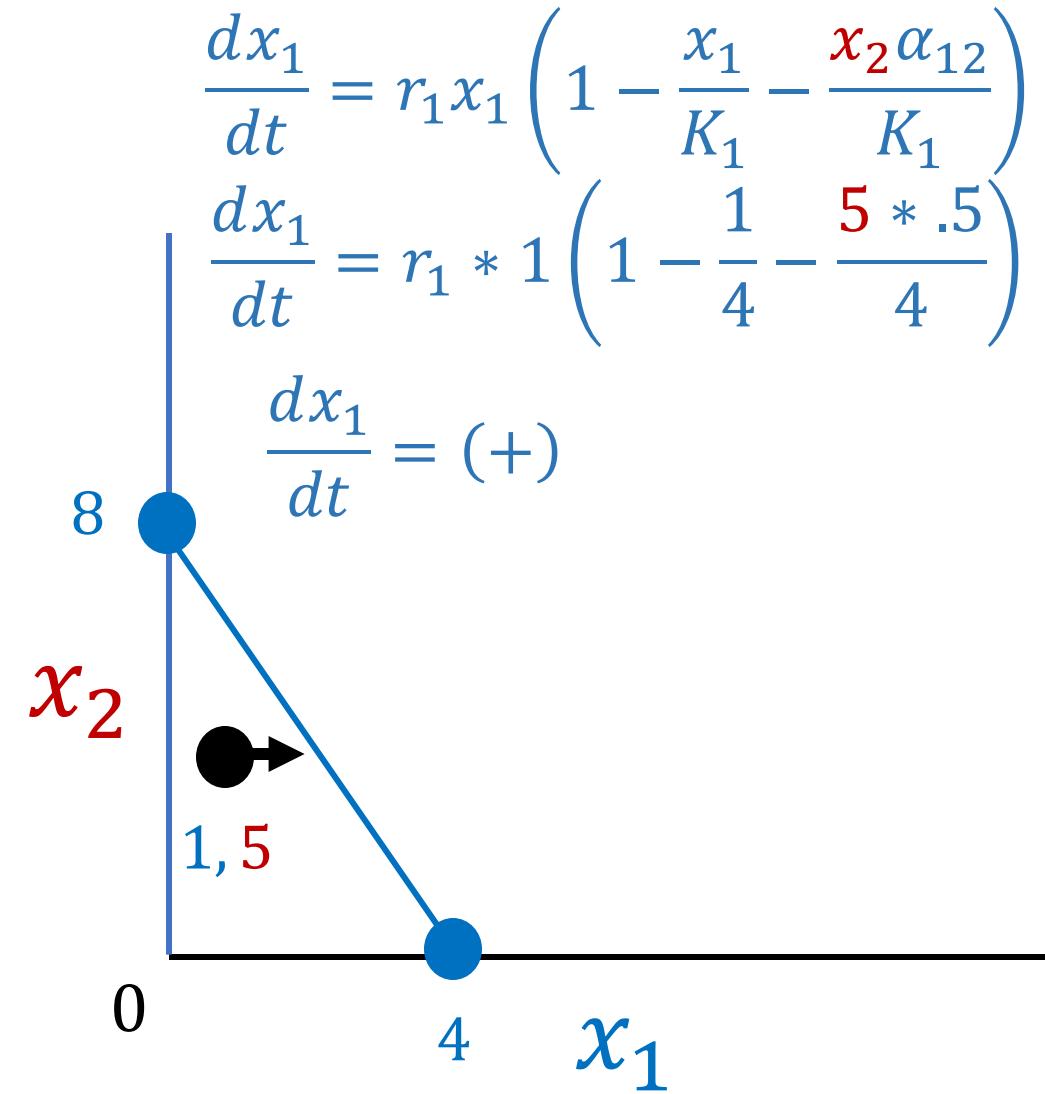
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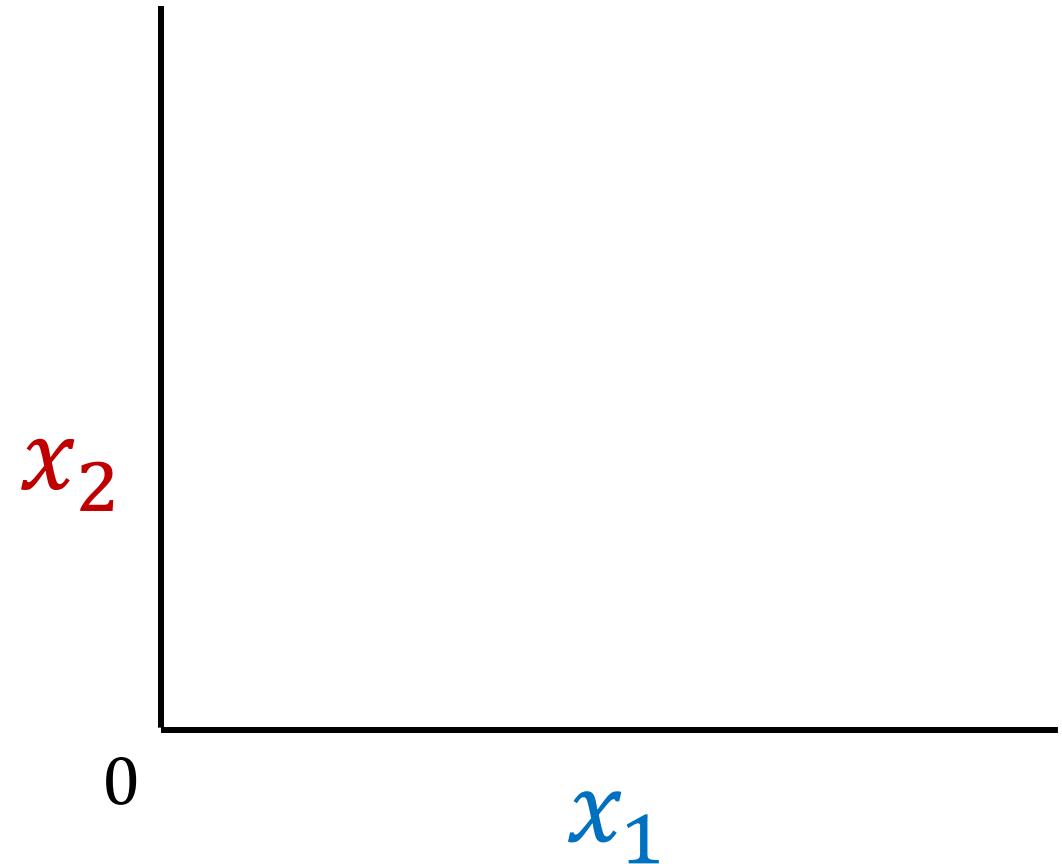
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Nullclines (or isoclines) of the Lotka-Volterra competition model

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



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

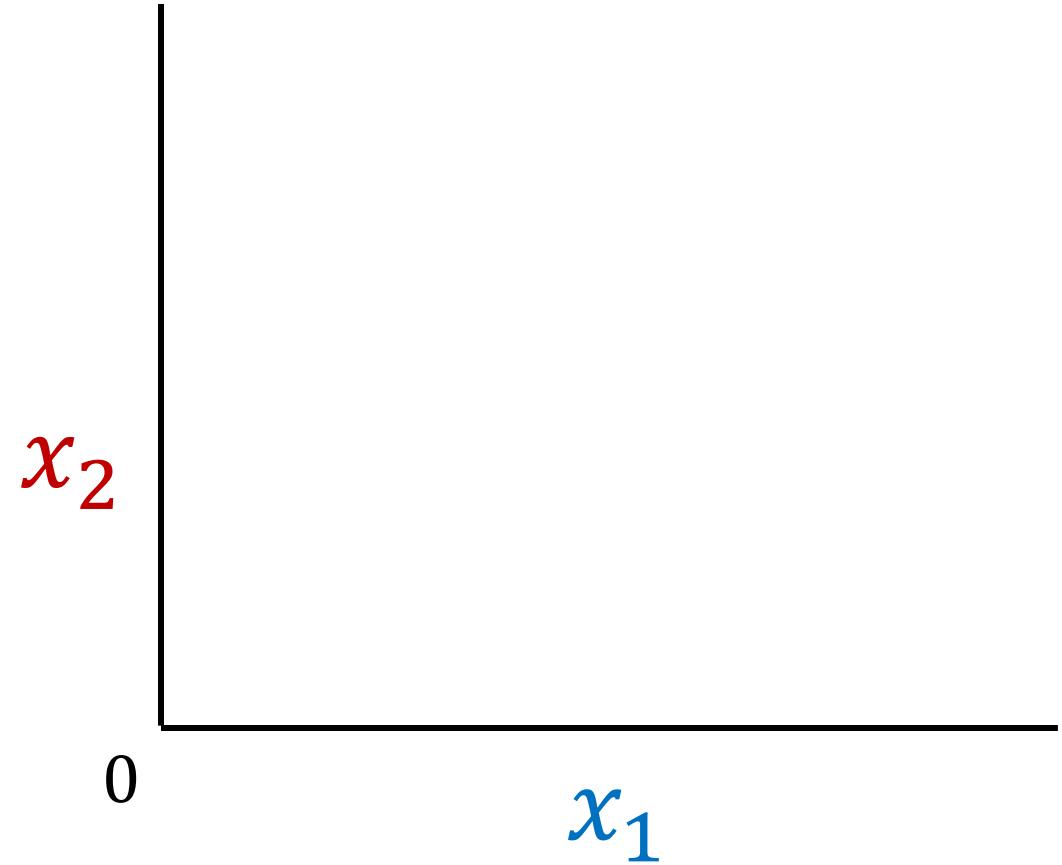
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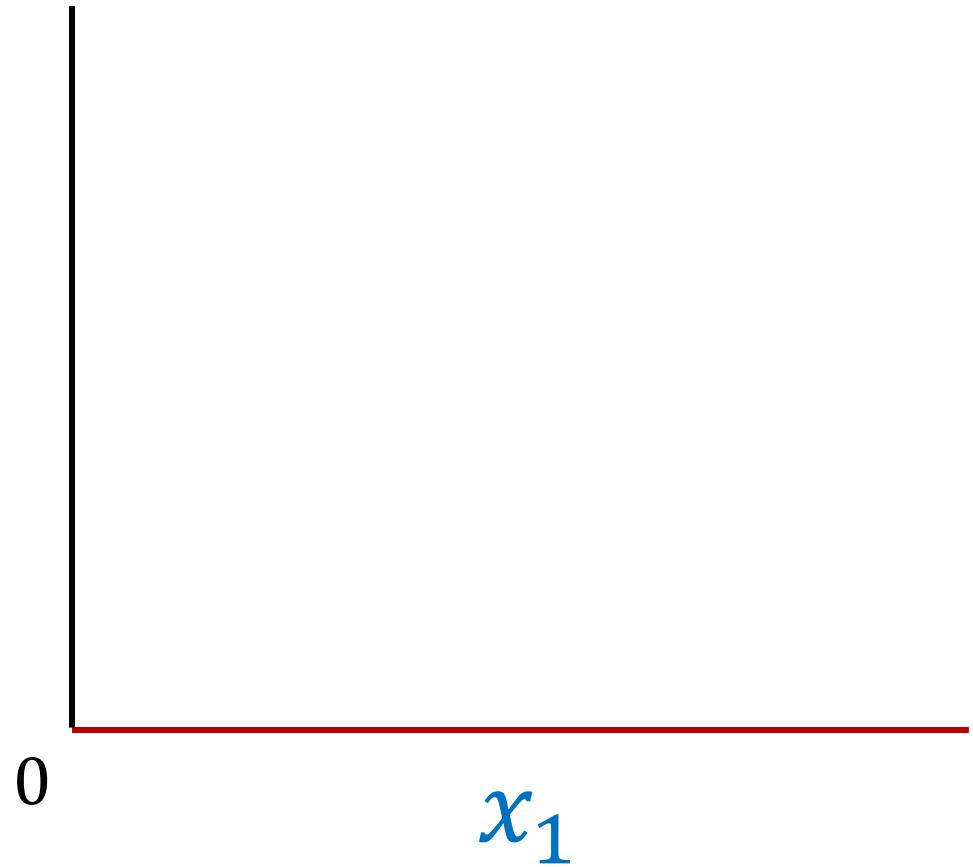
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first nullcline at $x_2 = 0$



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

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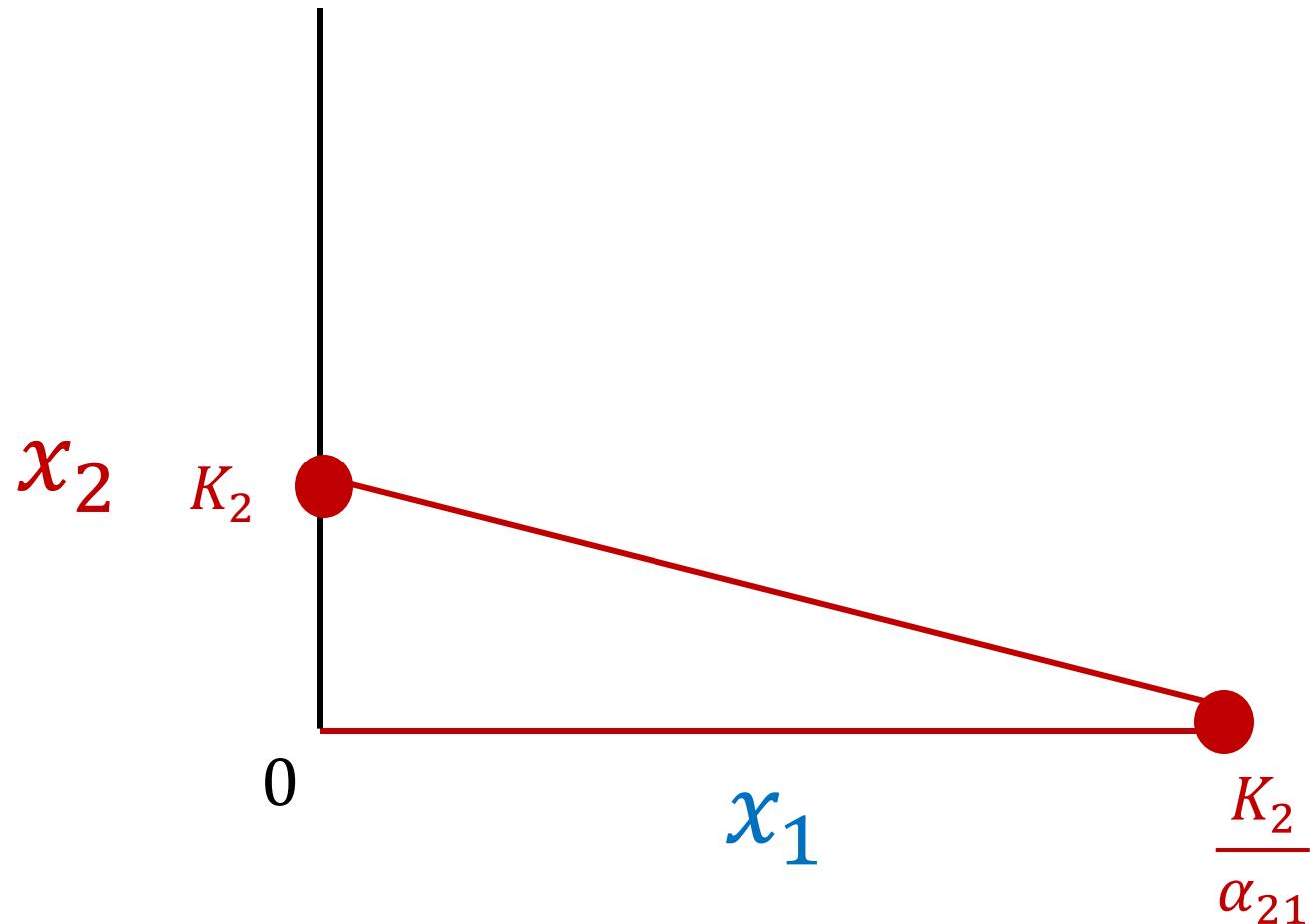
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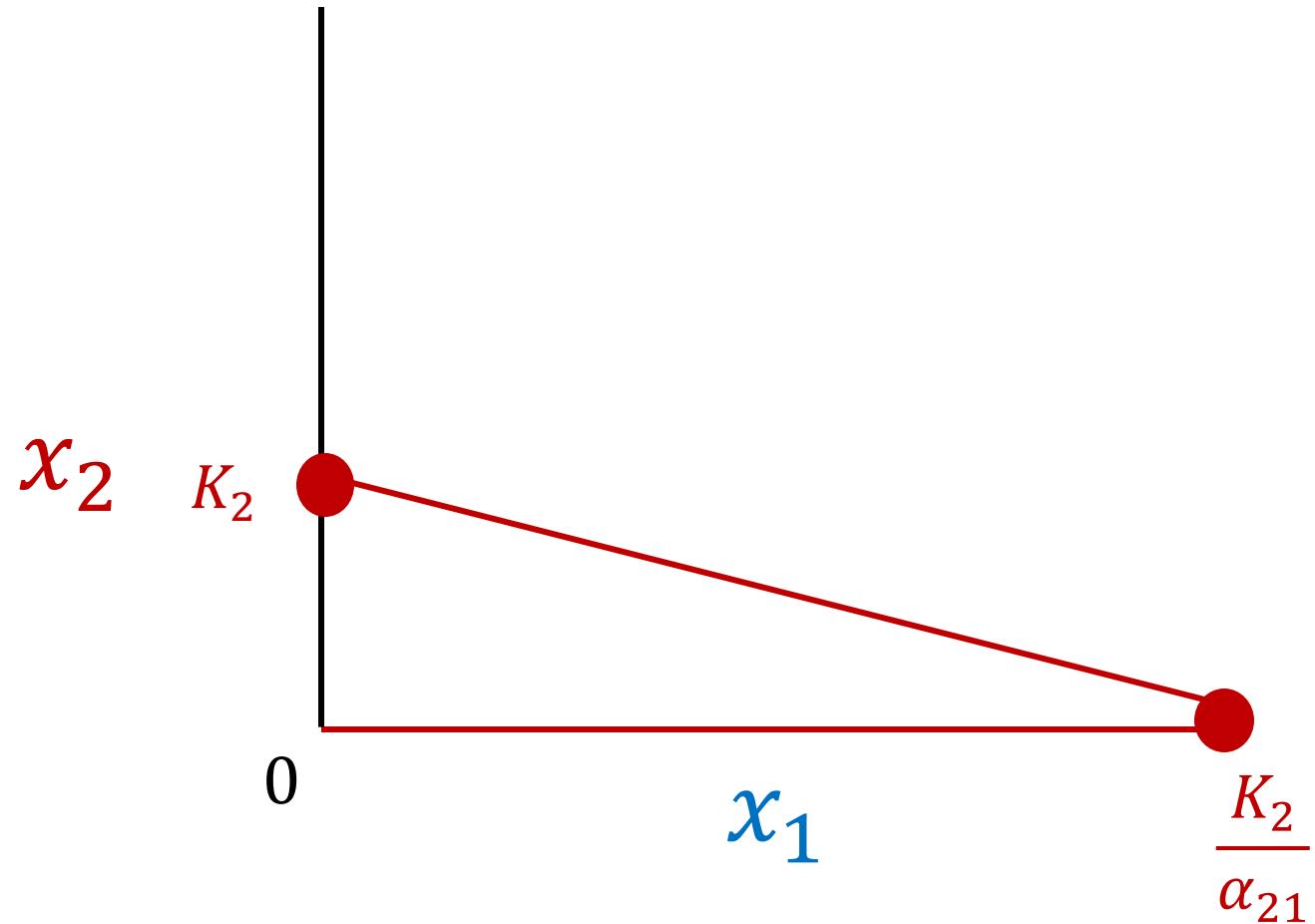
first nullcline at $x_2 = 0$

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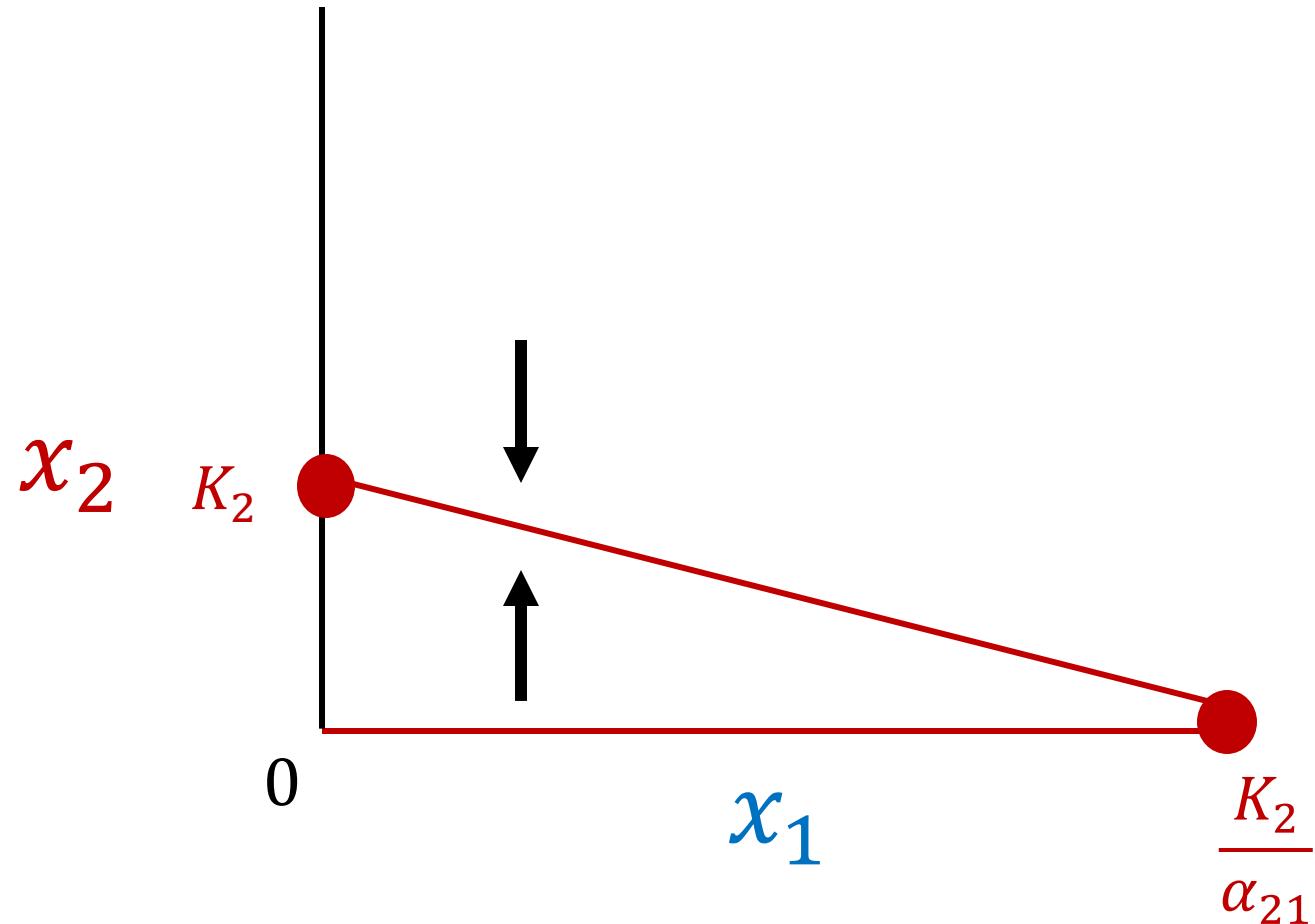
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- Following a perturbation, the population should return to equilibrium!



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

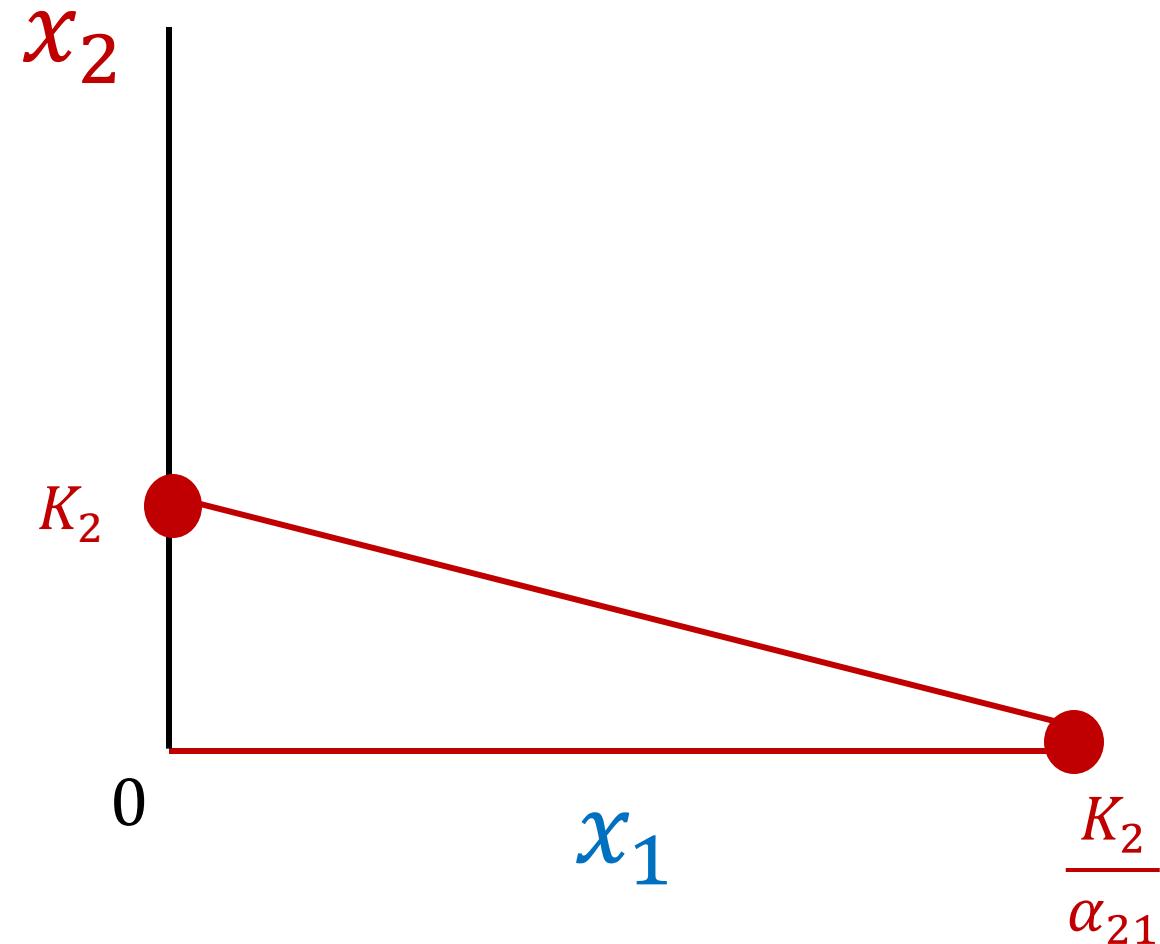
- Following a perturbation, the population should return to equilibrium!
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Nullclines (or isoclines) of the Lotka-Volterra competition model

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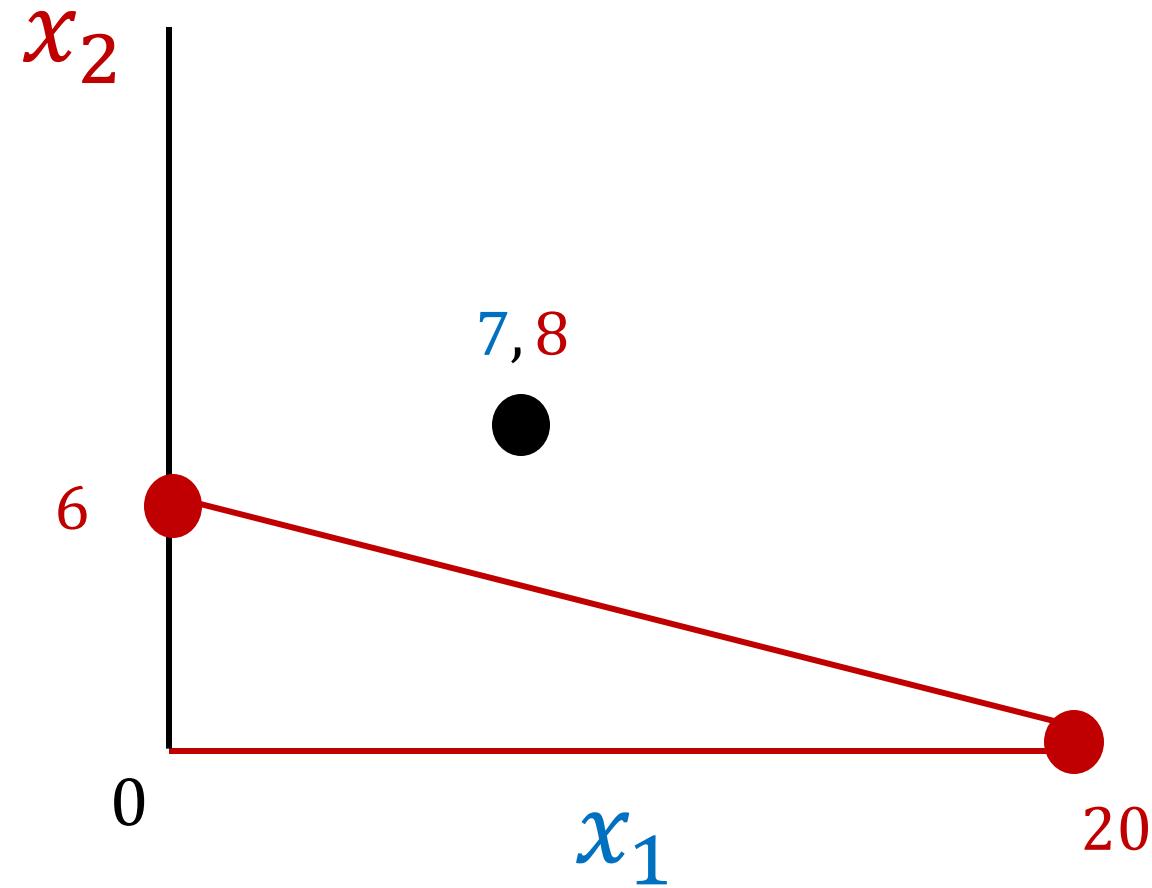
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Nullclines (or isoclines) of the Lotka-Volterra competition model

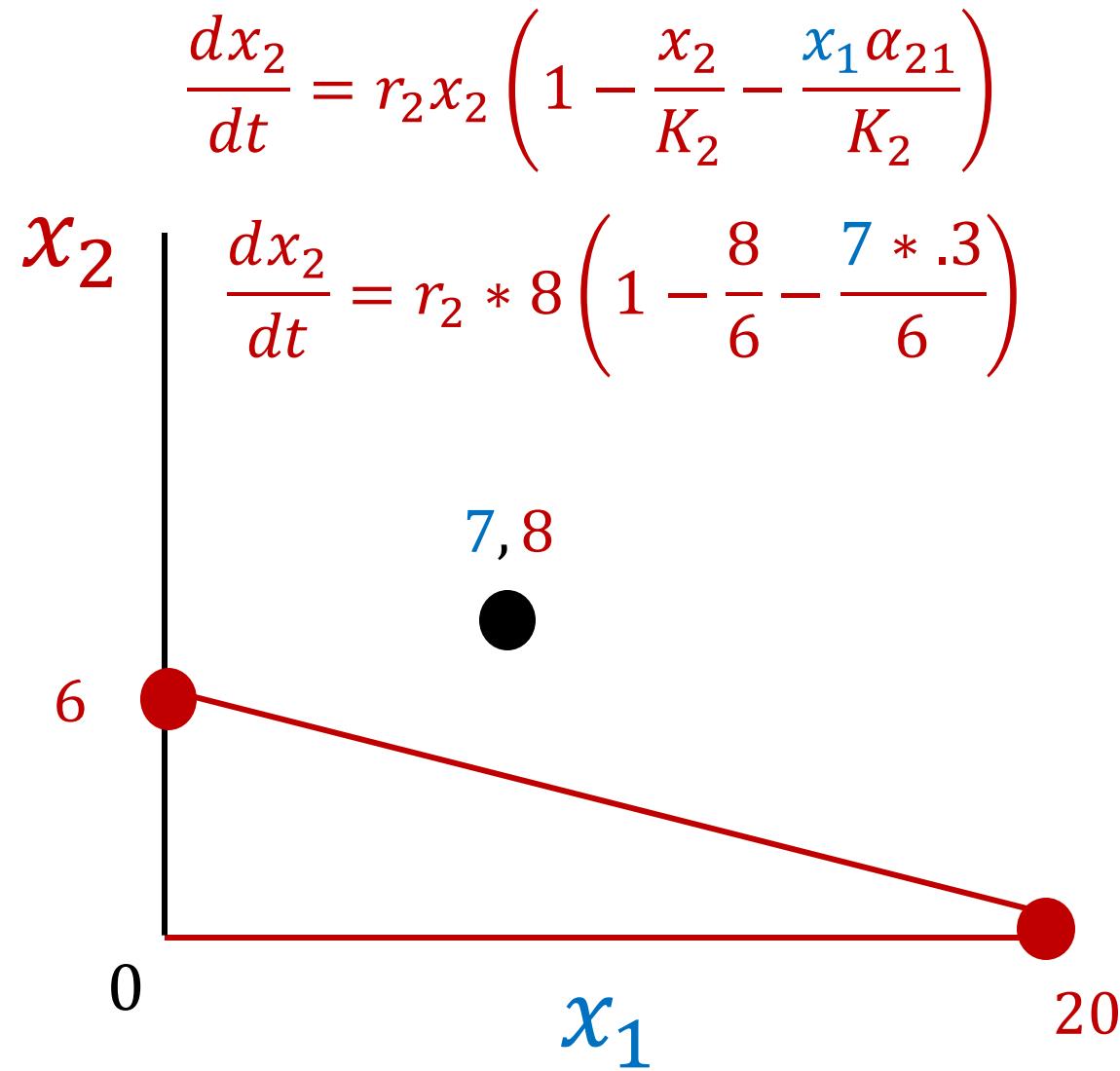
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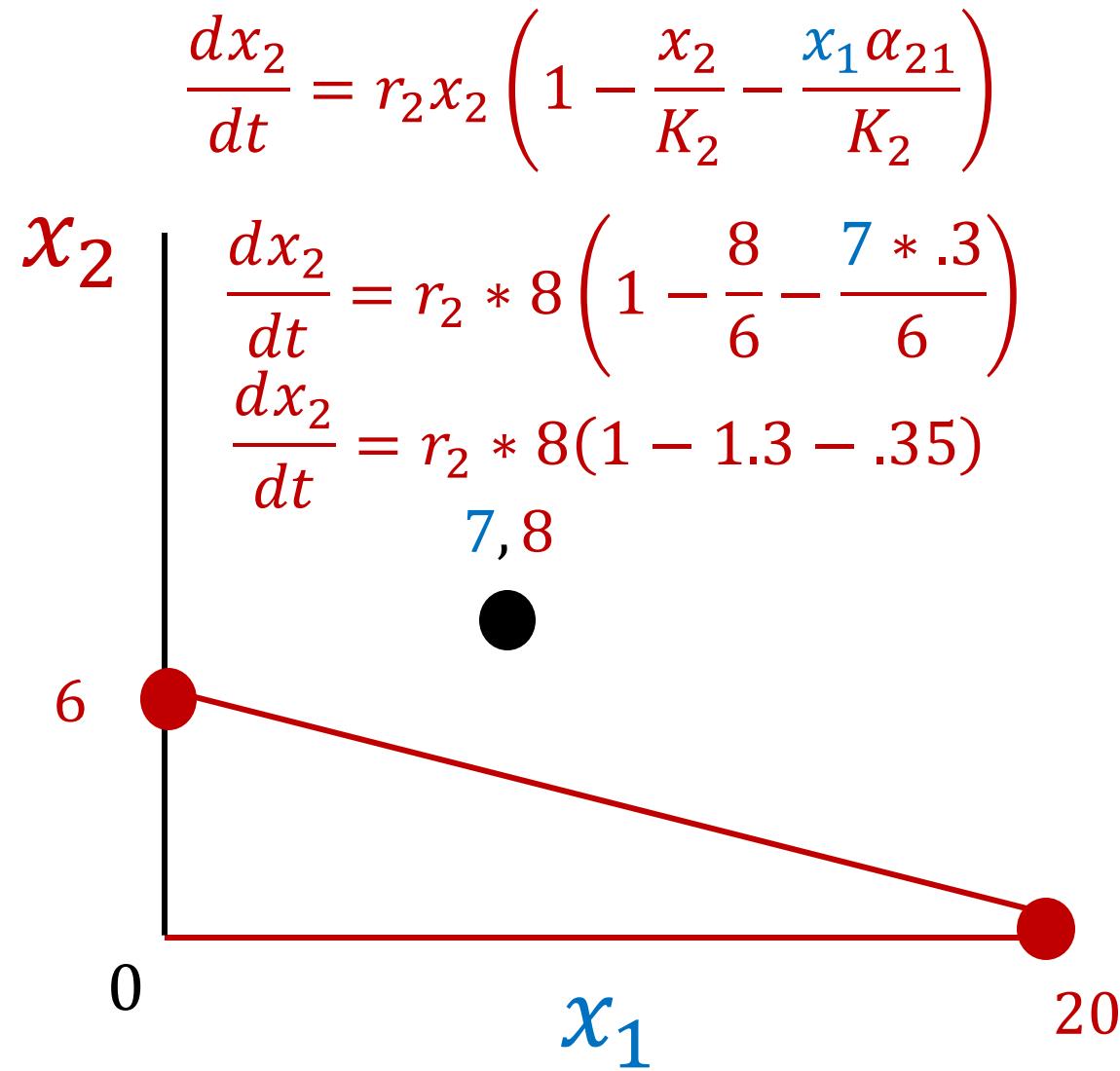
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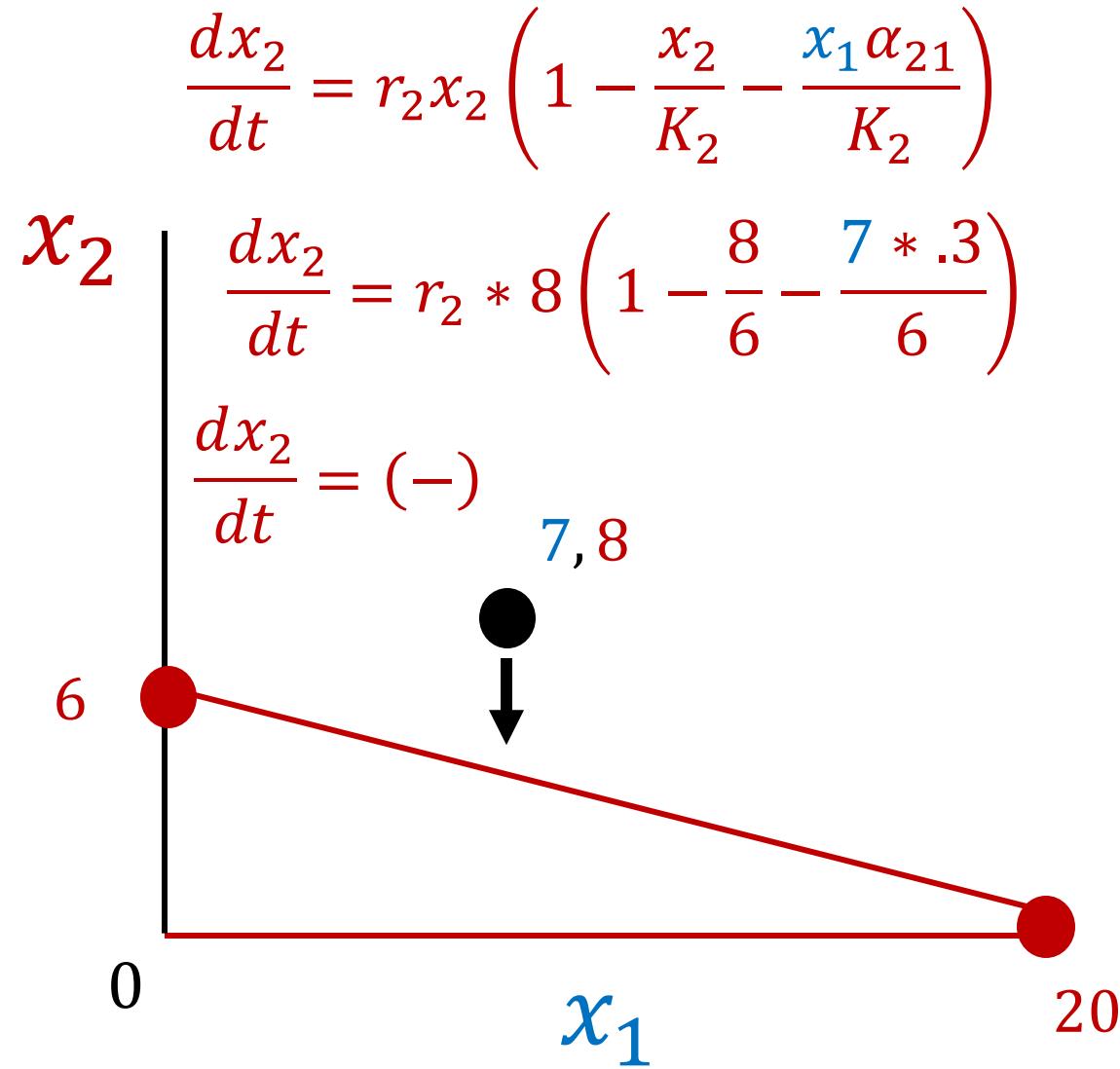
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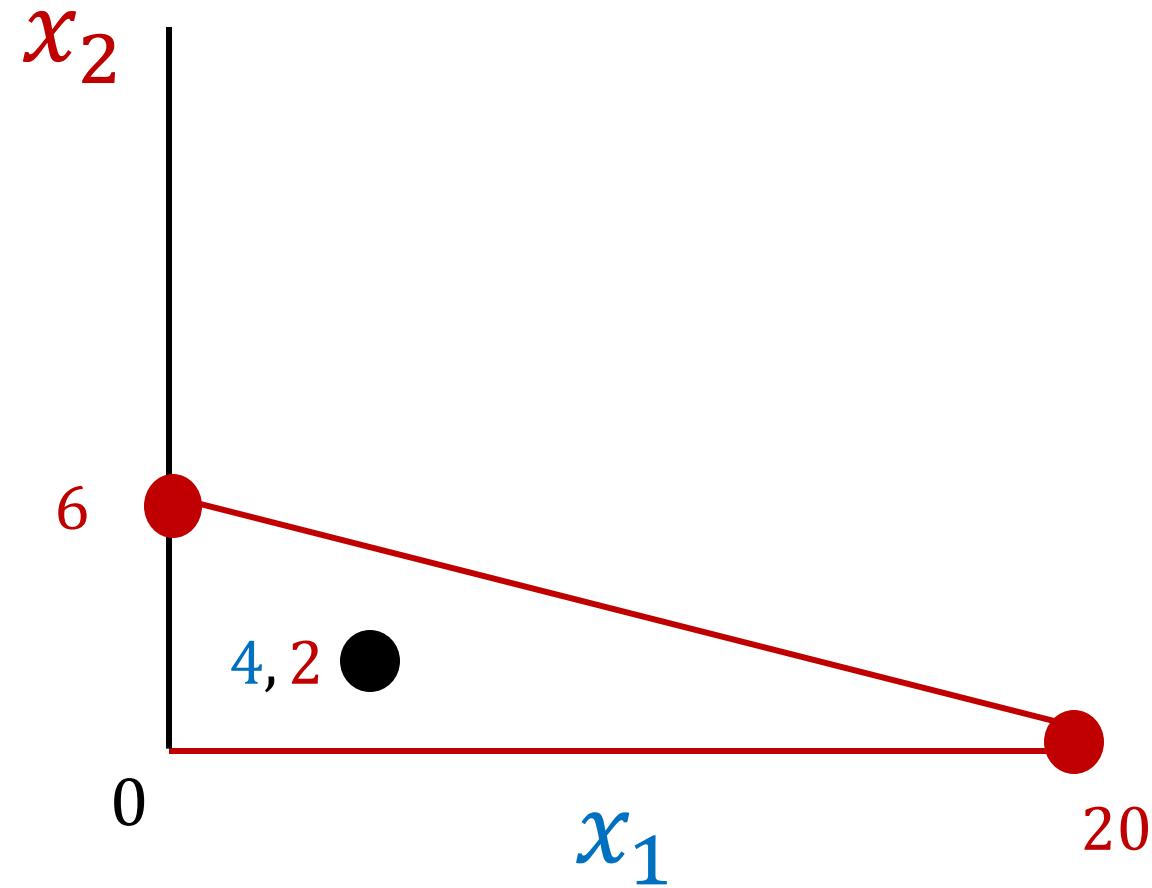
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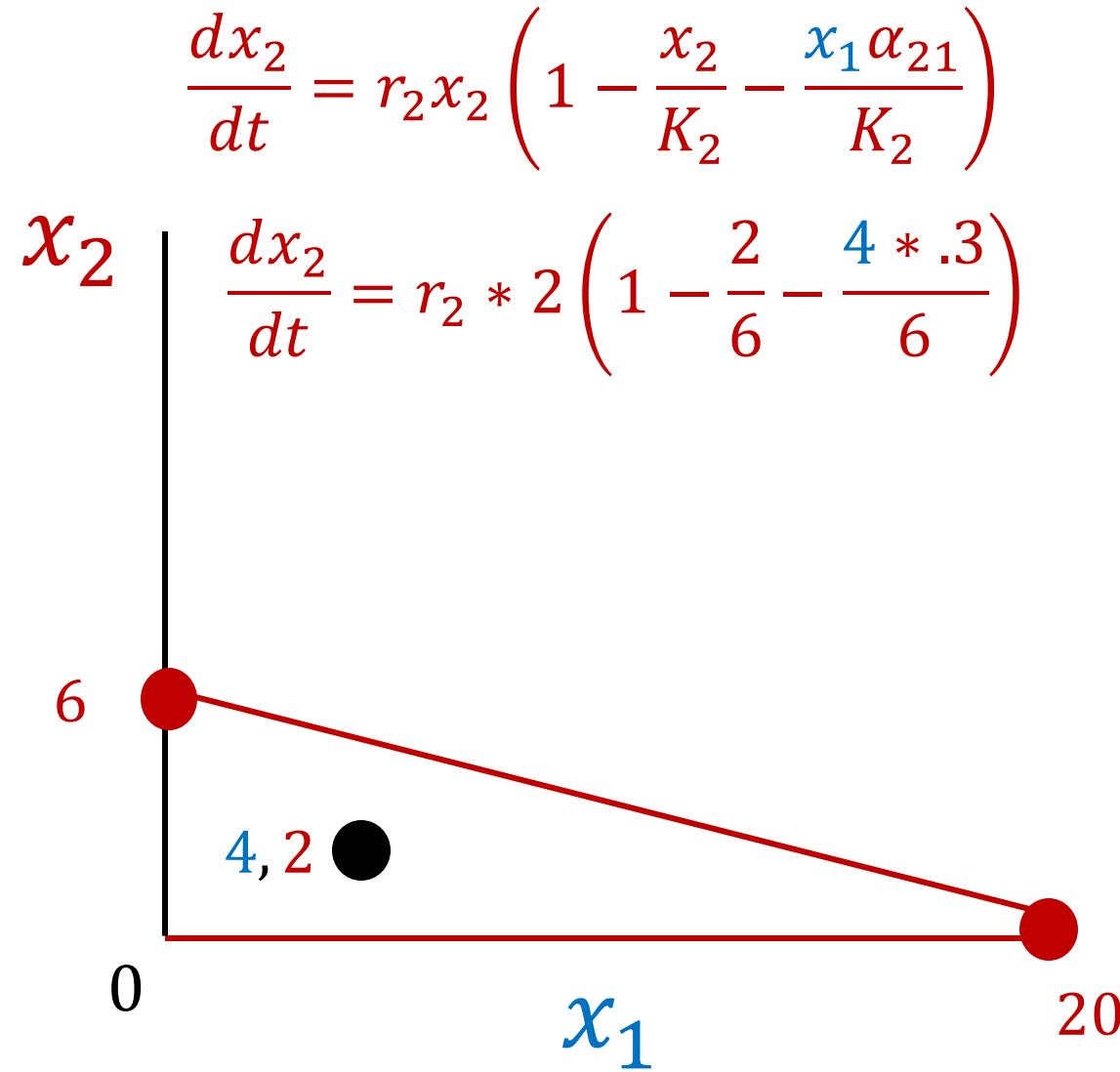
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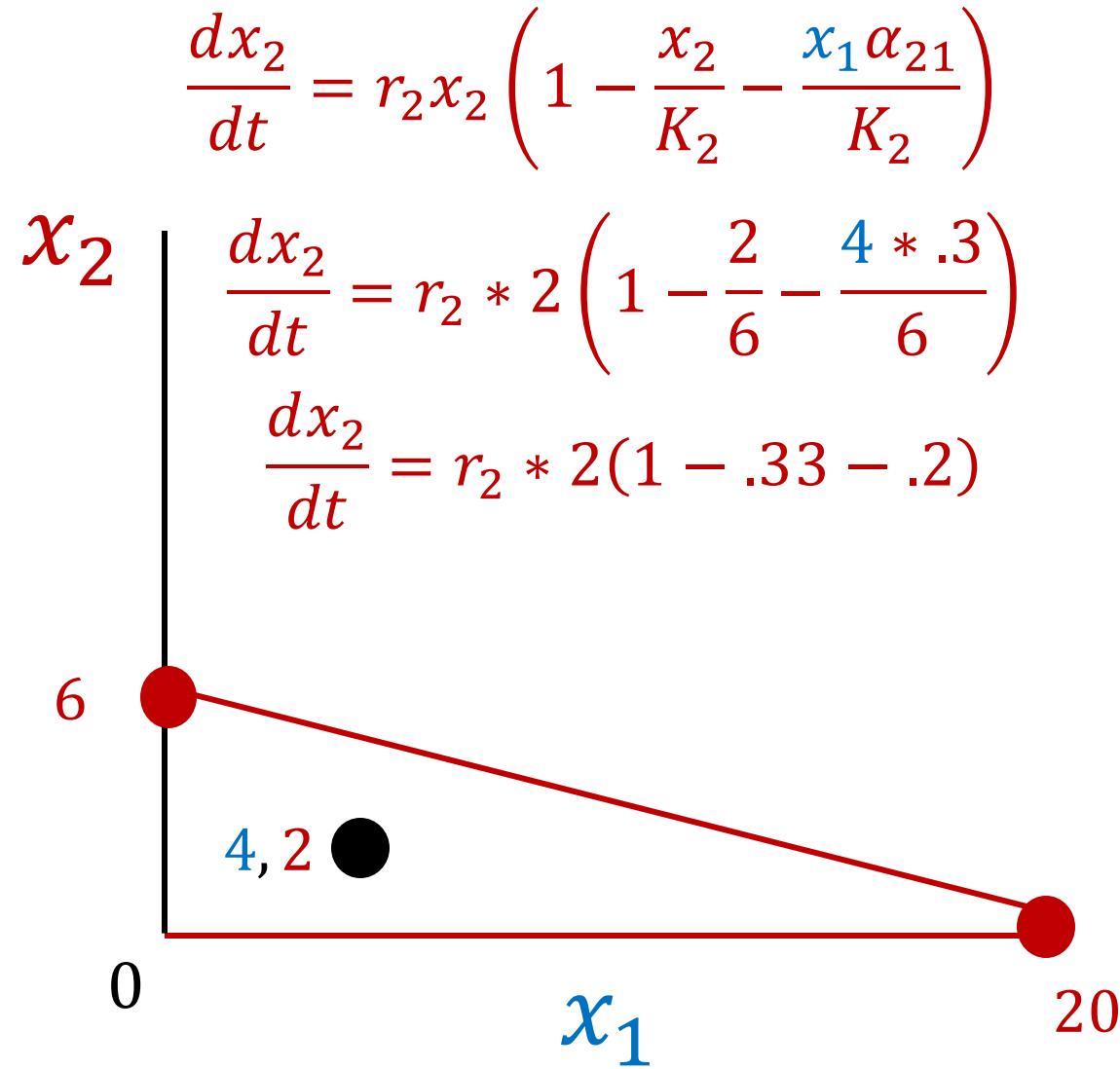
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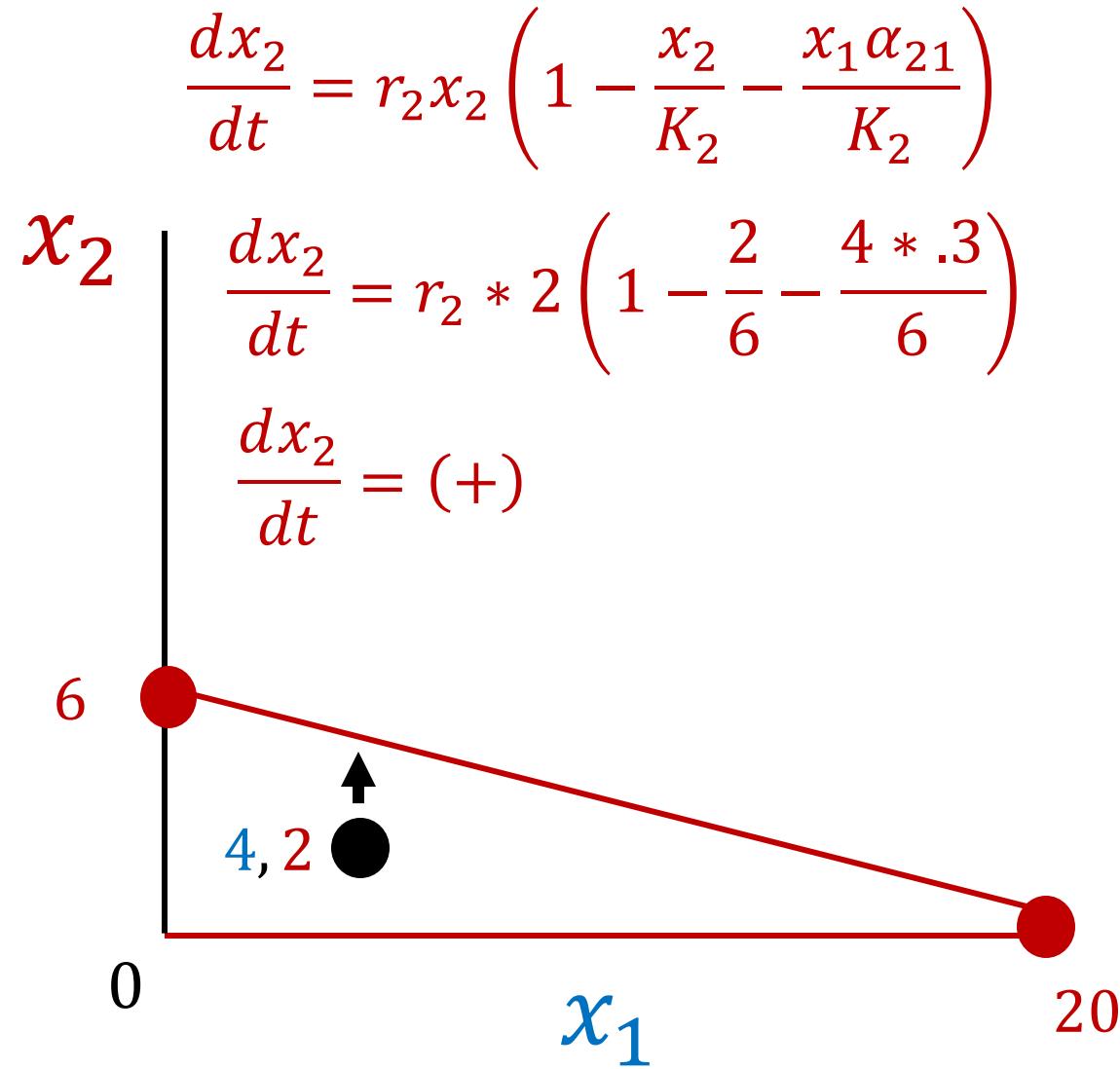
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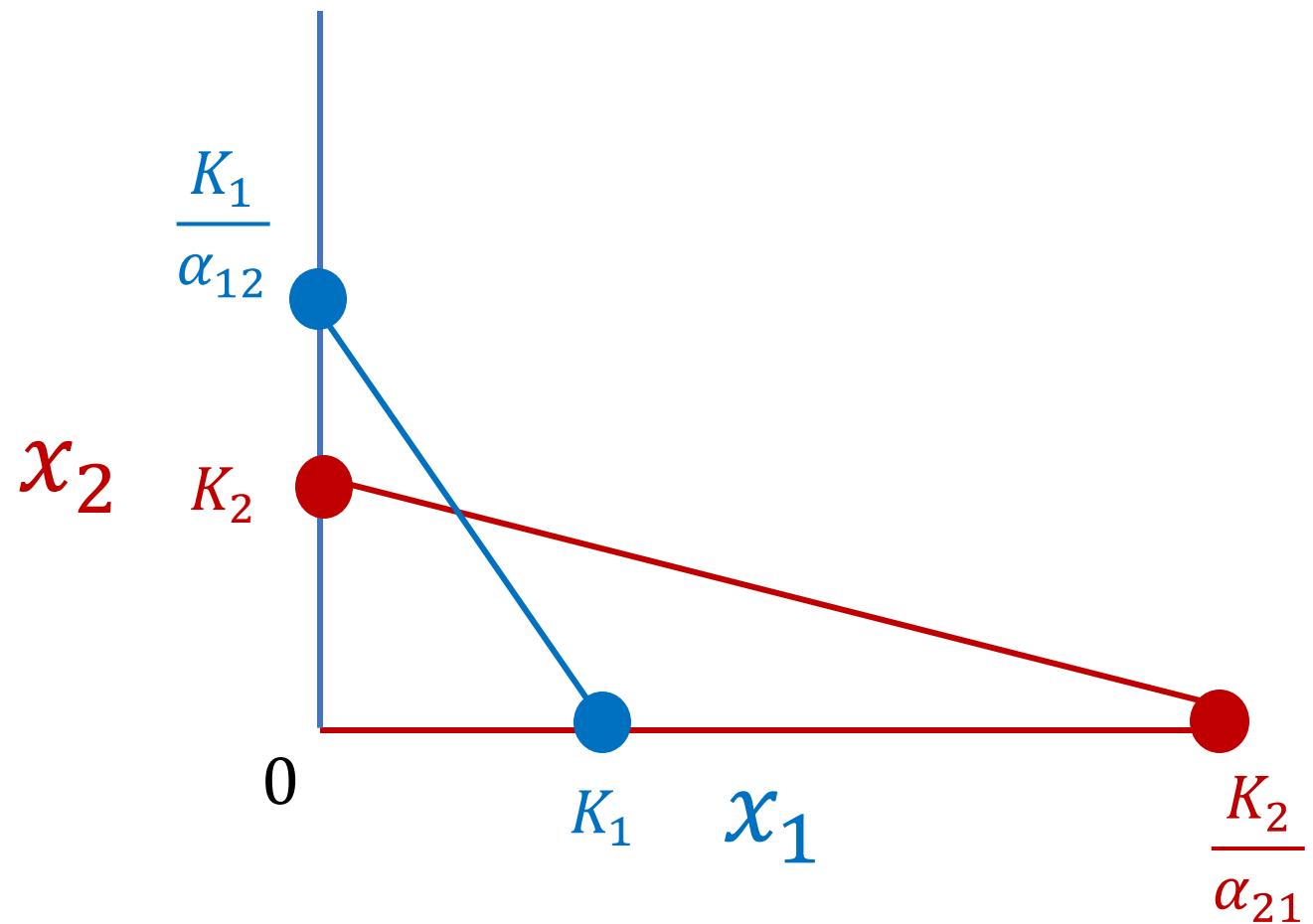


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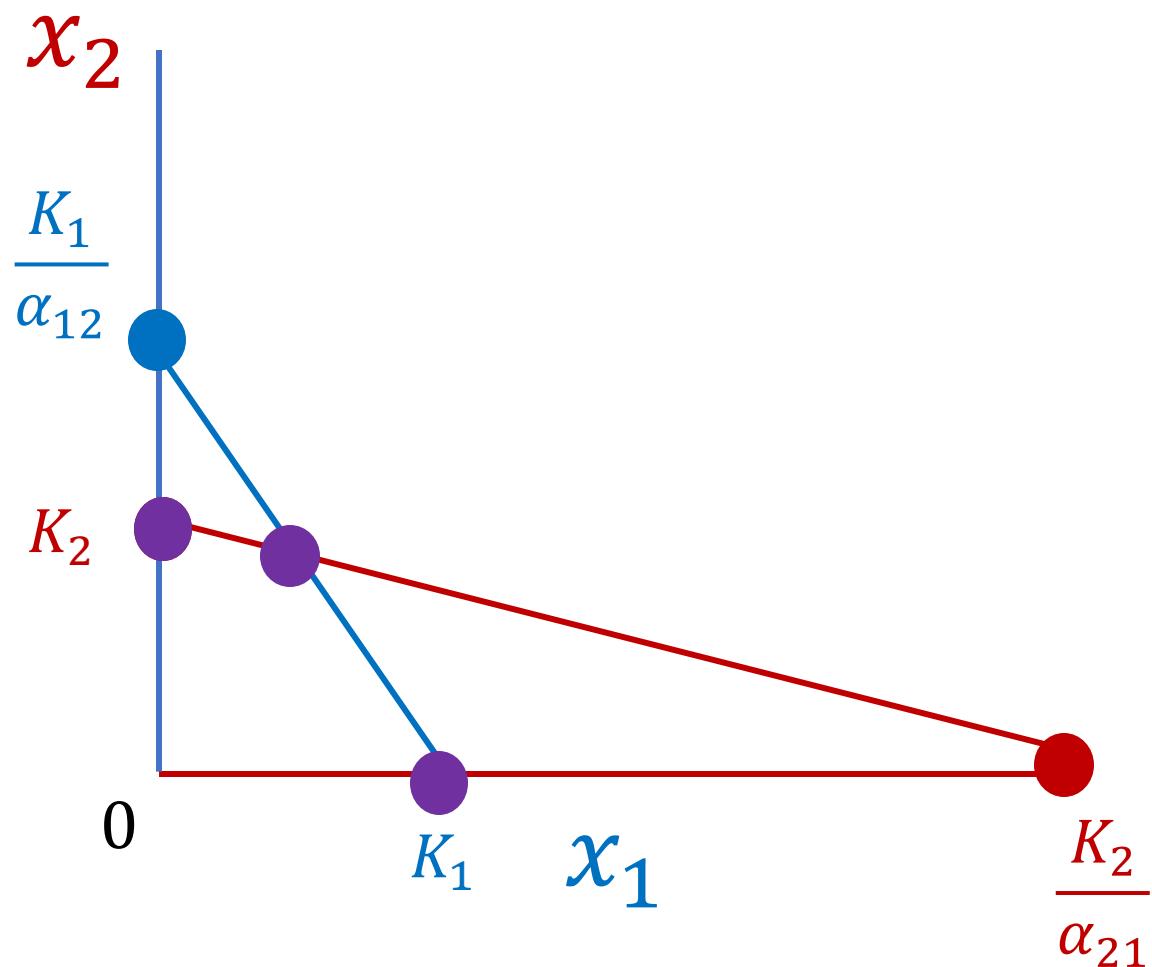


Given different combinations of x_1 and x_2 what is the outcome of competition?

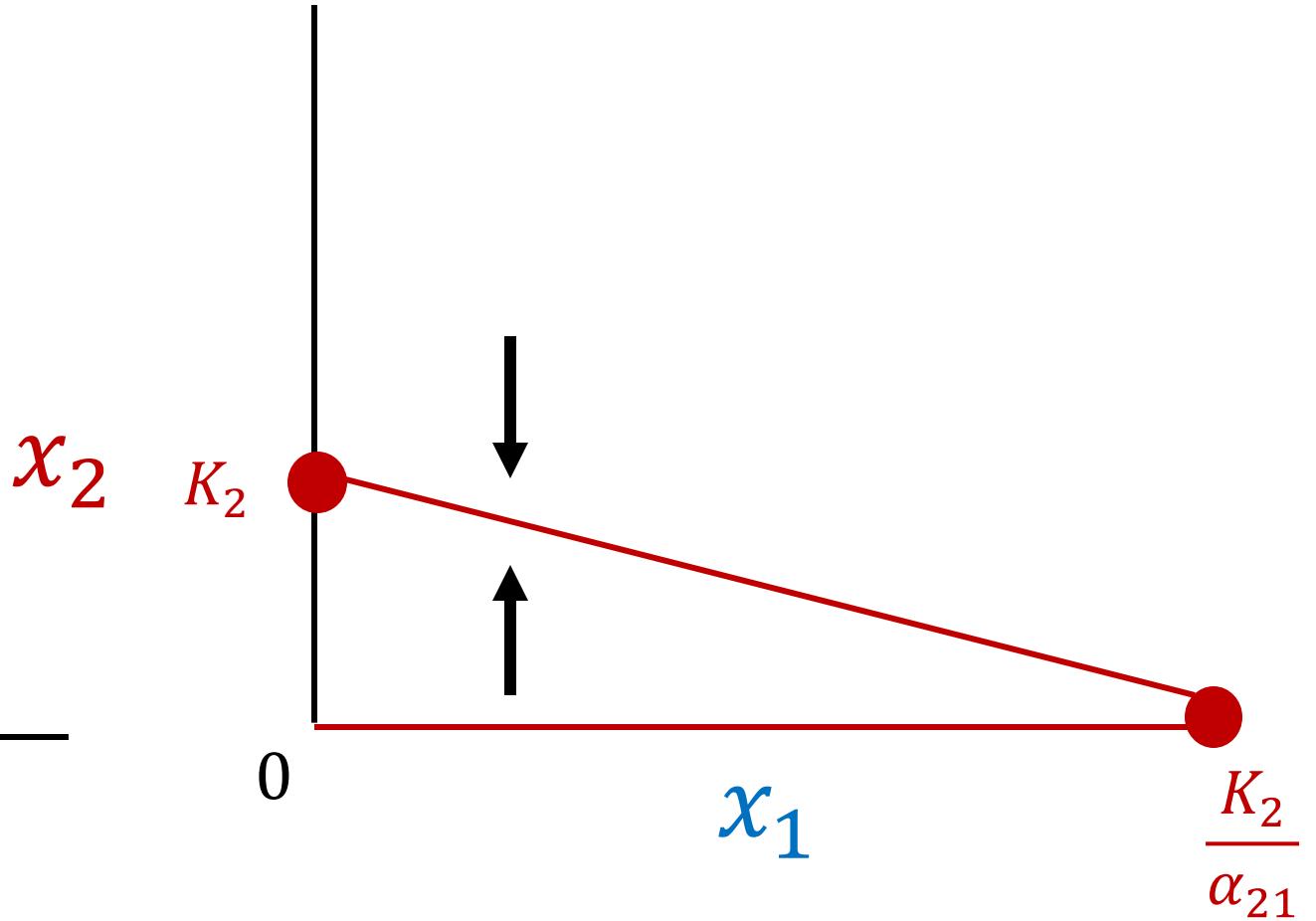
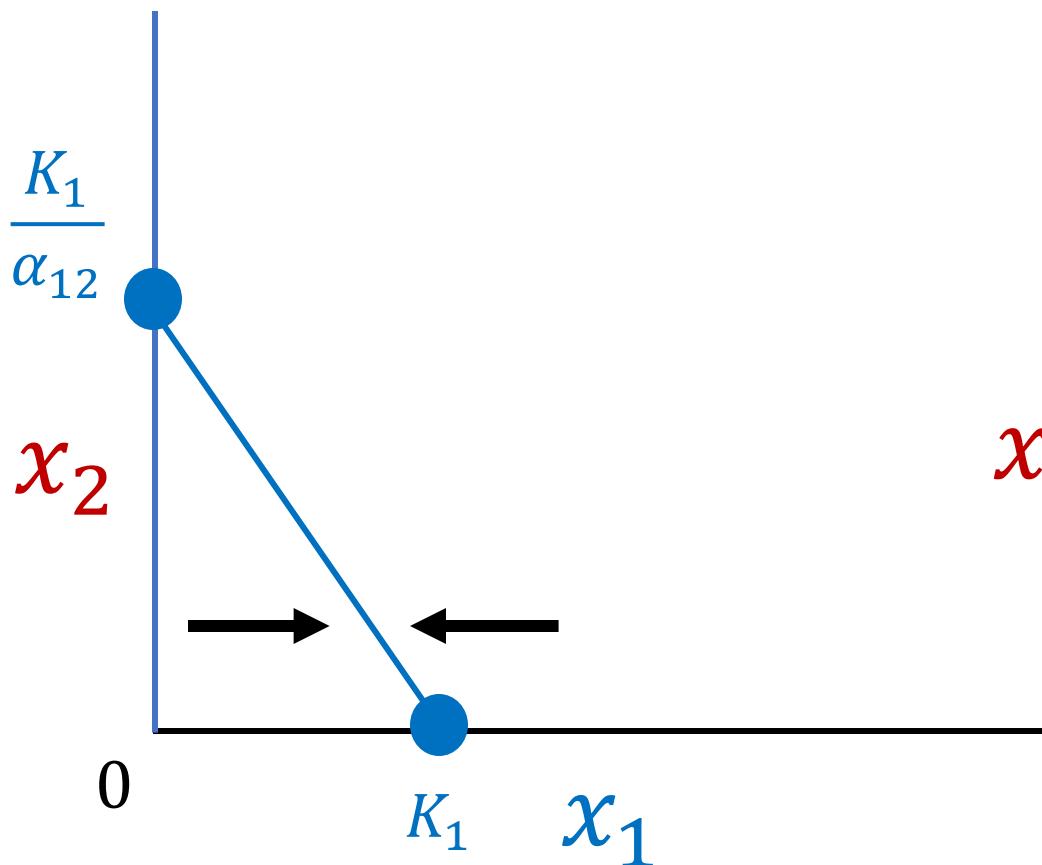


Given different combinations of x_1 and x_2 what is the outcome of competition?

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



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

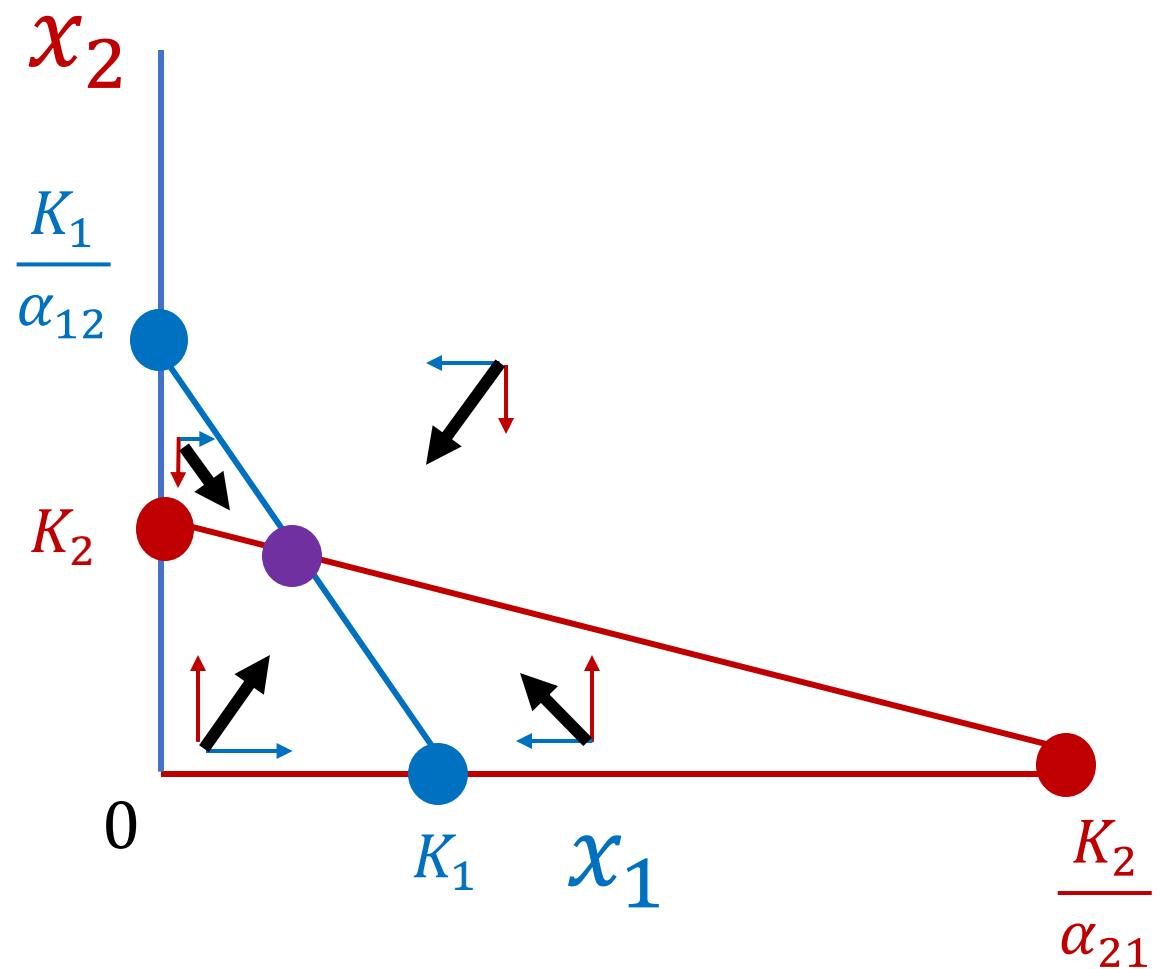


We can use vector addition from the individual nullclines to determine the outcome of competition.

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

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



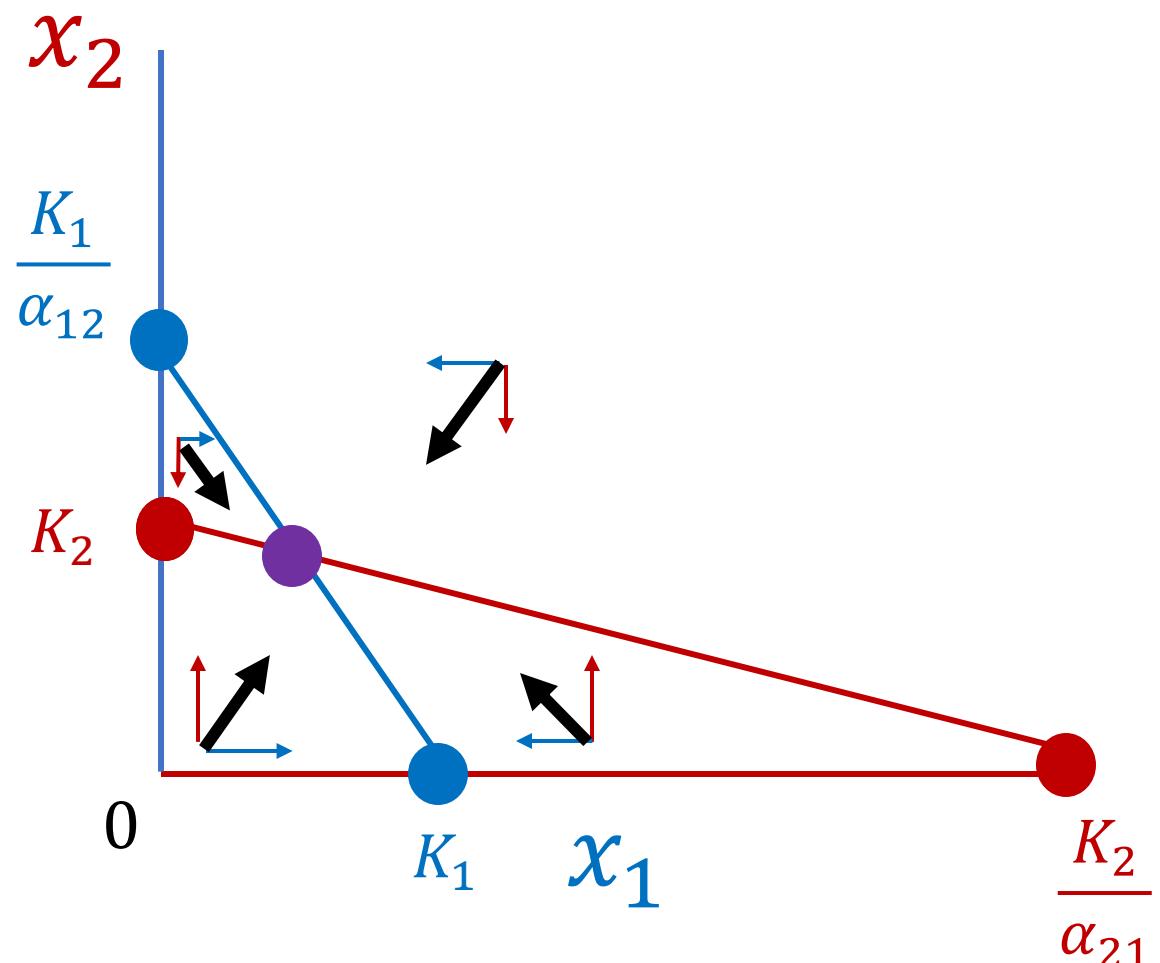
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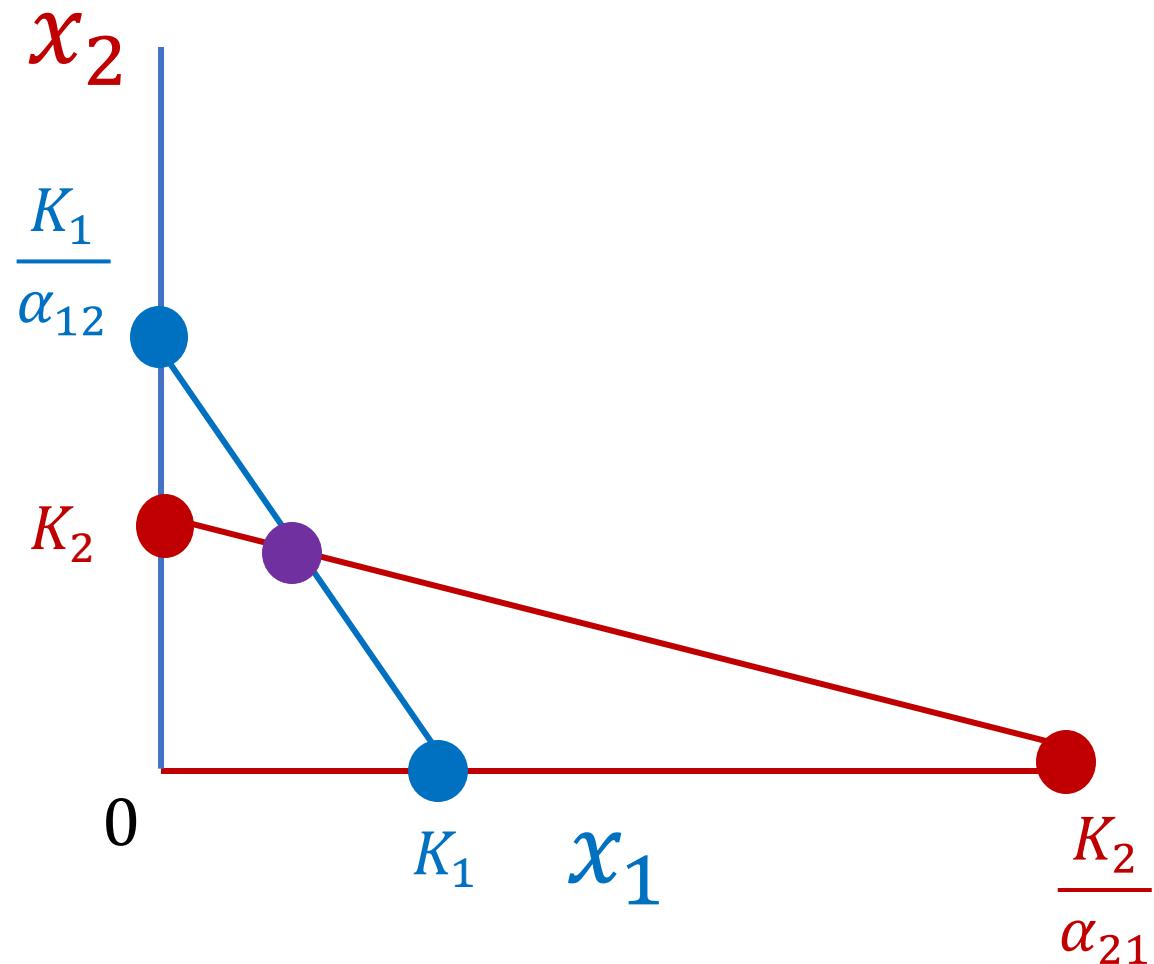
This configuration is a **stable equilibrium**, indicating **stable coexistence** at:

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



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

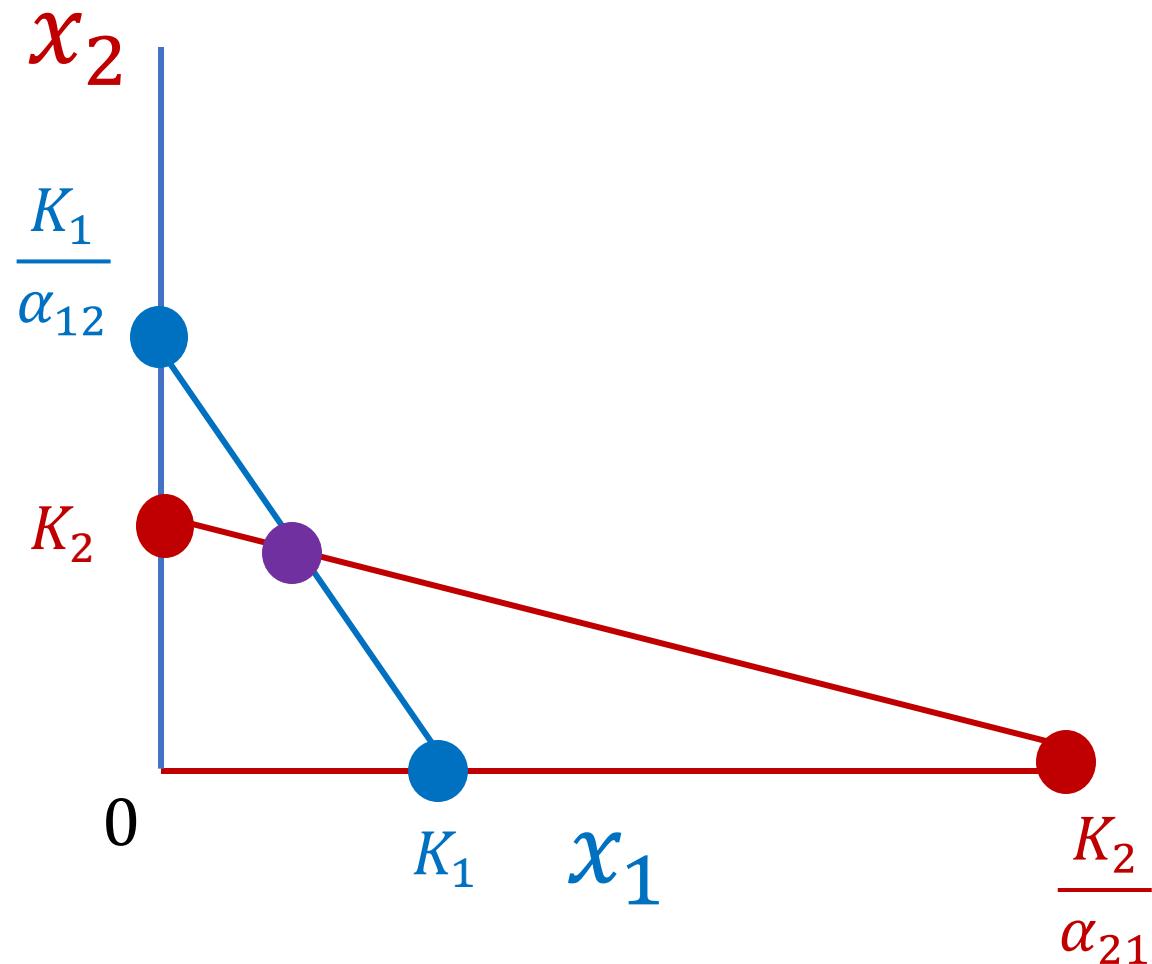
Like before, we can also solve $\frac{dx_1}{dt}$ at different combinations of x_1 and x_2 to test the direction the x_1 population will move during competition (always along the x-axis).



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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).

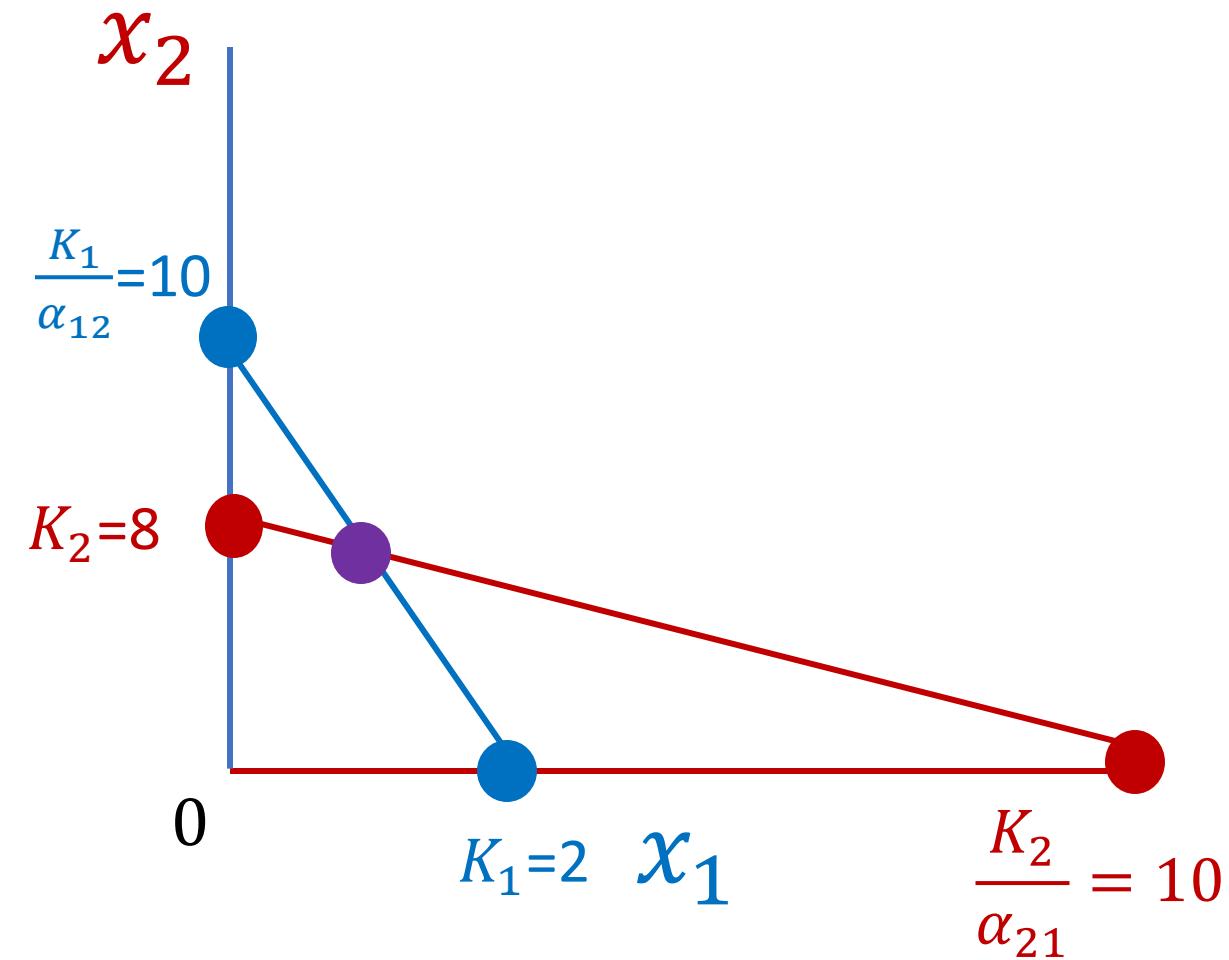


Given different combinations of x_1 and x_2 what is the outcome of competition?

Let's try it!

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

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



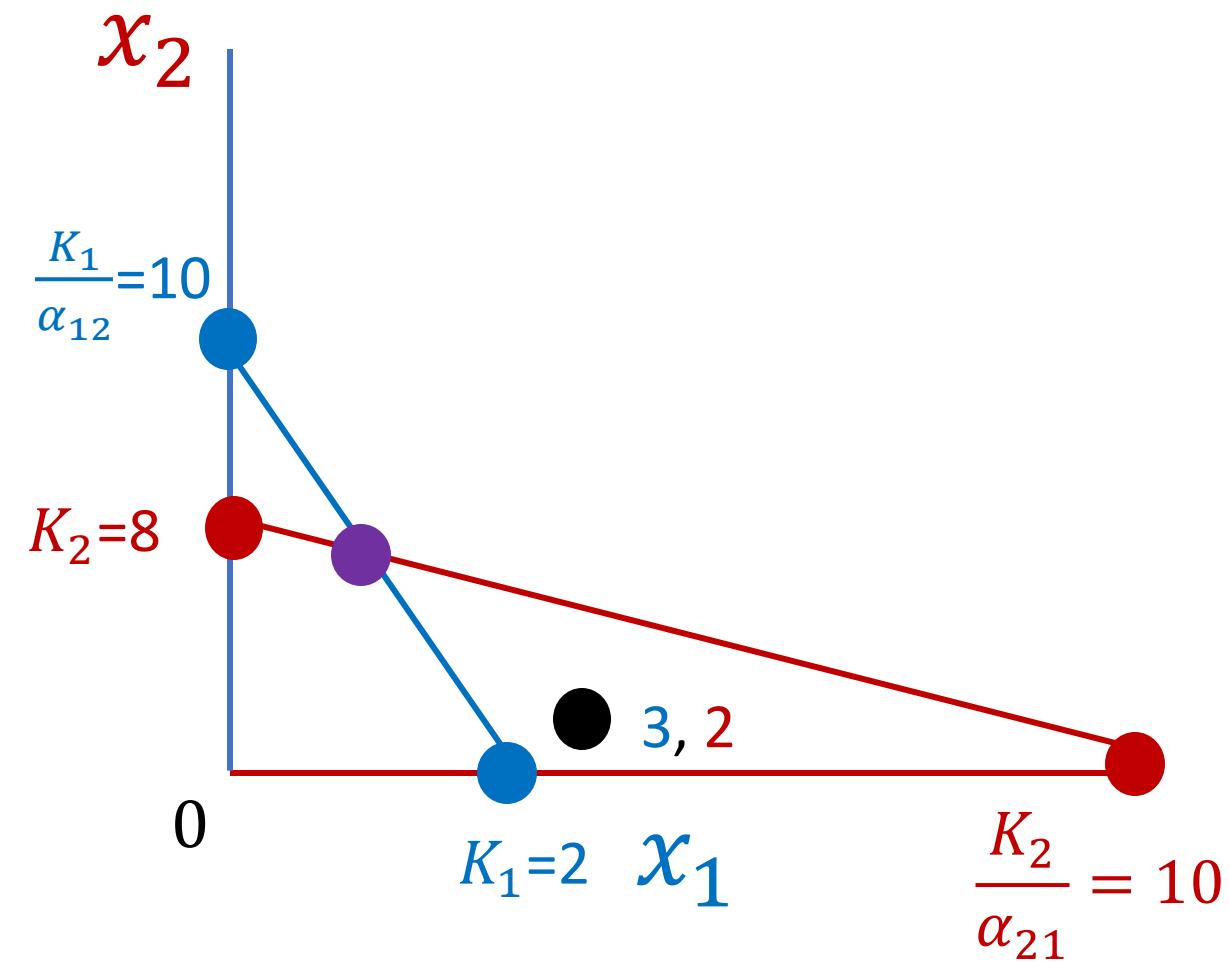
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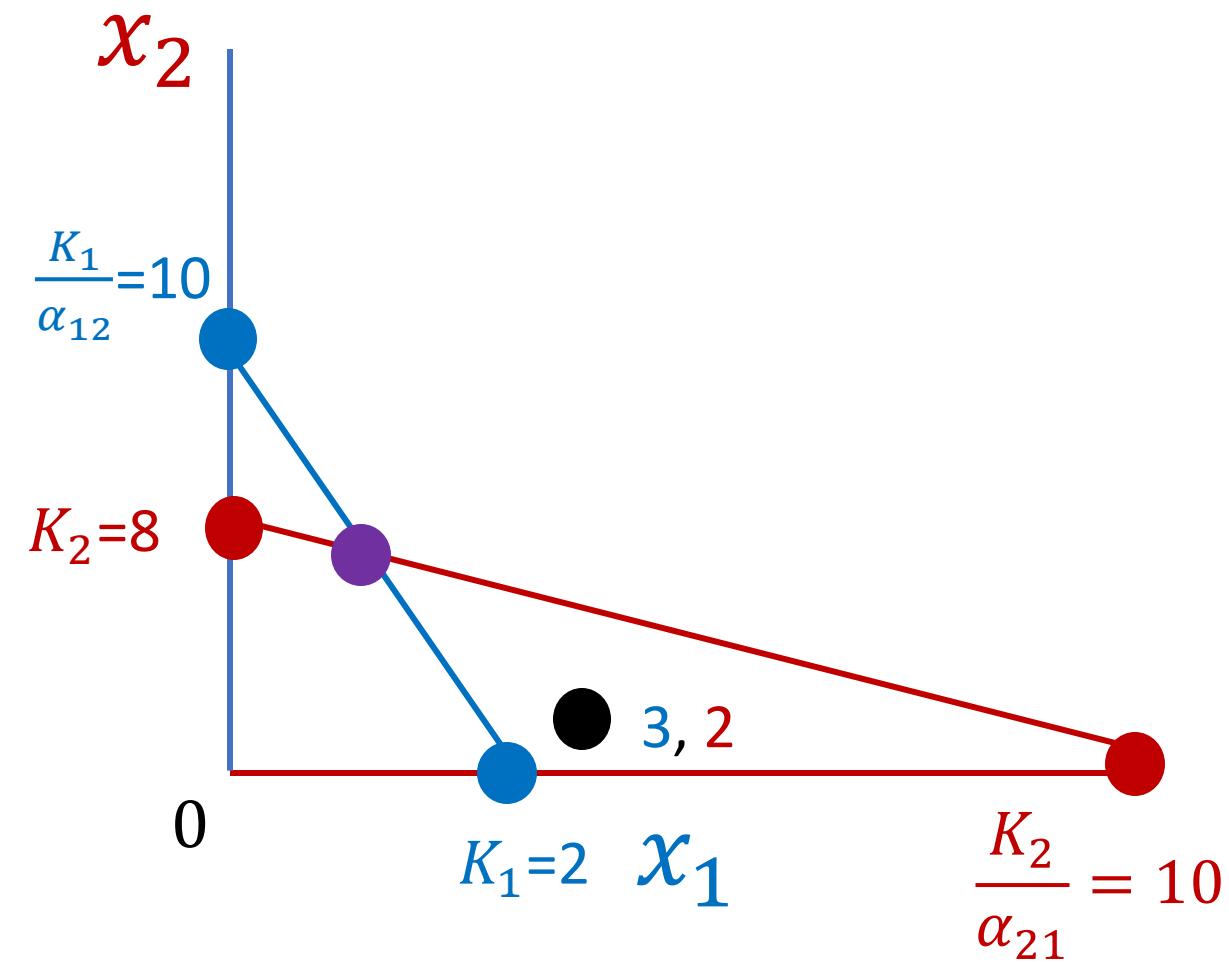
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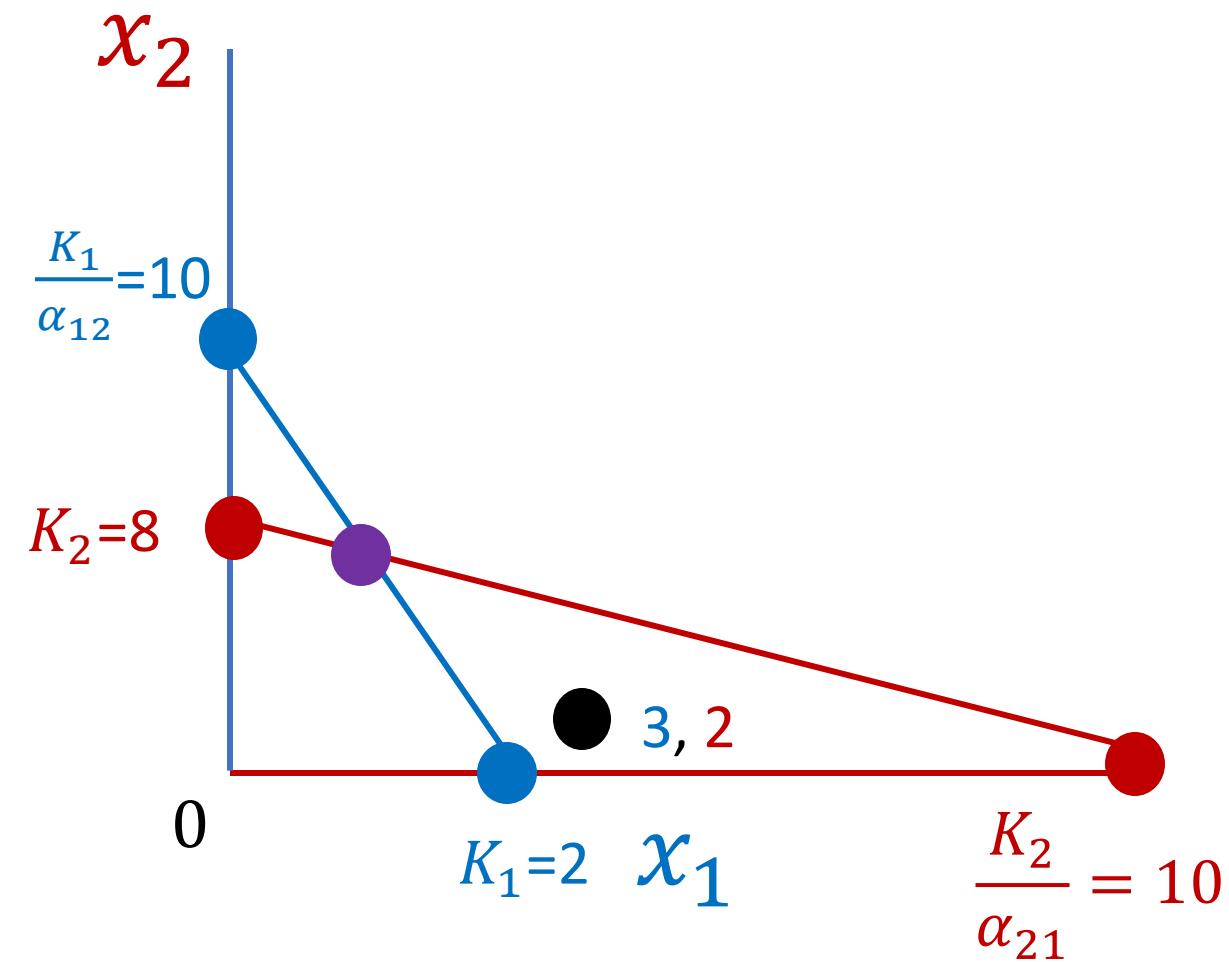
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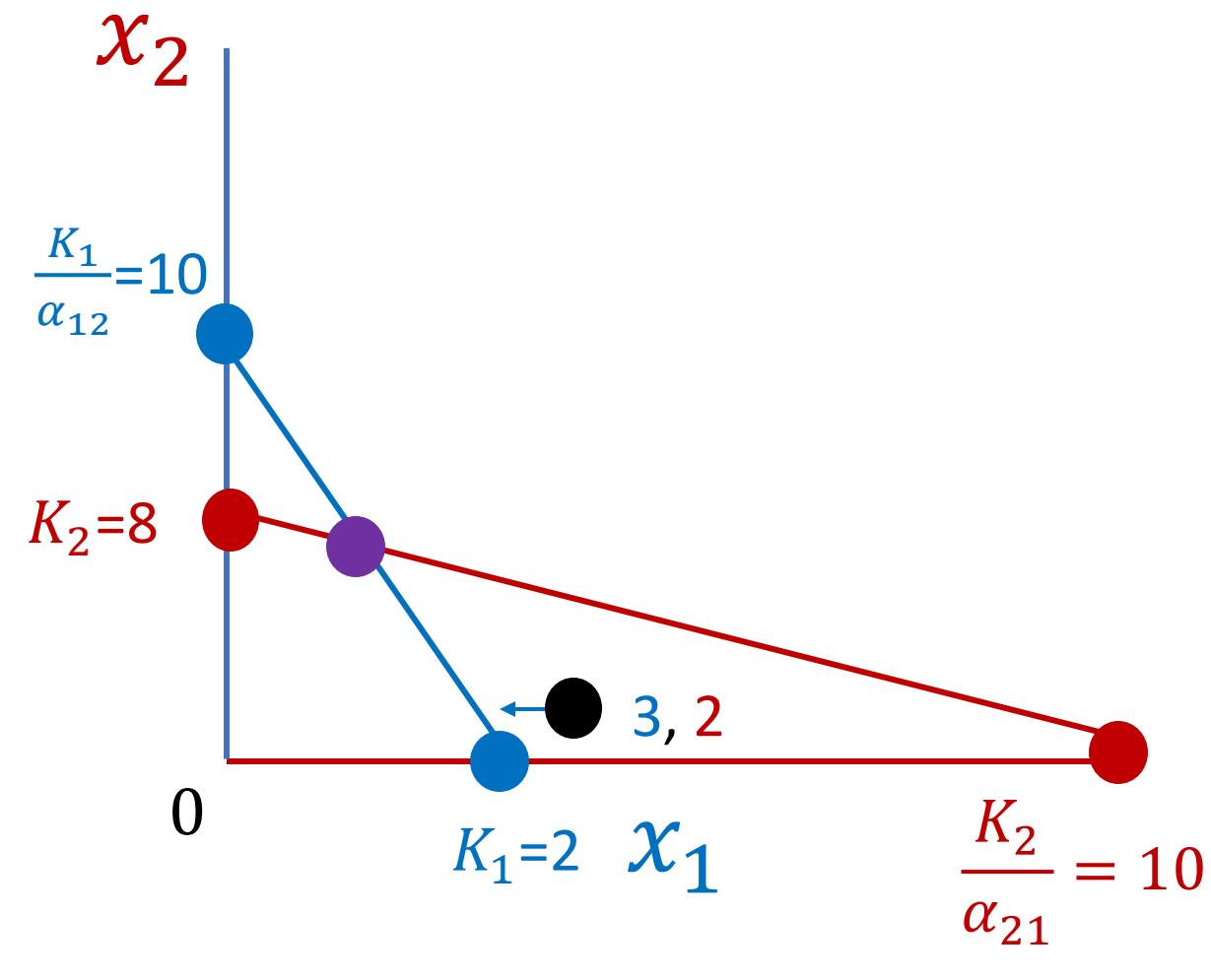
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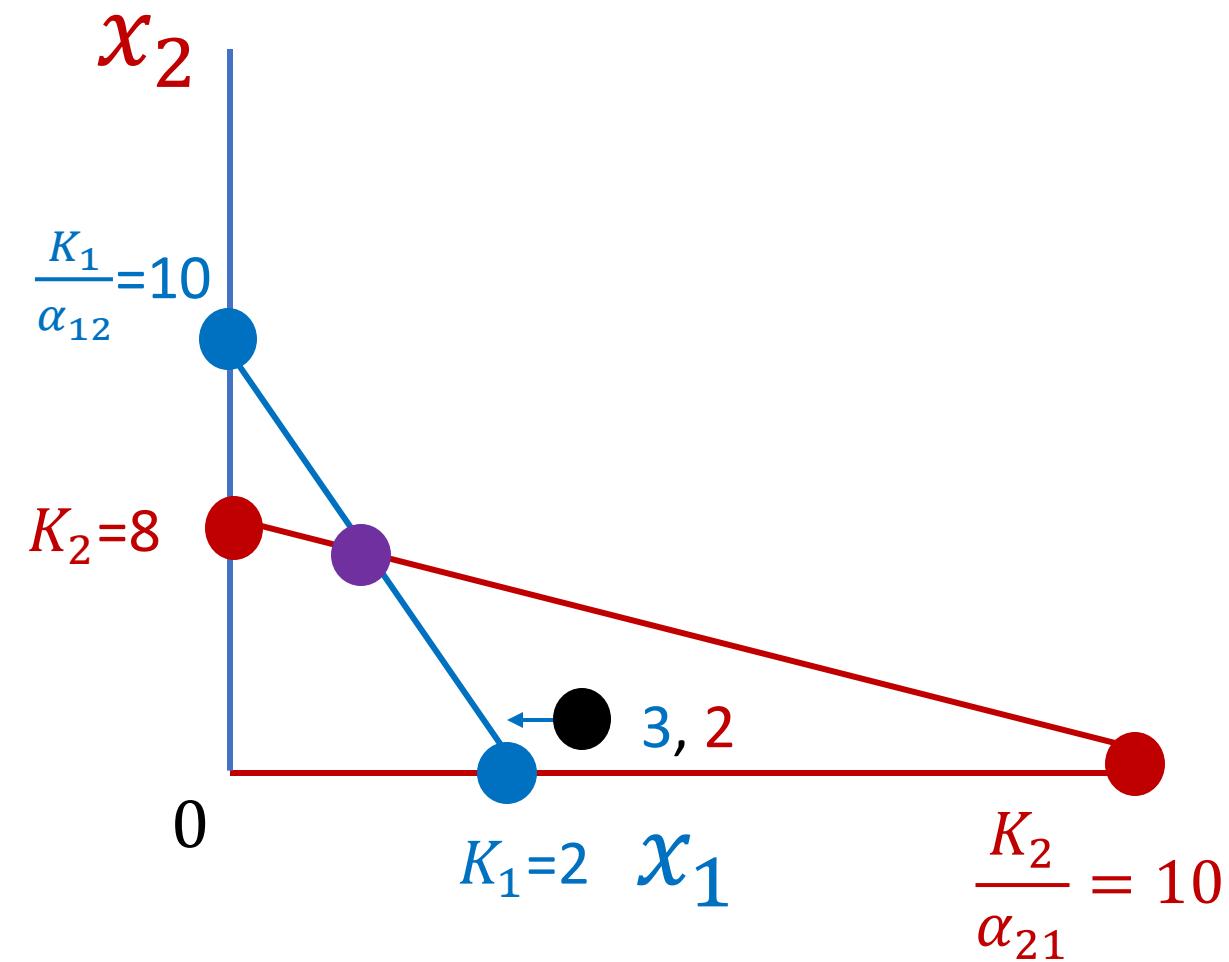
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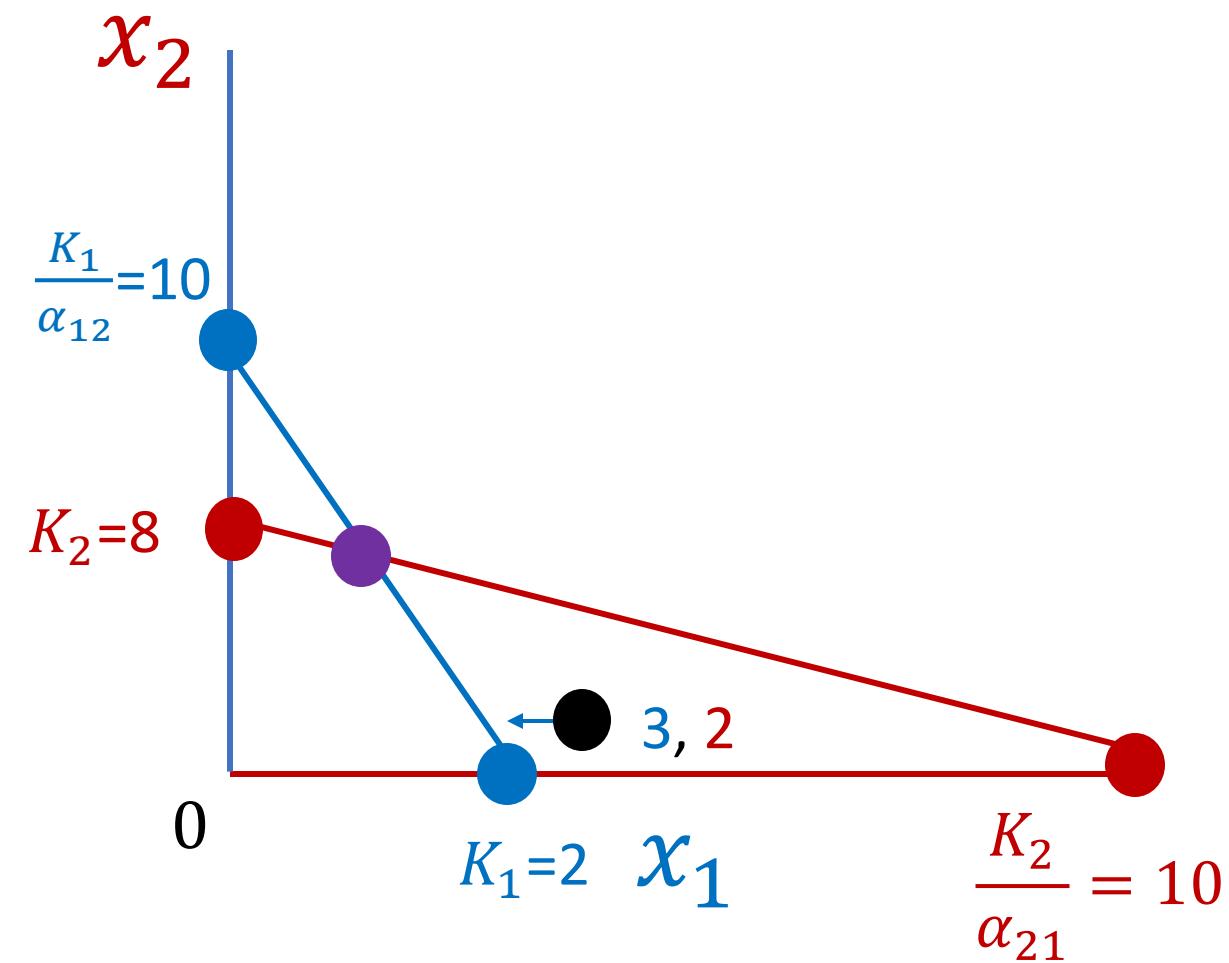
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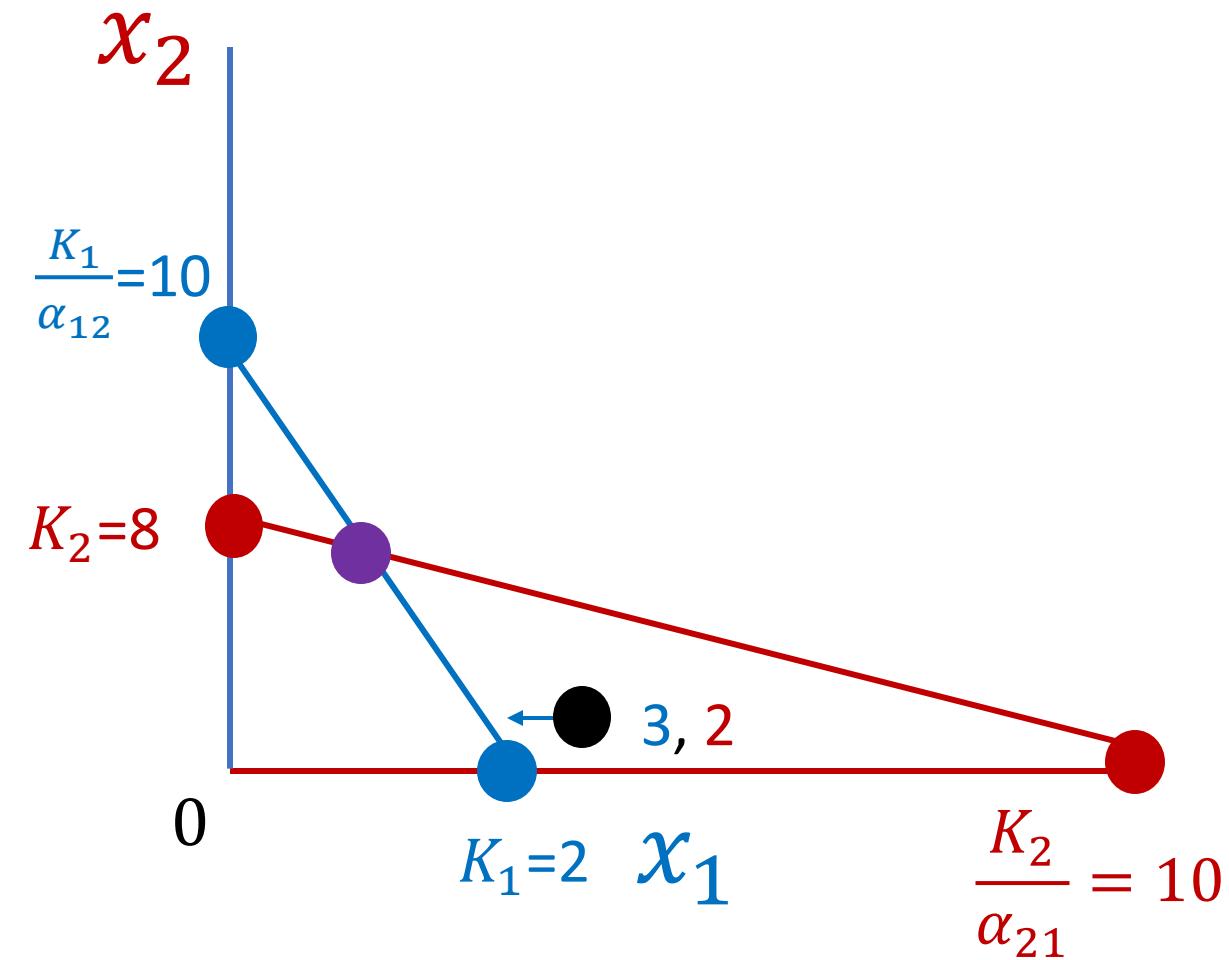
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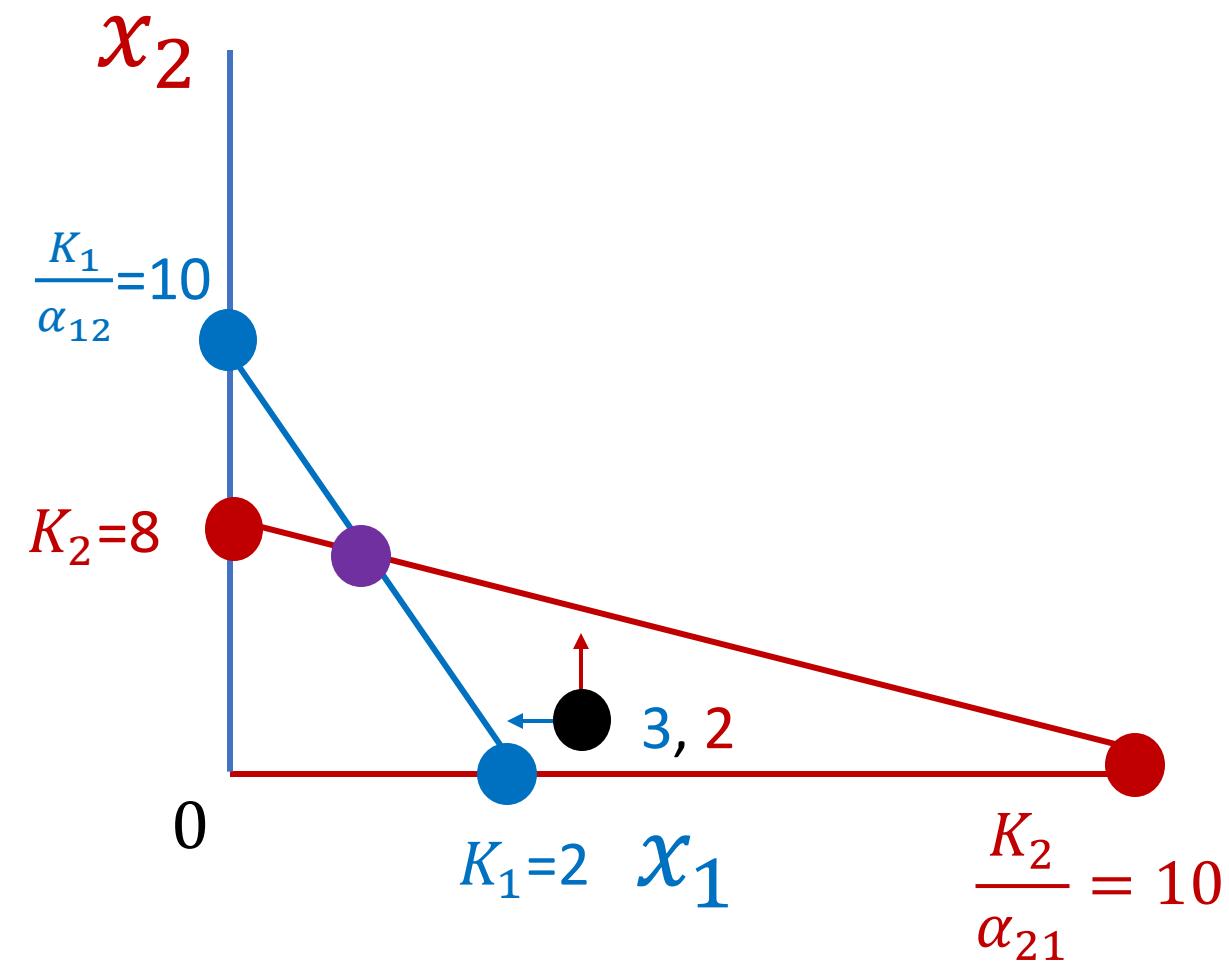
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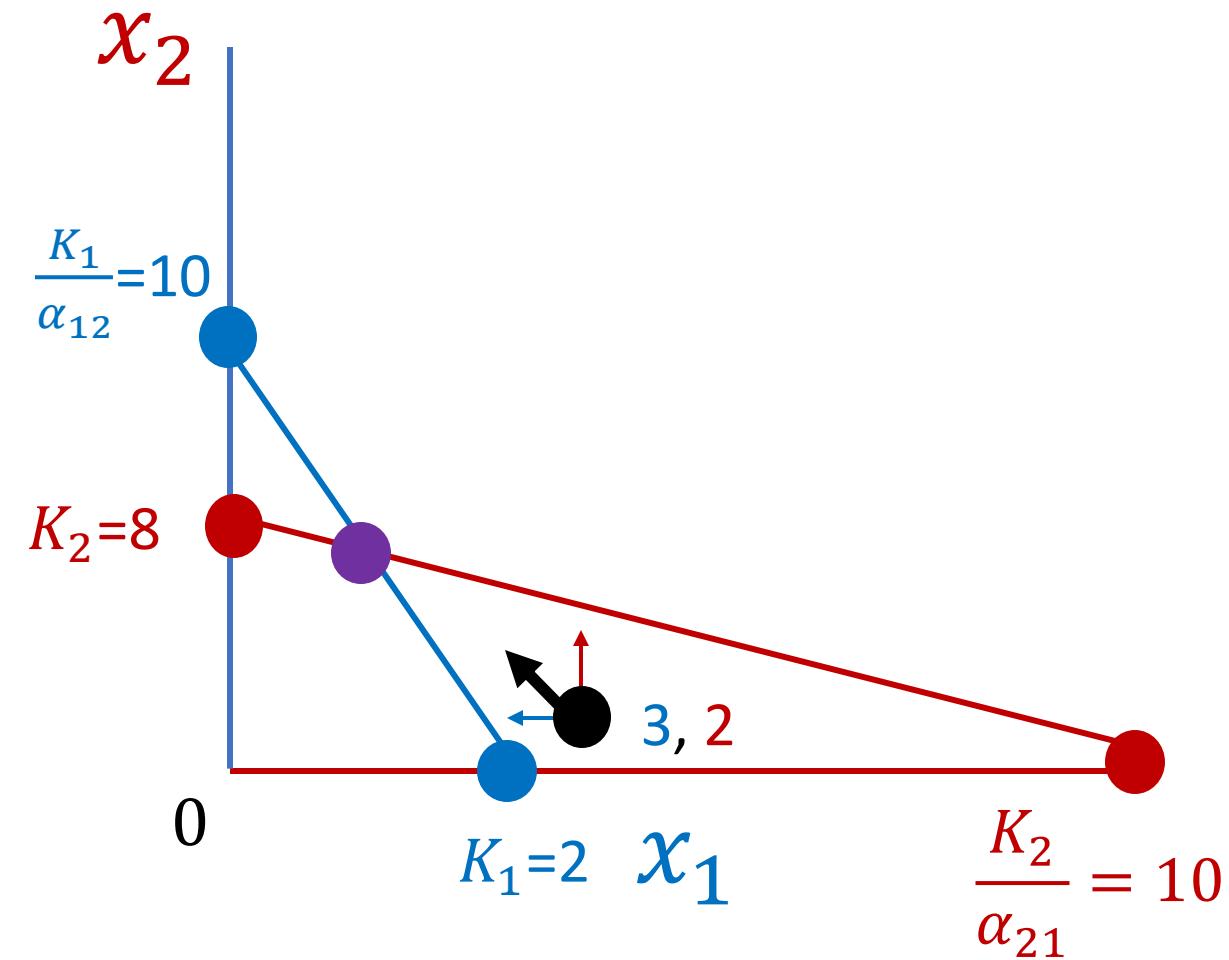
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Results replicate graphical approach!

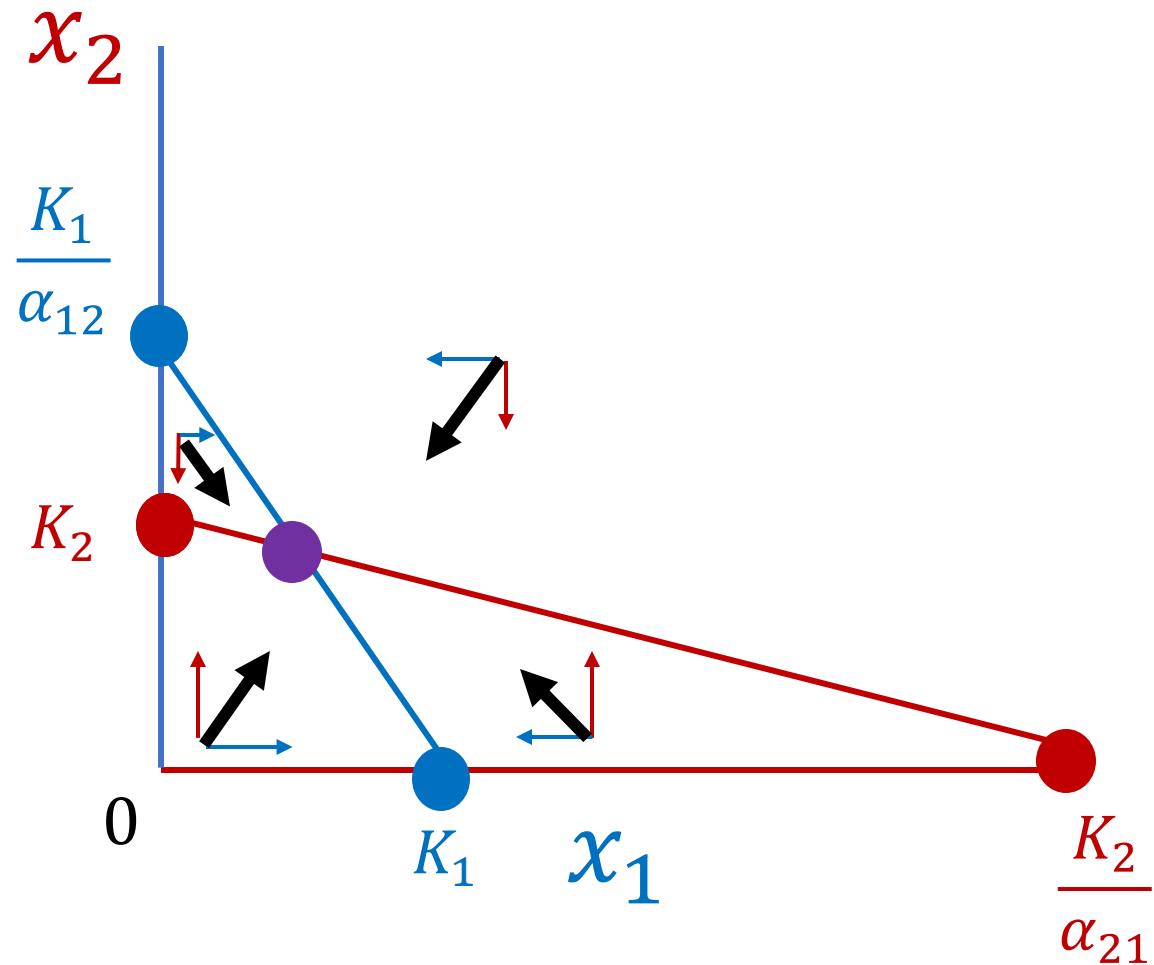


Four possible outcomes for competition

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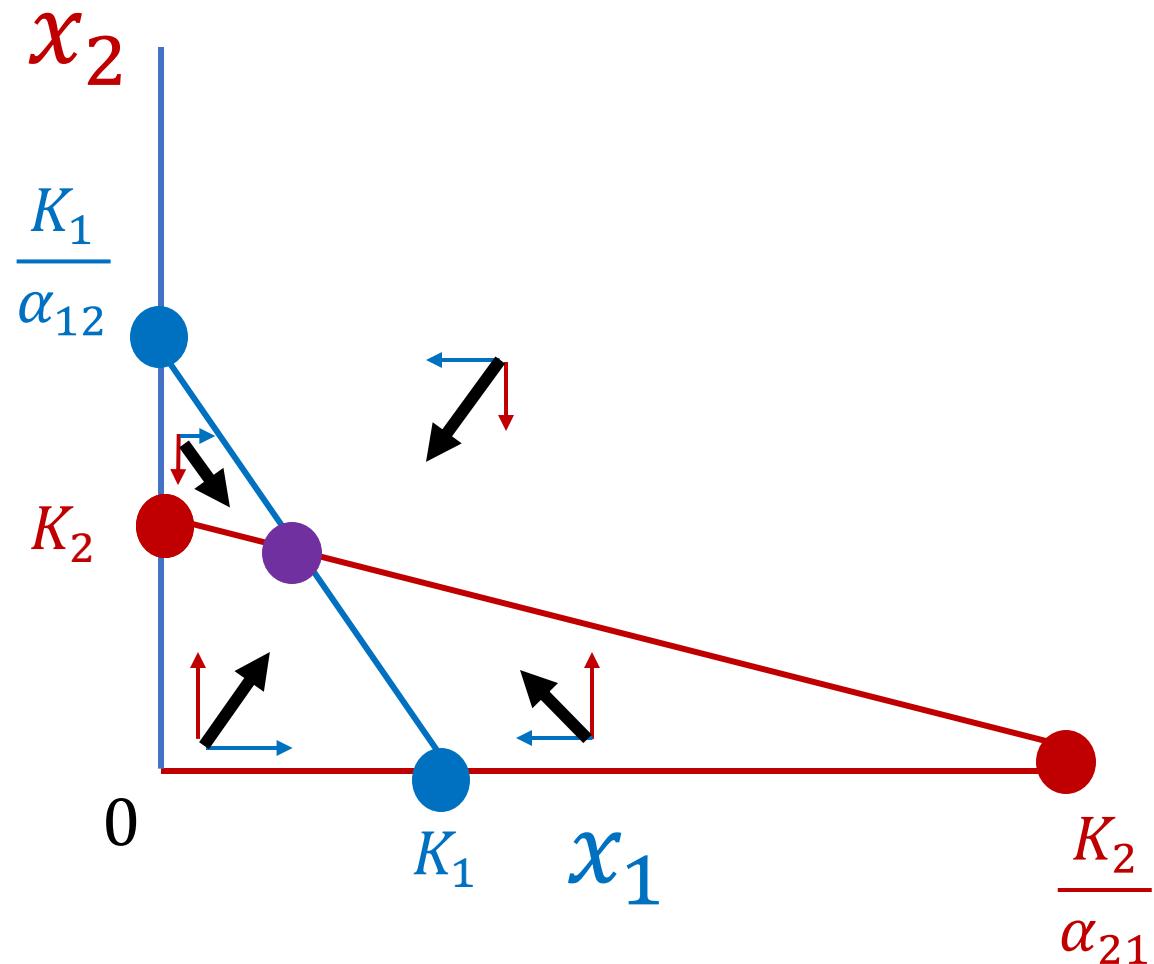
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$$\frac{K_1}{\alpha_{12}} > K_2 \text{ & } \frac{K_2}{\alpha_{21}} > K_1$$

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



Four possible outcomes for competition

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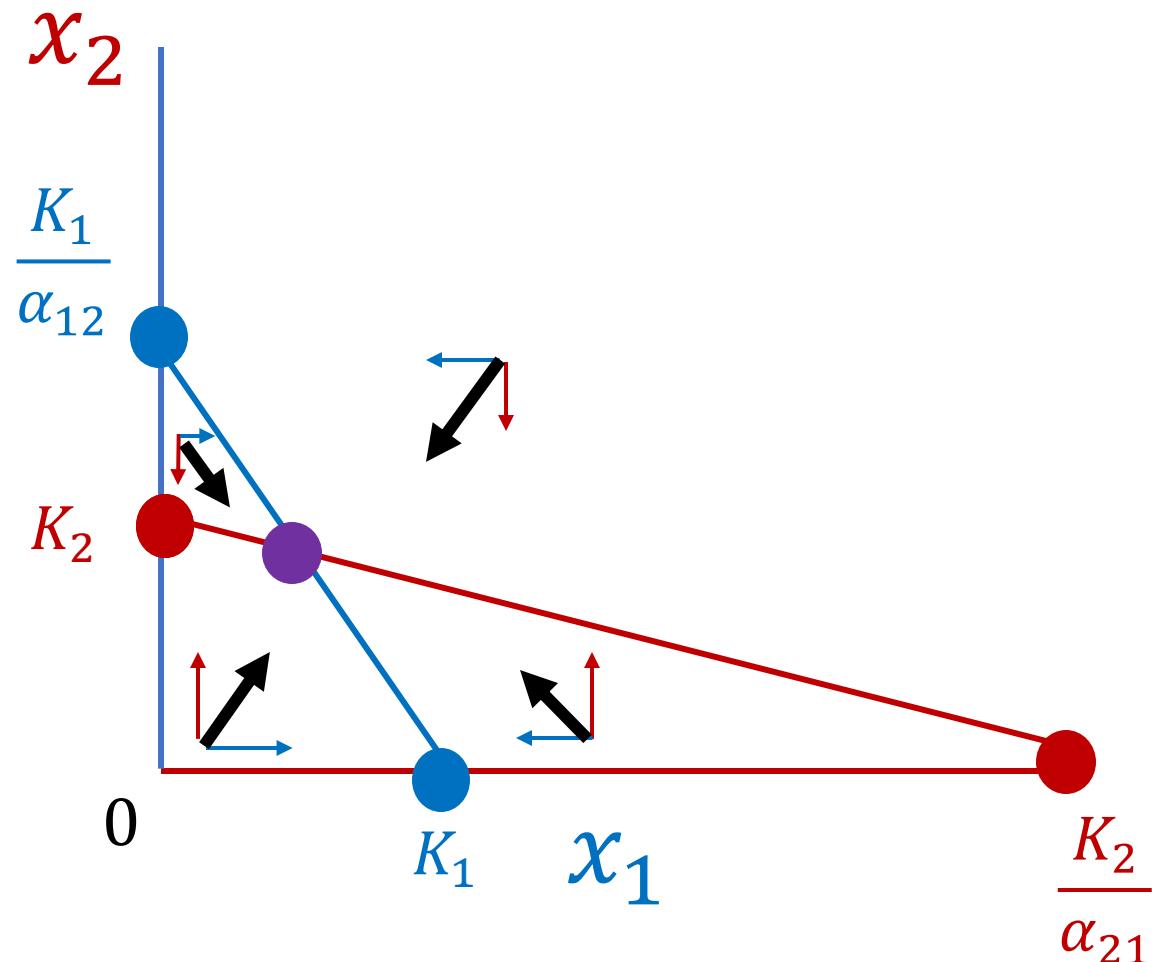
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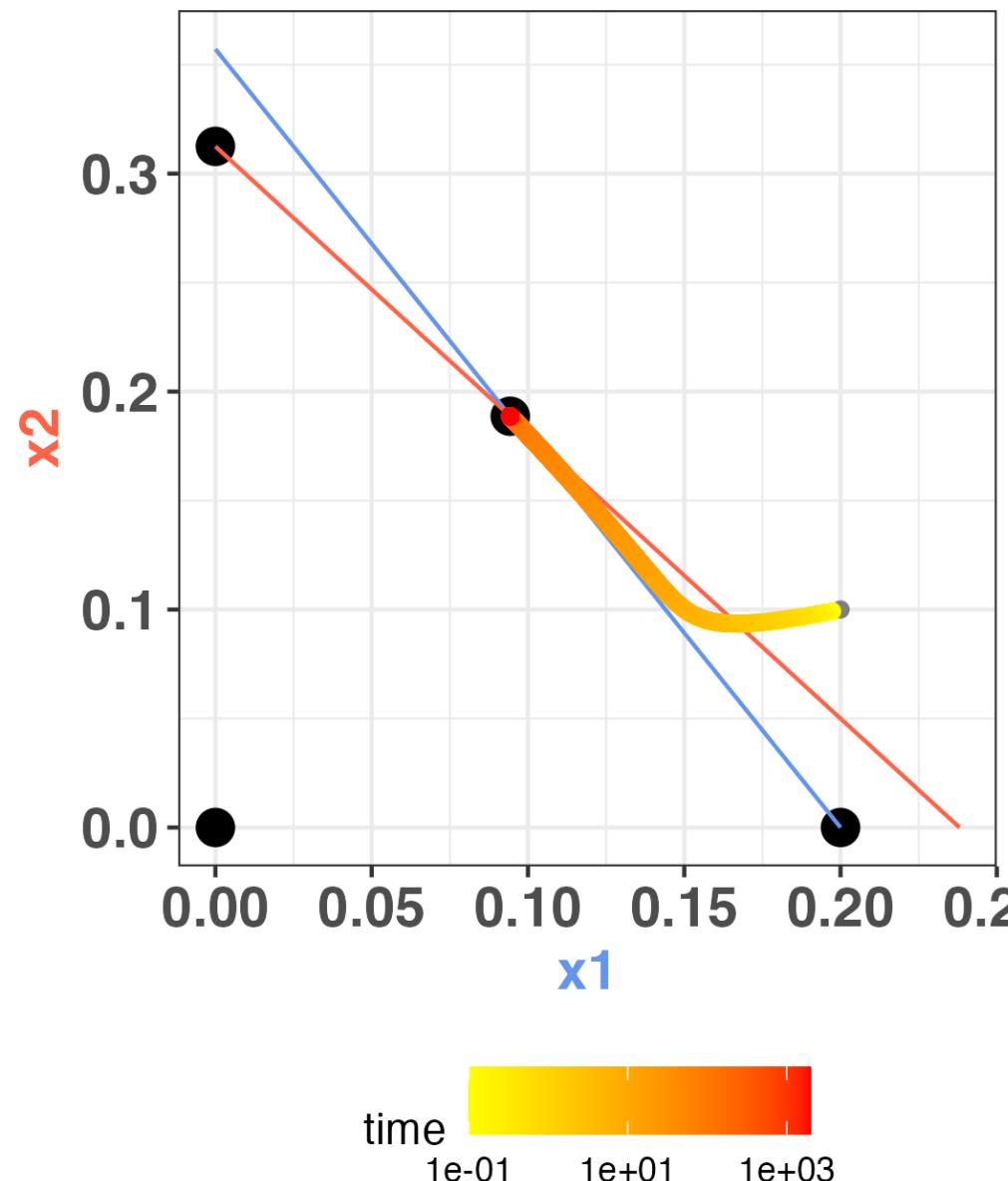
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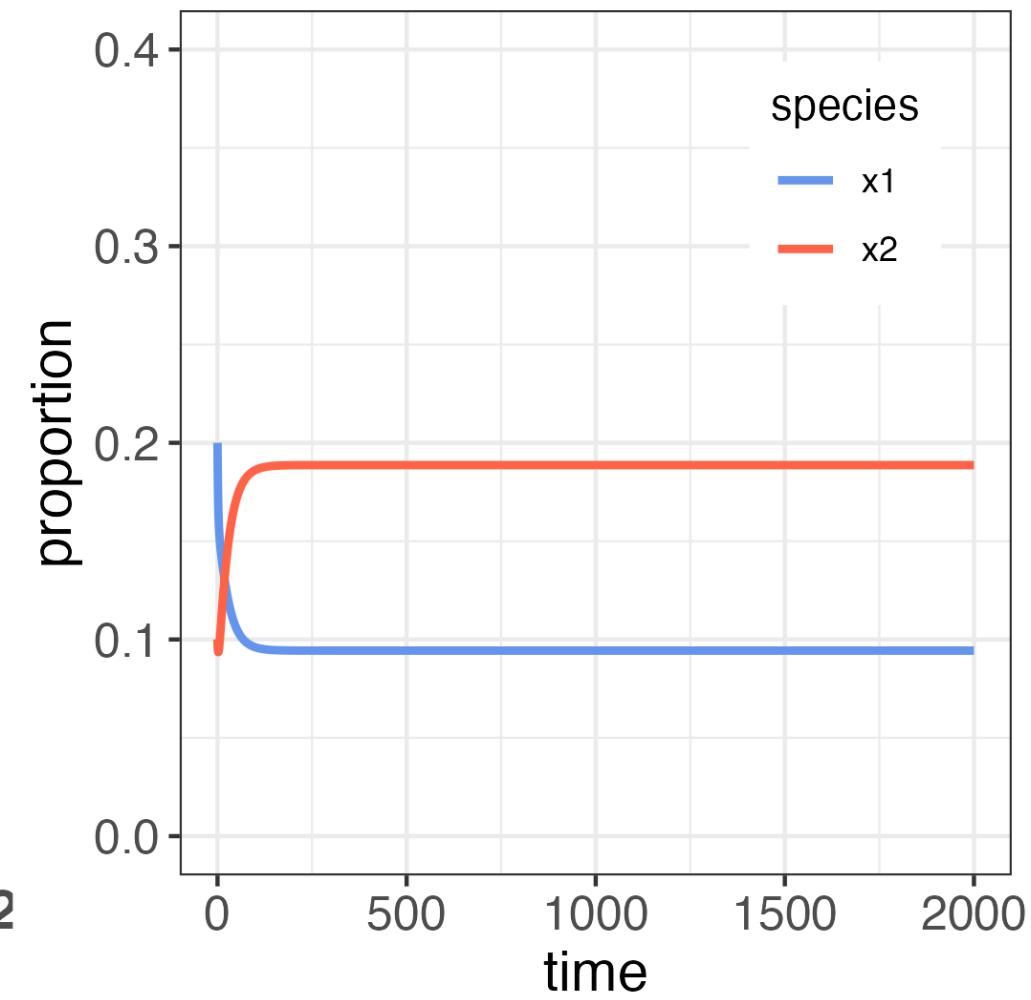
- Species coexist stably but **below carrying capacity** for each individual population.
- Intraspecific** competition is stronger than **interspecific** competition.



Case 1:
Stable equilibrium, with coexistence:



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

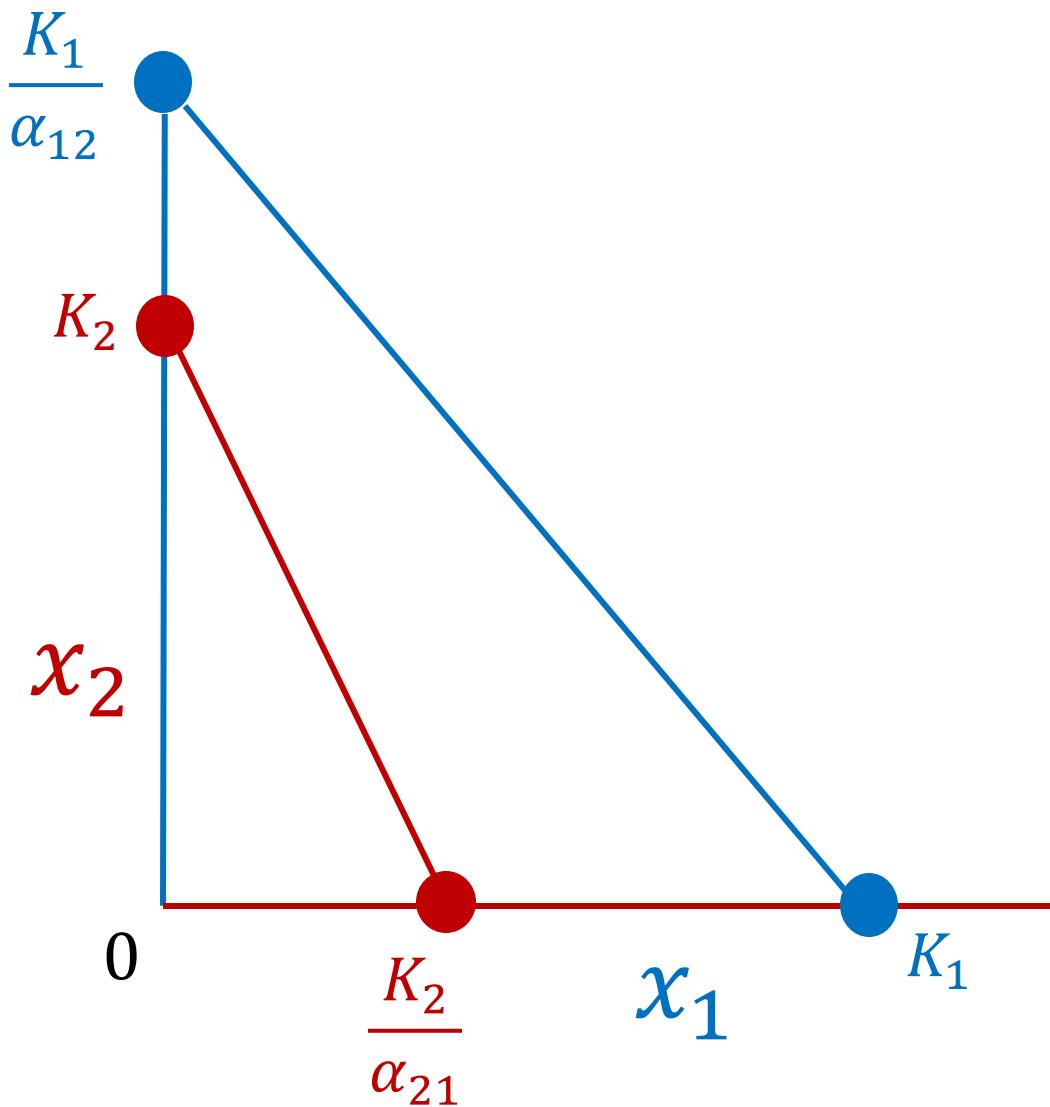


Four possible outcomes for competition

Case 2:

Species 1 outcompetes species 2

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



Four possible outcomes for competition

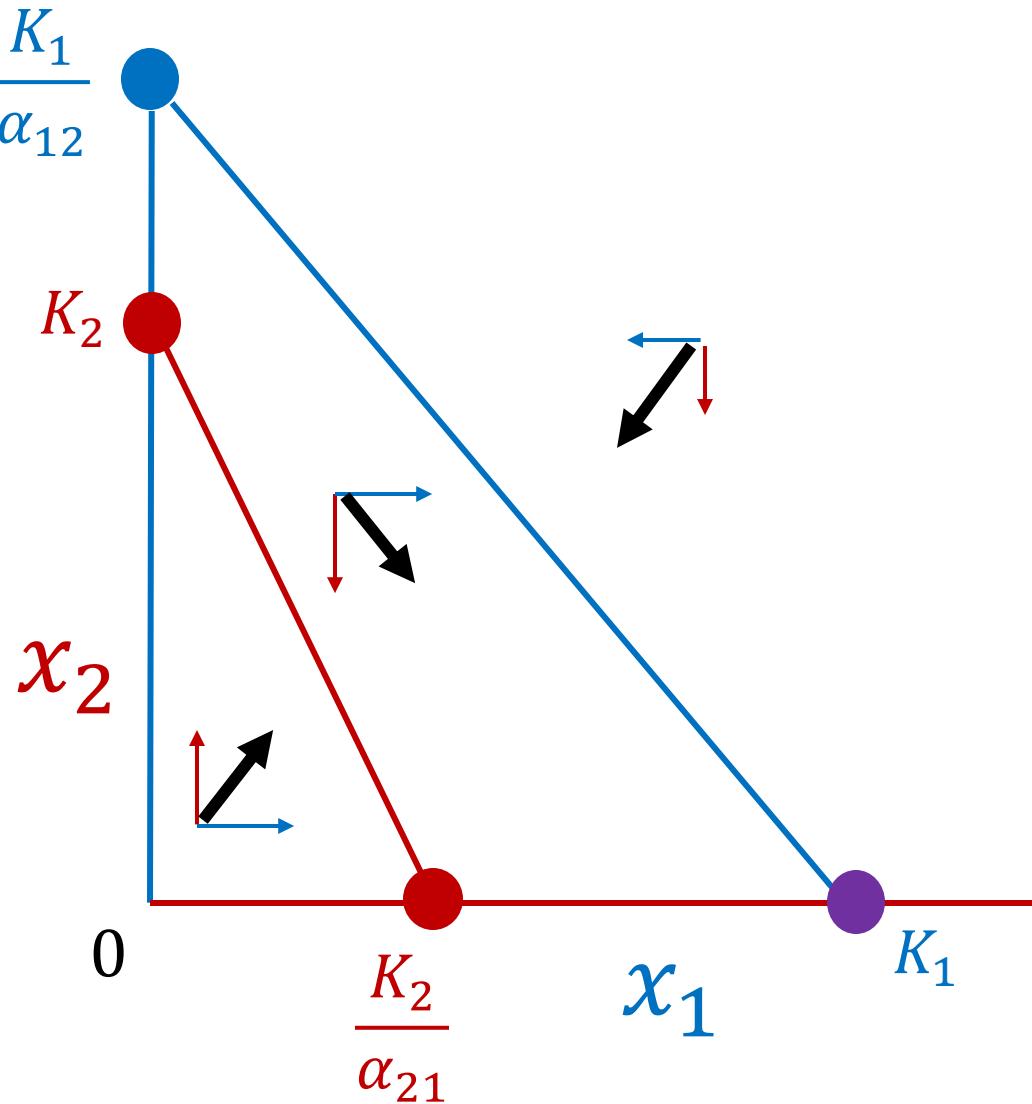
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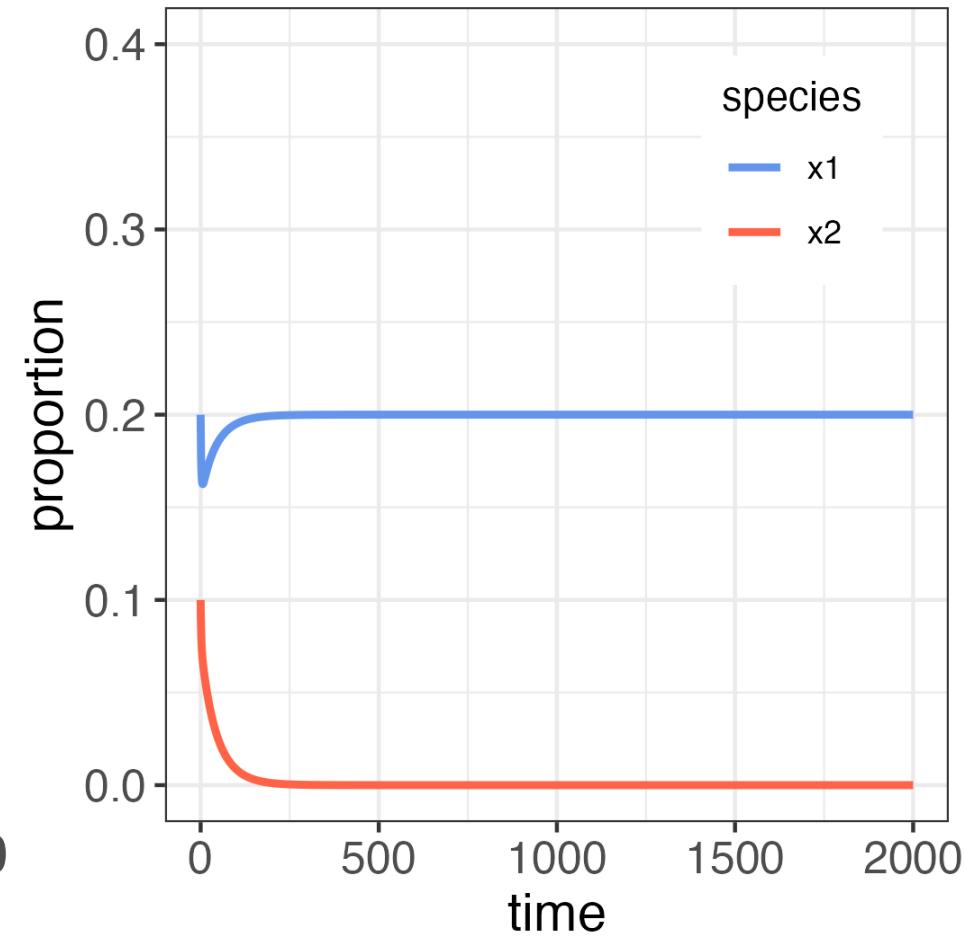
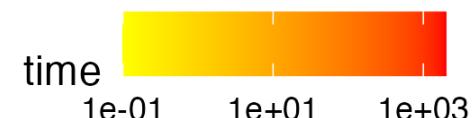
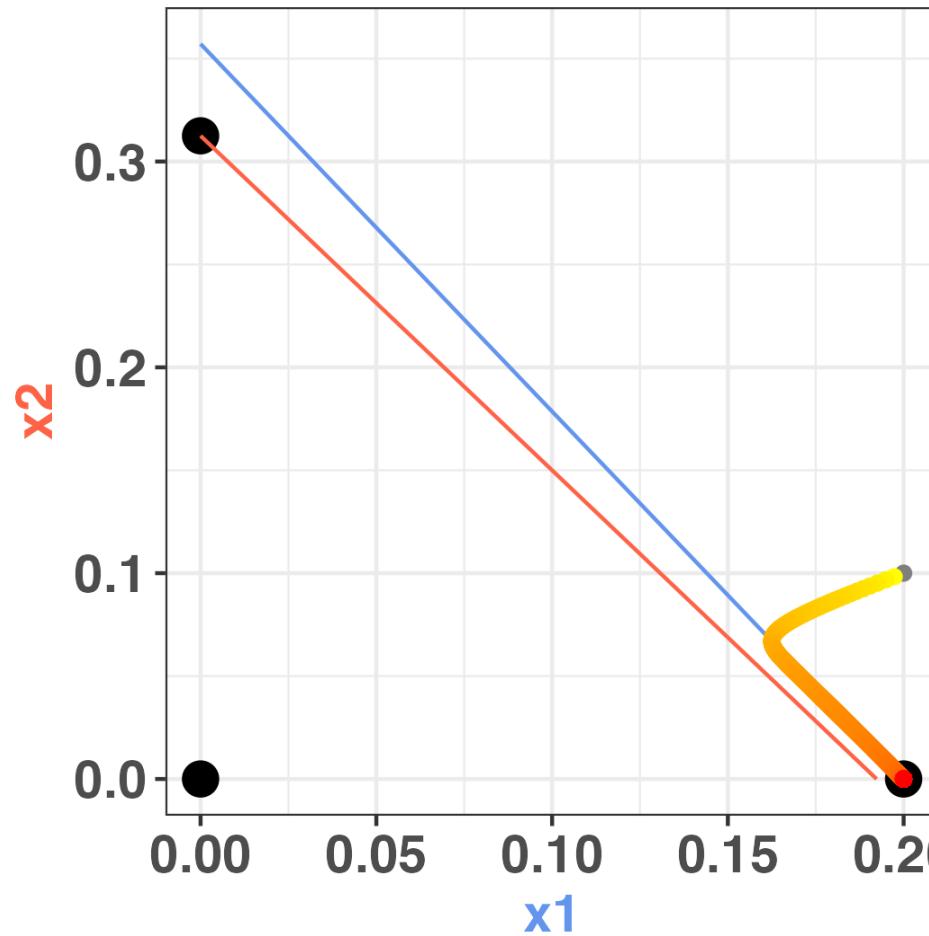
System collapses to equilibrium:

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



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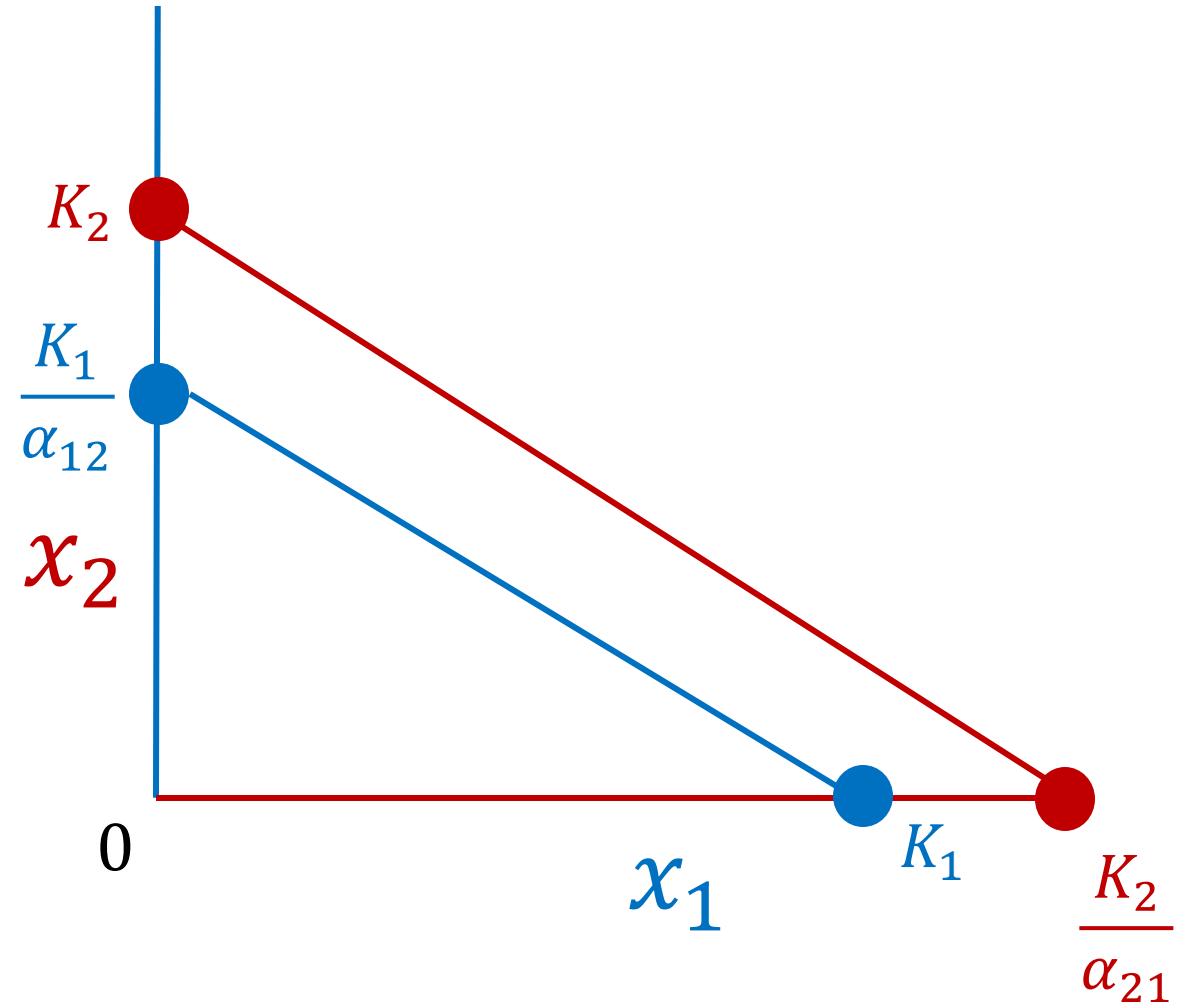


Four possible outcomes for competition

Case 3:

Species 2 outcompetes species 1

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Four possible outcomes for competition

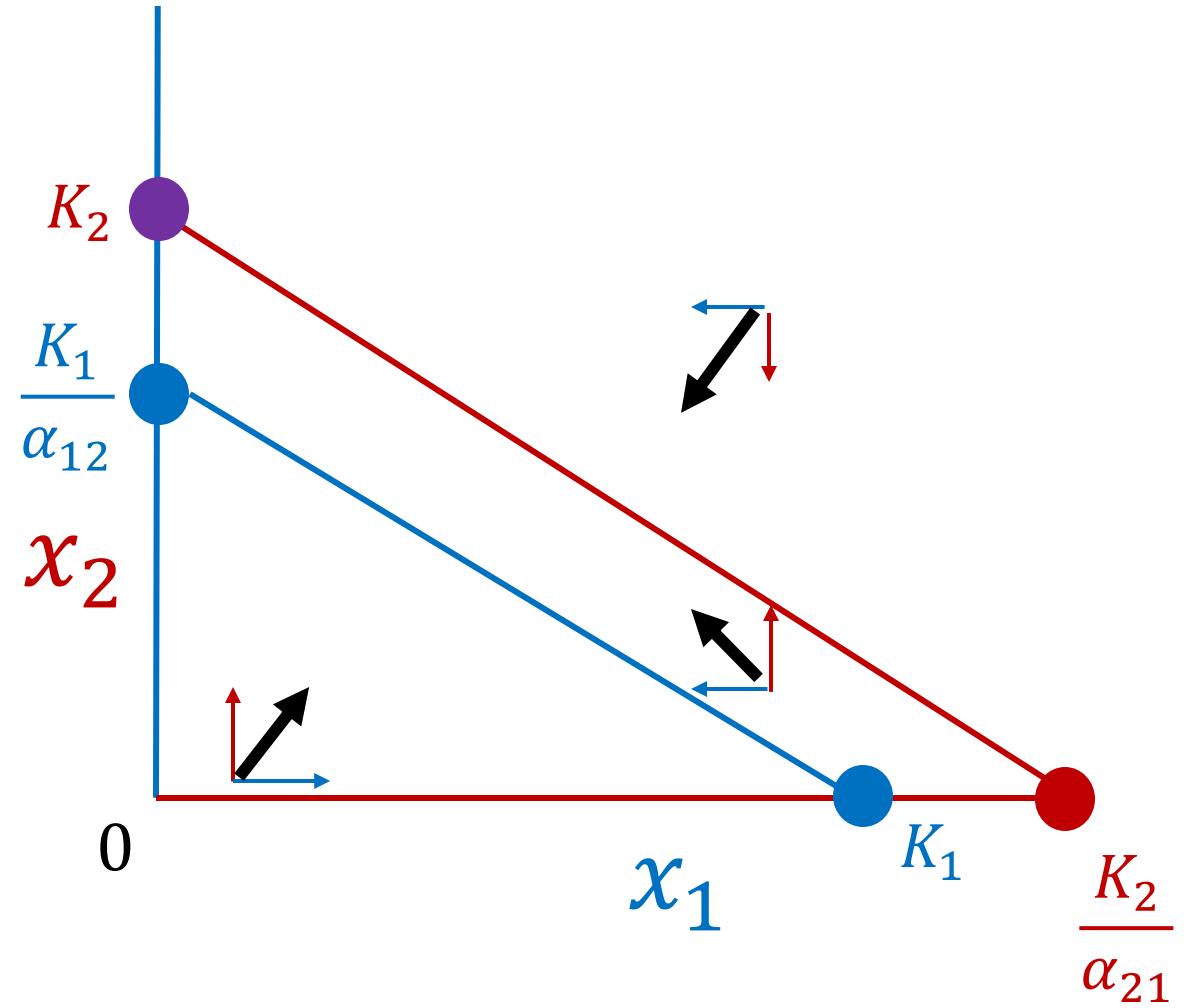
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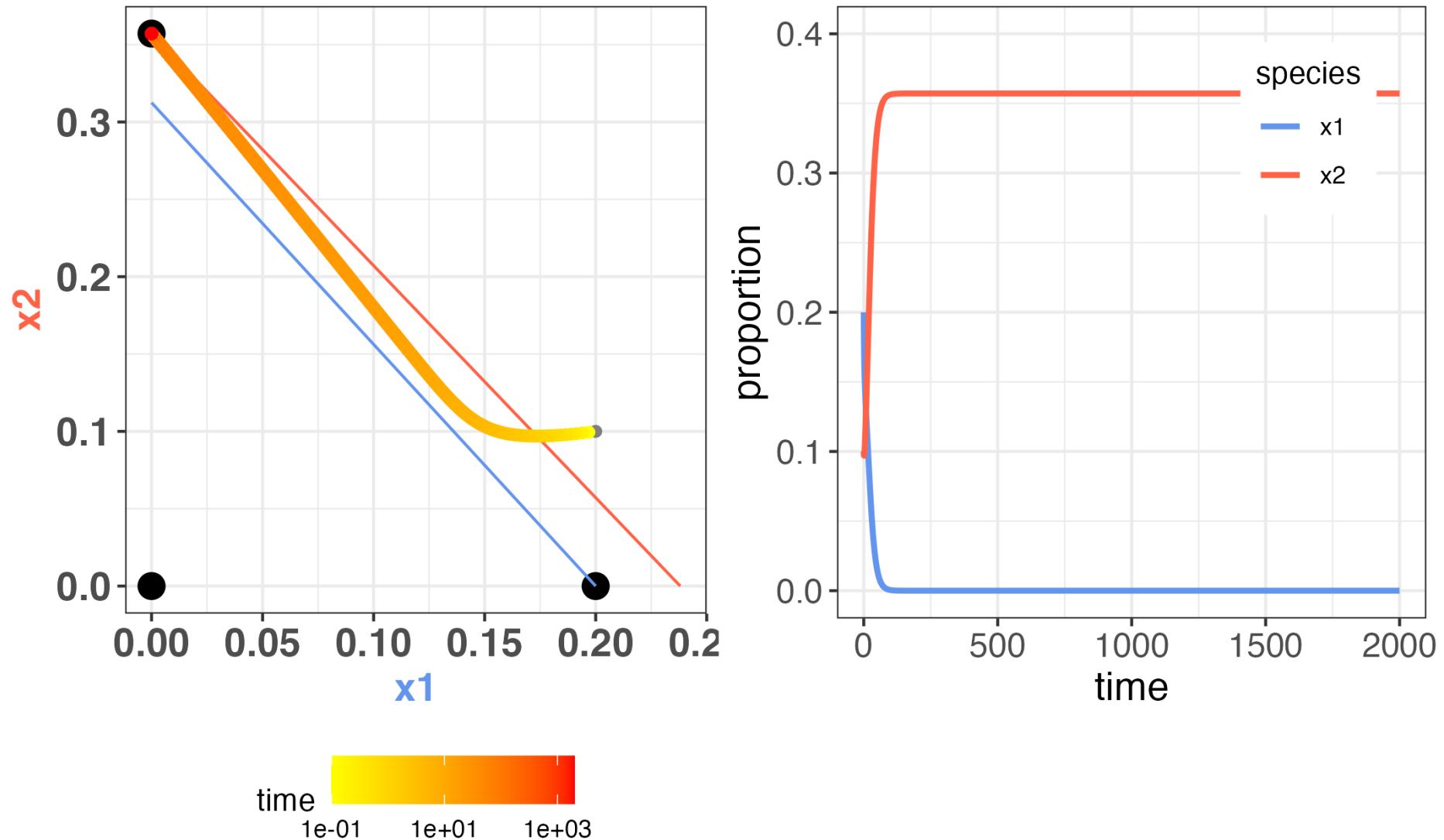
System collapses to equilibrium:

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



Case 3:
Species 2 outcompetes species 1

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

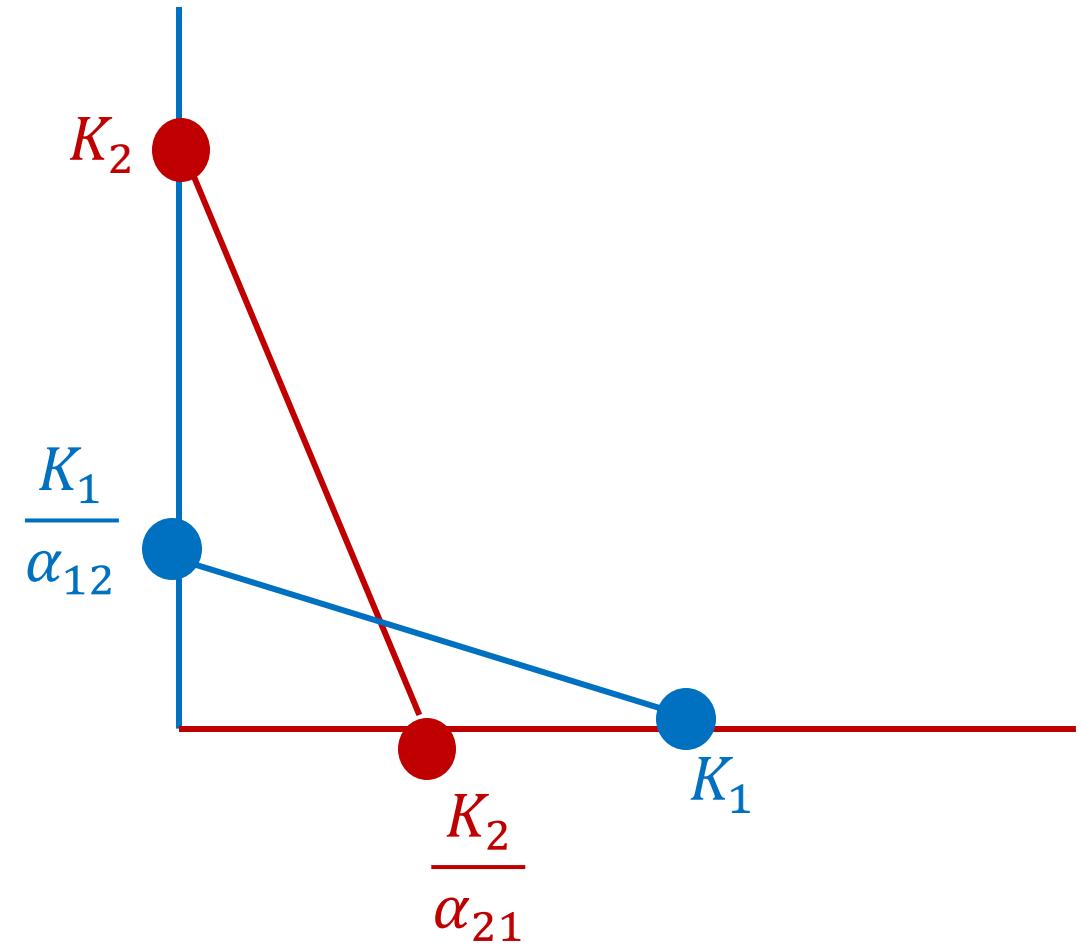


Four possible outcomes for competition

Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.



Four possible outcomes for competition

Case 4: Precedence

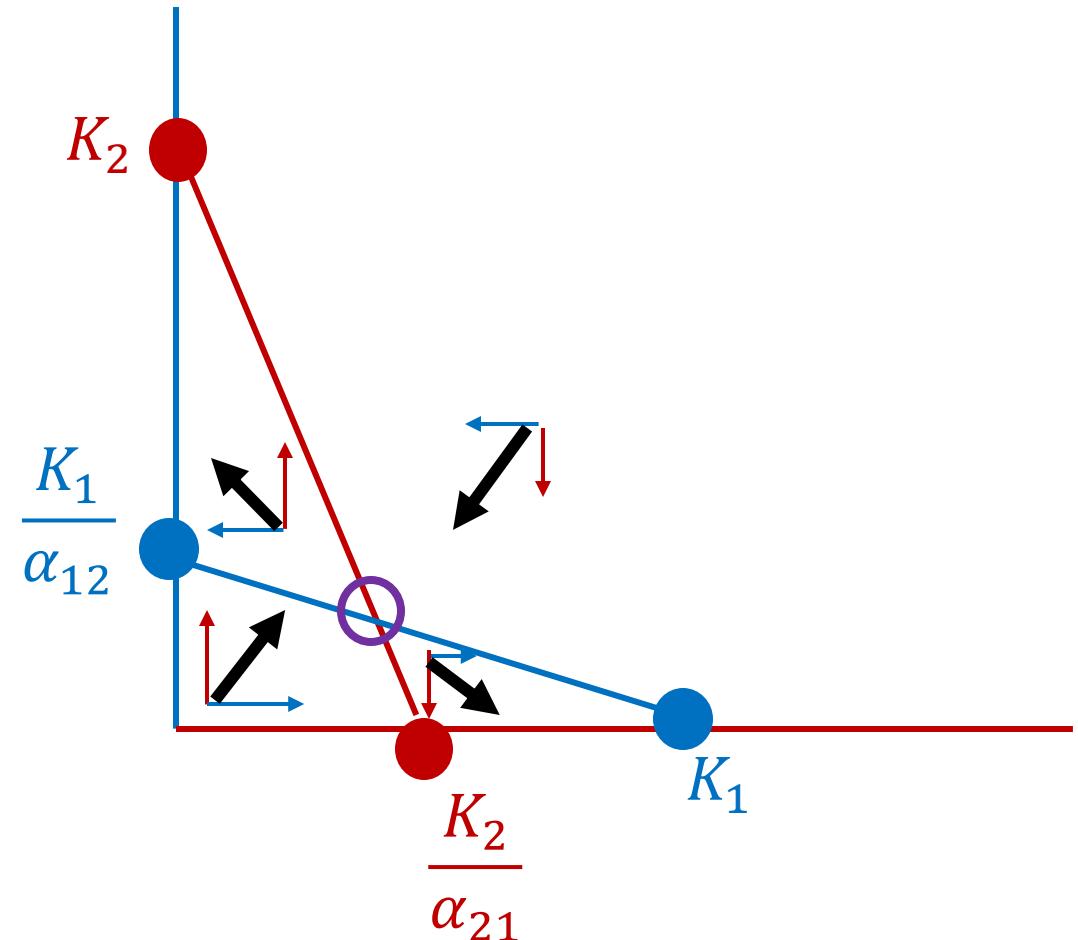
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$$\frac{K_1}{\alpha_{12}} < K_2 \text{ & } \frac{K_2}{\alpha_{21}} < K_1$$

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

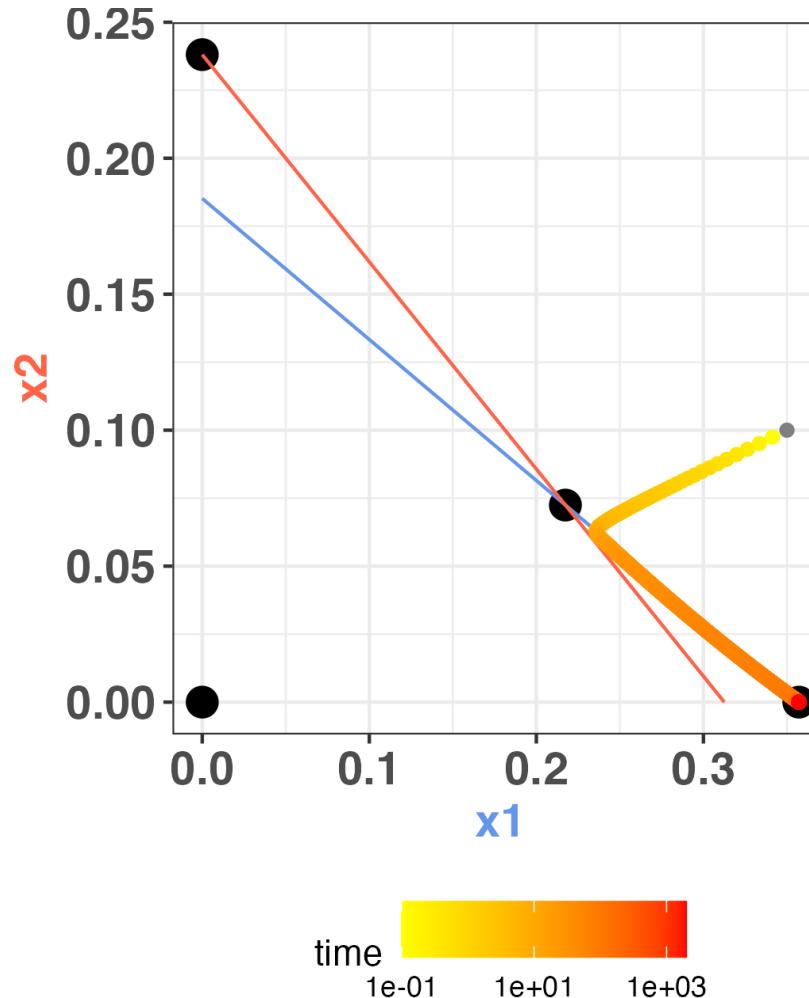
- **System will move towards either single species equilibria** ($x_1^* = 0$; $x_2^* = K_2$ OR $x_1^* = K_1$; $x_2^* = 0$), depending on starting conditions.
- Under extremely unrealistic starting conditions, system will sit at an **unstable equilibrium** that will collapse in either direction following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



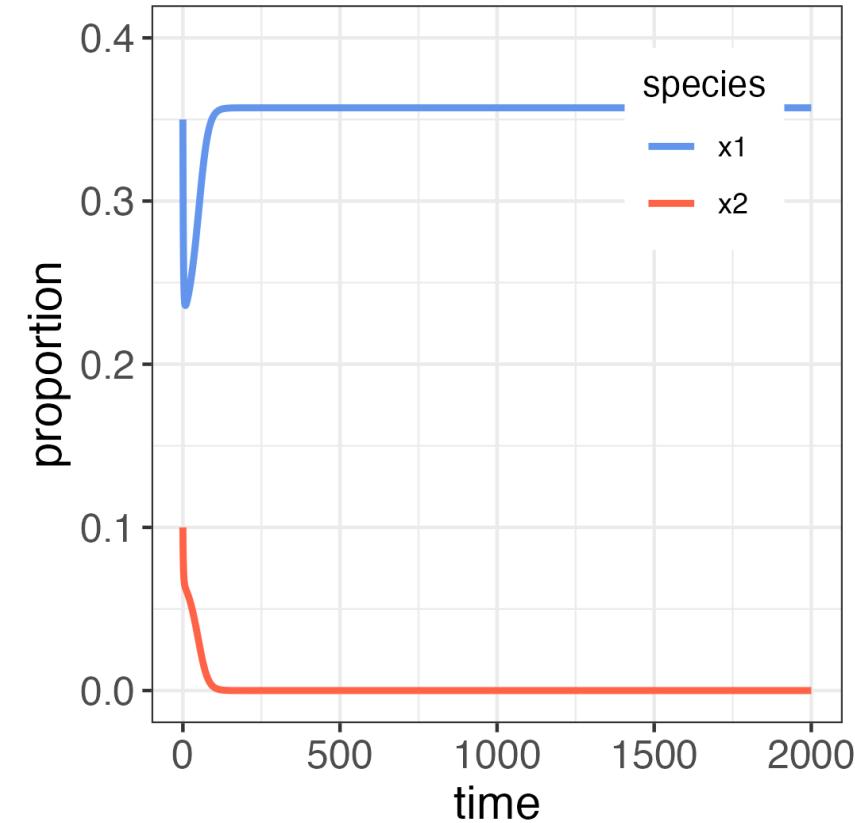
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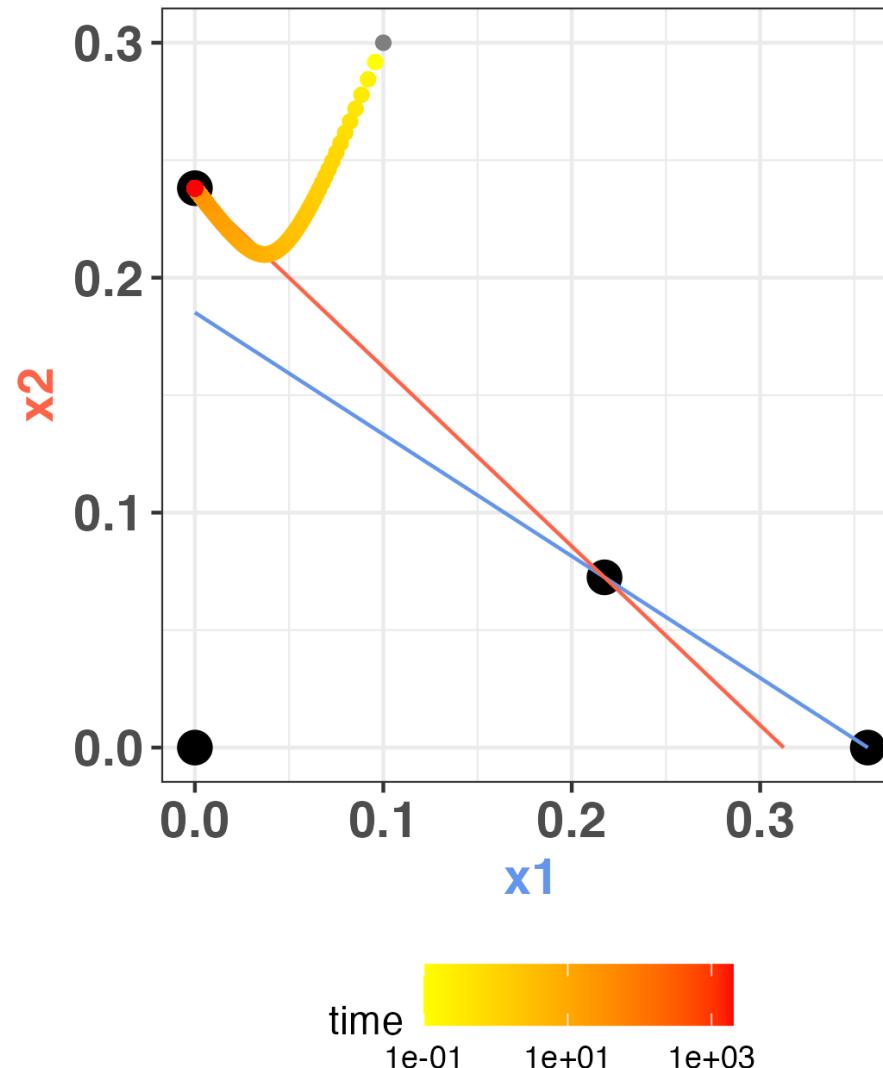
Here, **x1 outcompetes x2**



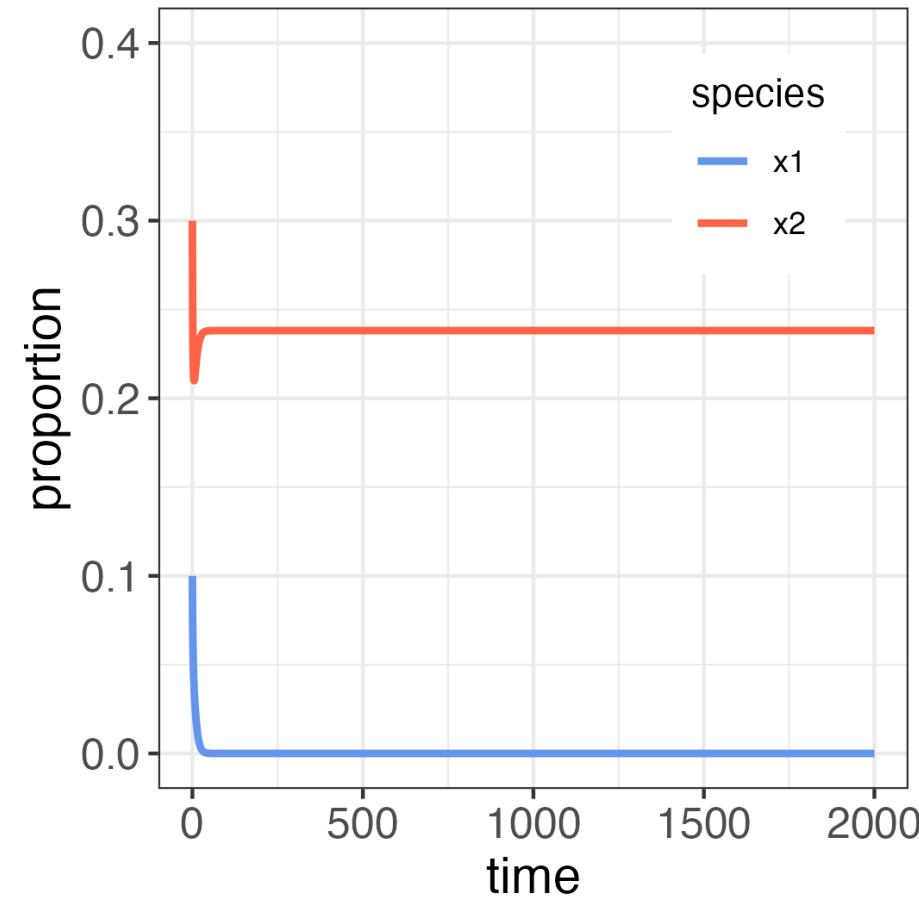
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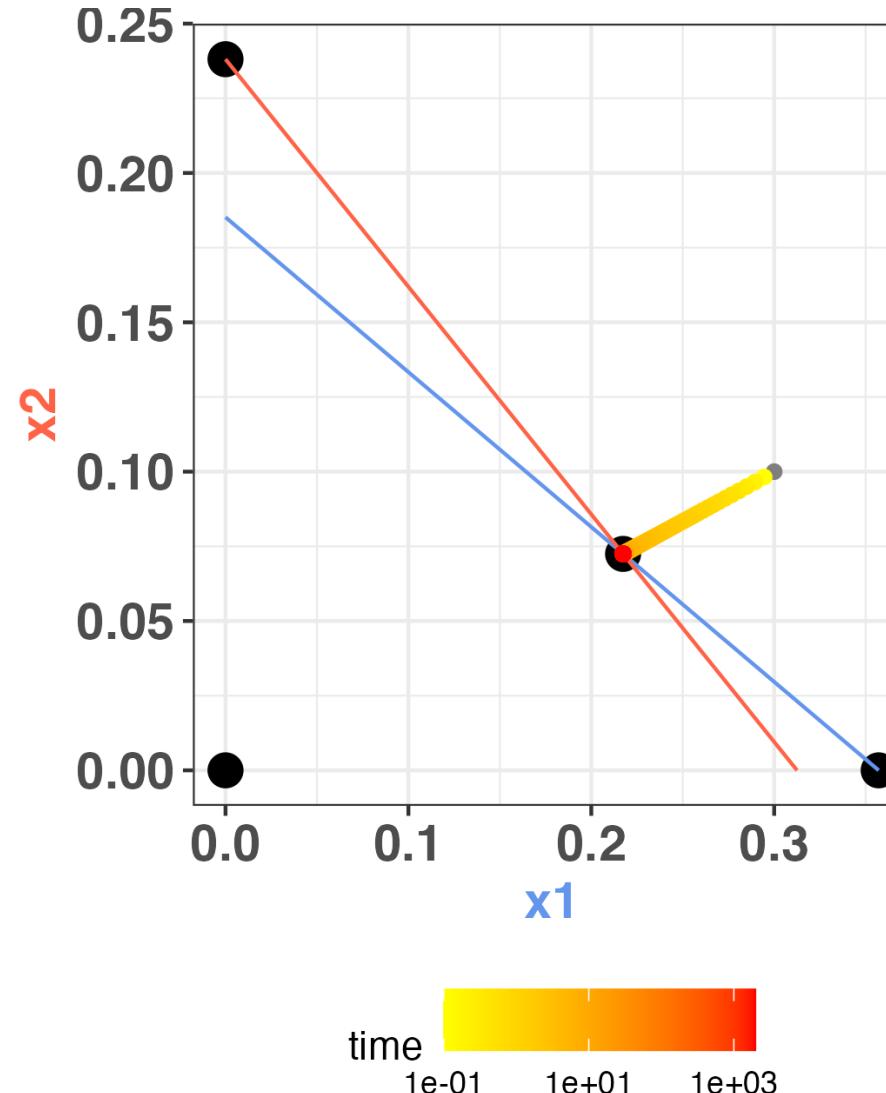
Here, **x_2 outcompetes x_1**



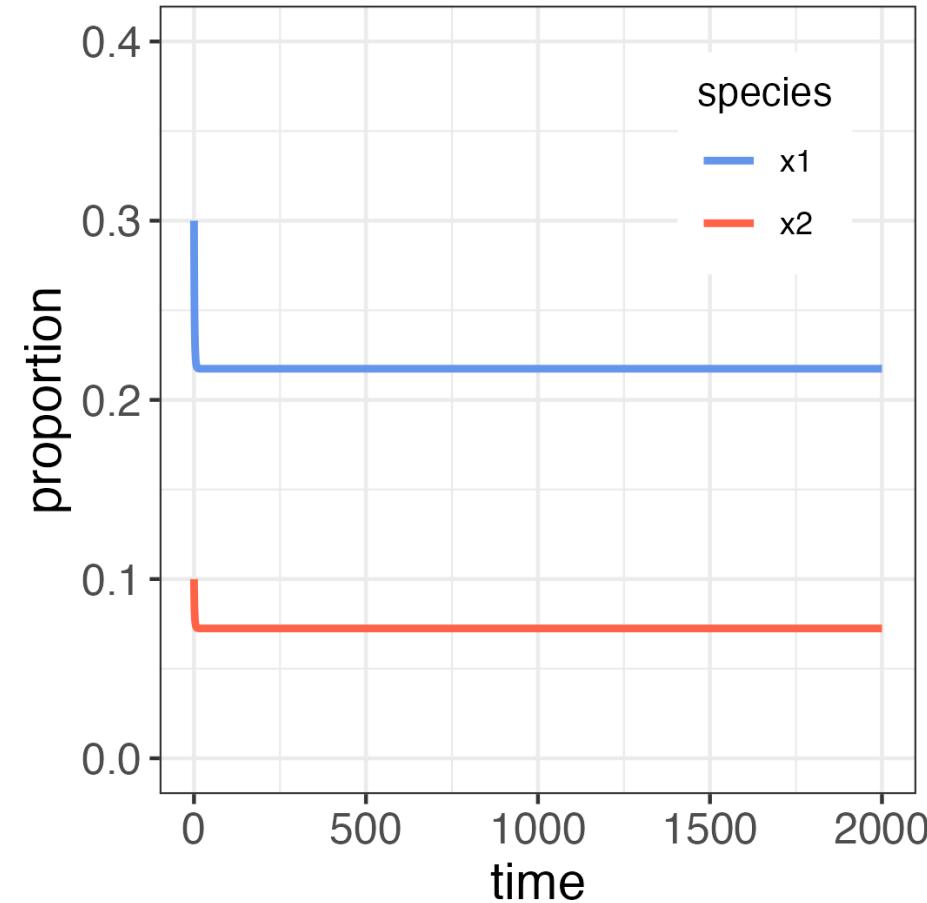
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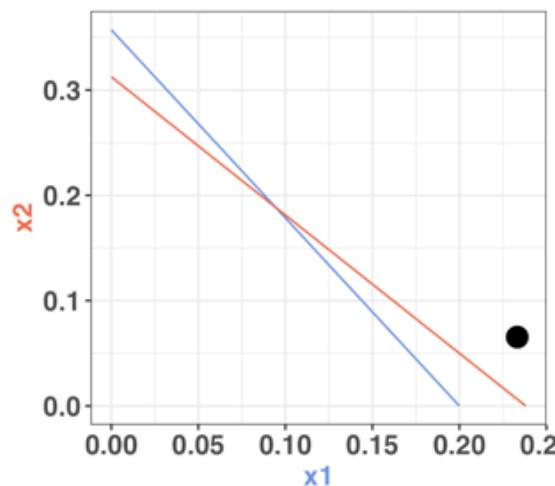


Here, **coexistence**





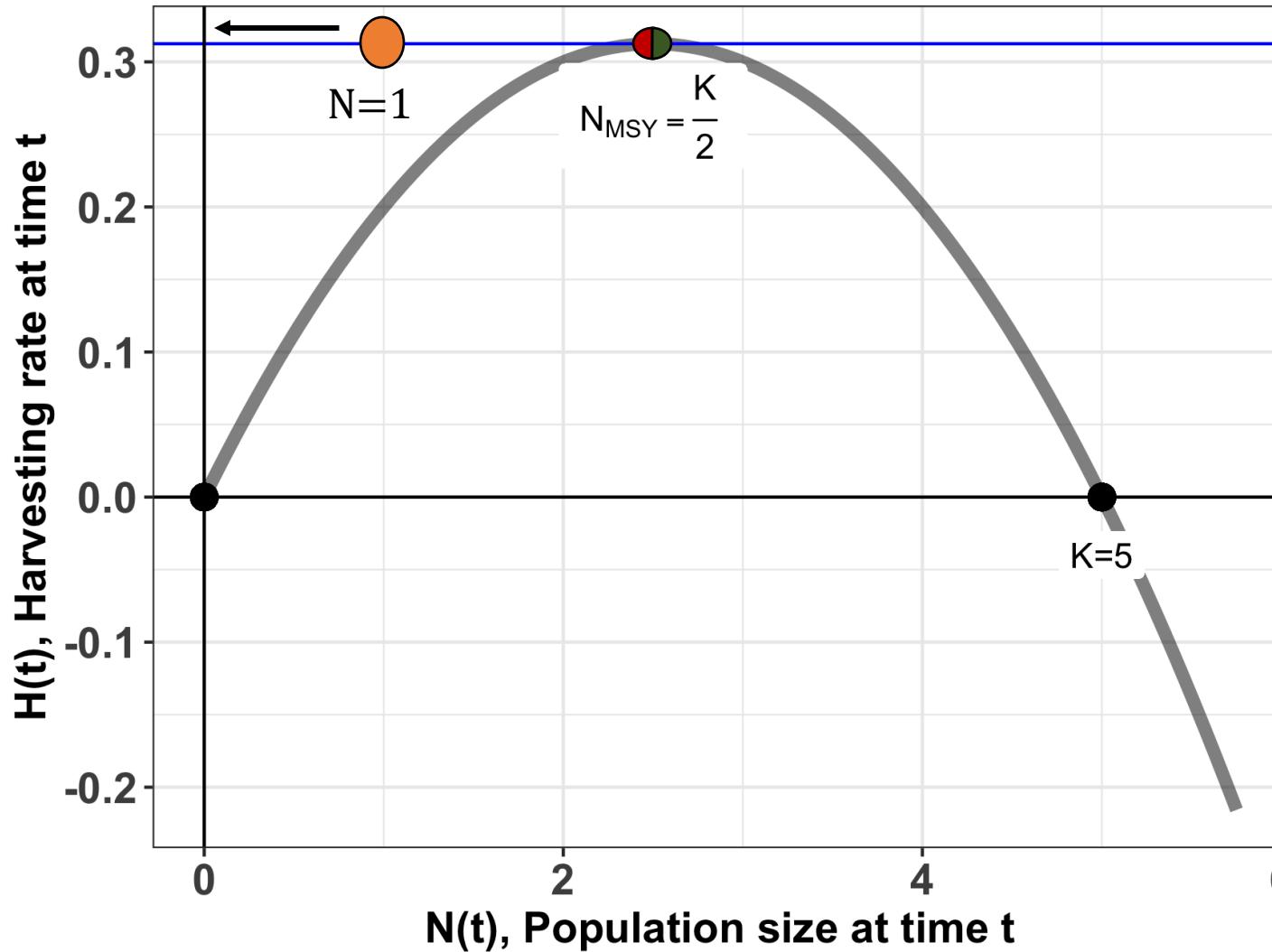
What will be the outcome of competition for a population with this nullcline structure, starting at the quantities shown by the black dot?



- A Species x2 ... 0%
- B Species x1 ... 0%
- C Both species ... 0%
- D The outco... 0%

Remember MSY, the semi-stable equilibrium:

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



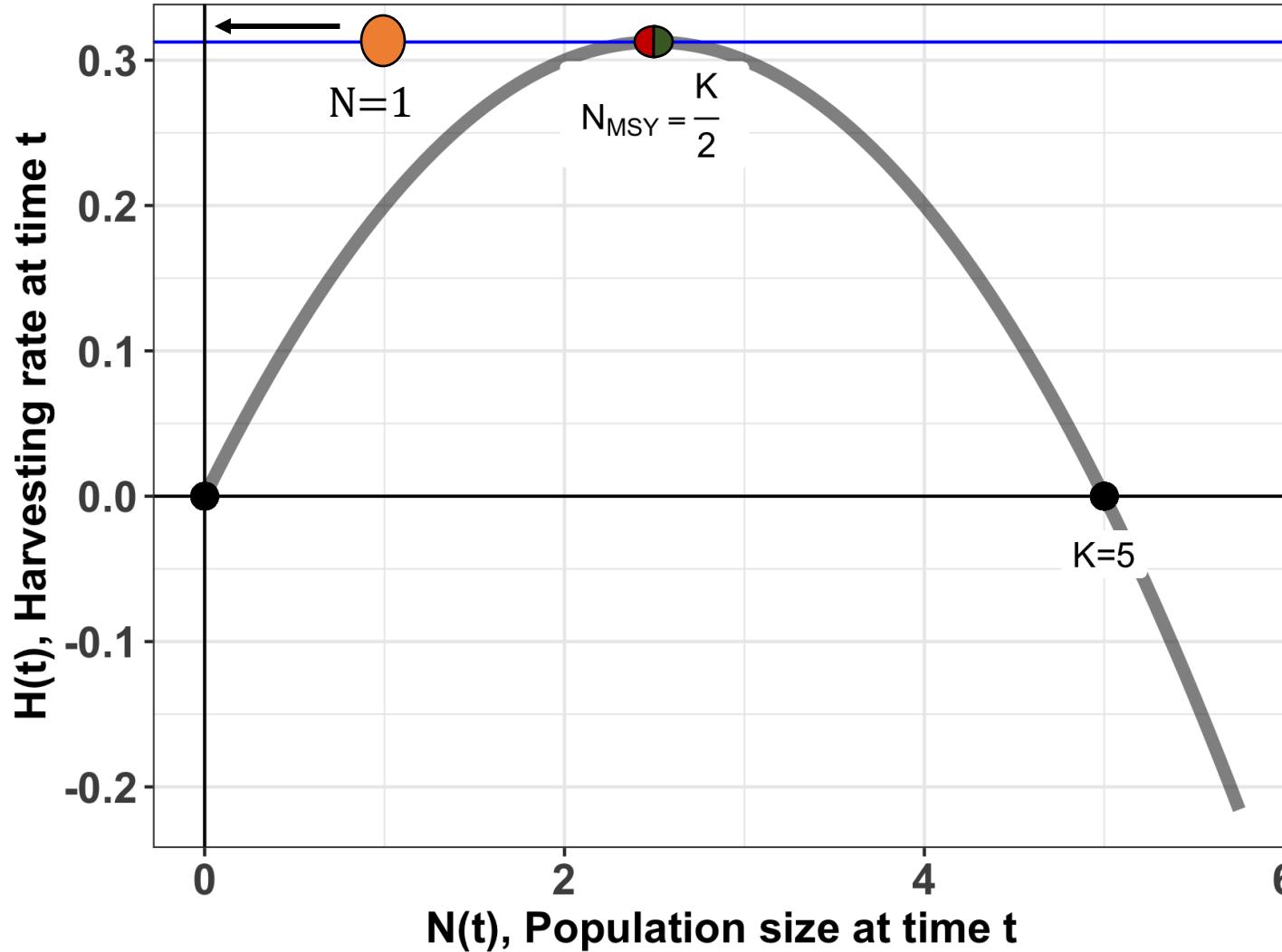
$$K=5$$
$$r=0.25$$
$$H=.3125$$

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

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

Remember MSY, the semi-stable equilibrium:

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



$$K=5$$

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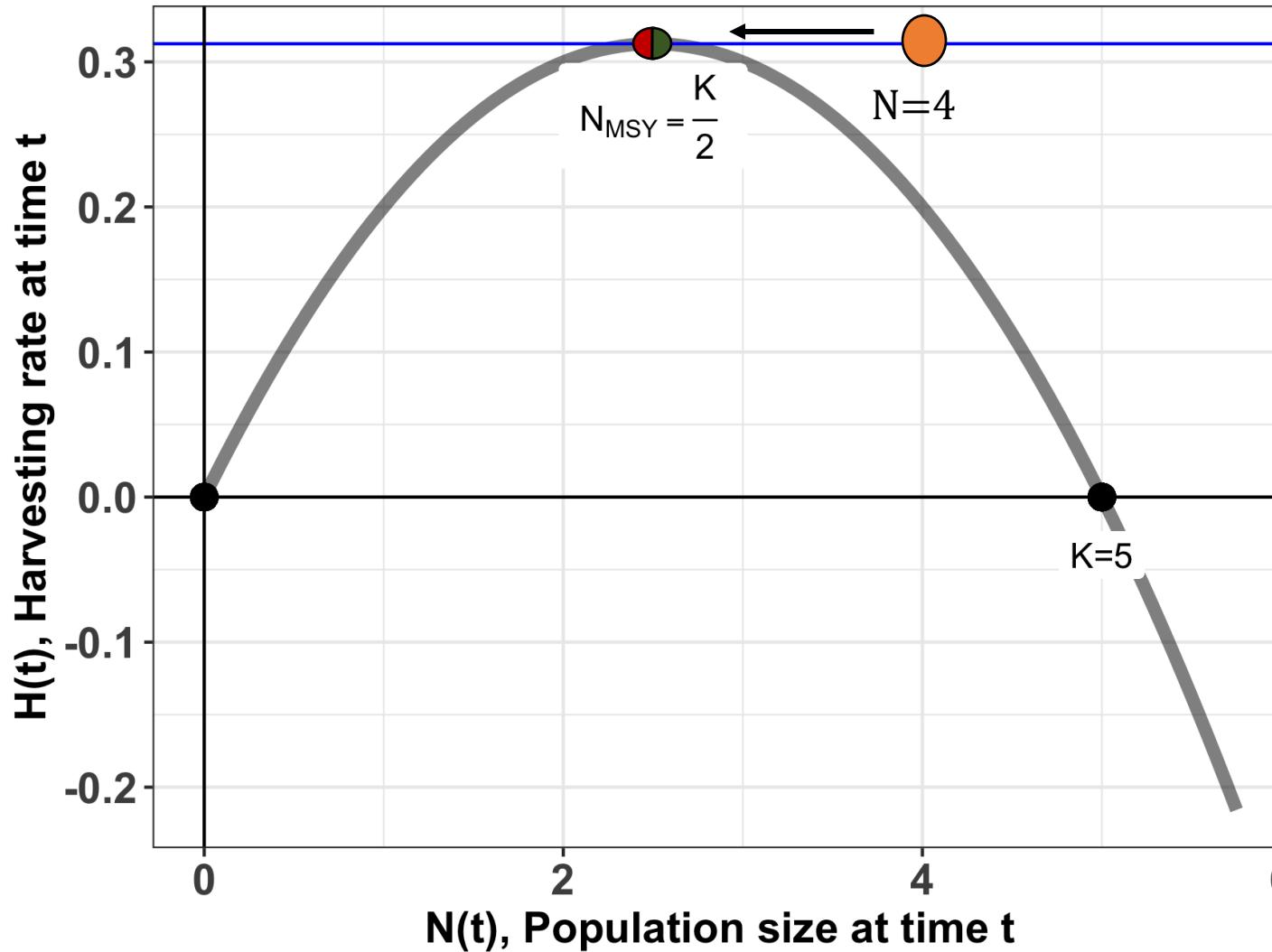
$$\frac{dN}{dt} = 0.25 * 1 \left(1 - \frac{1}{5}\right) - .3125$$

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

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

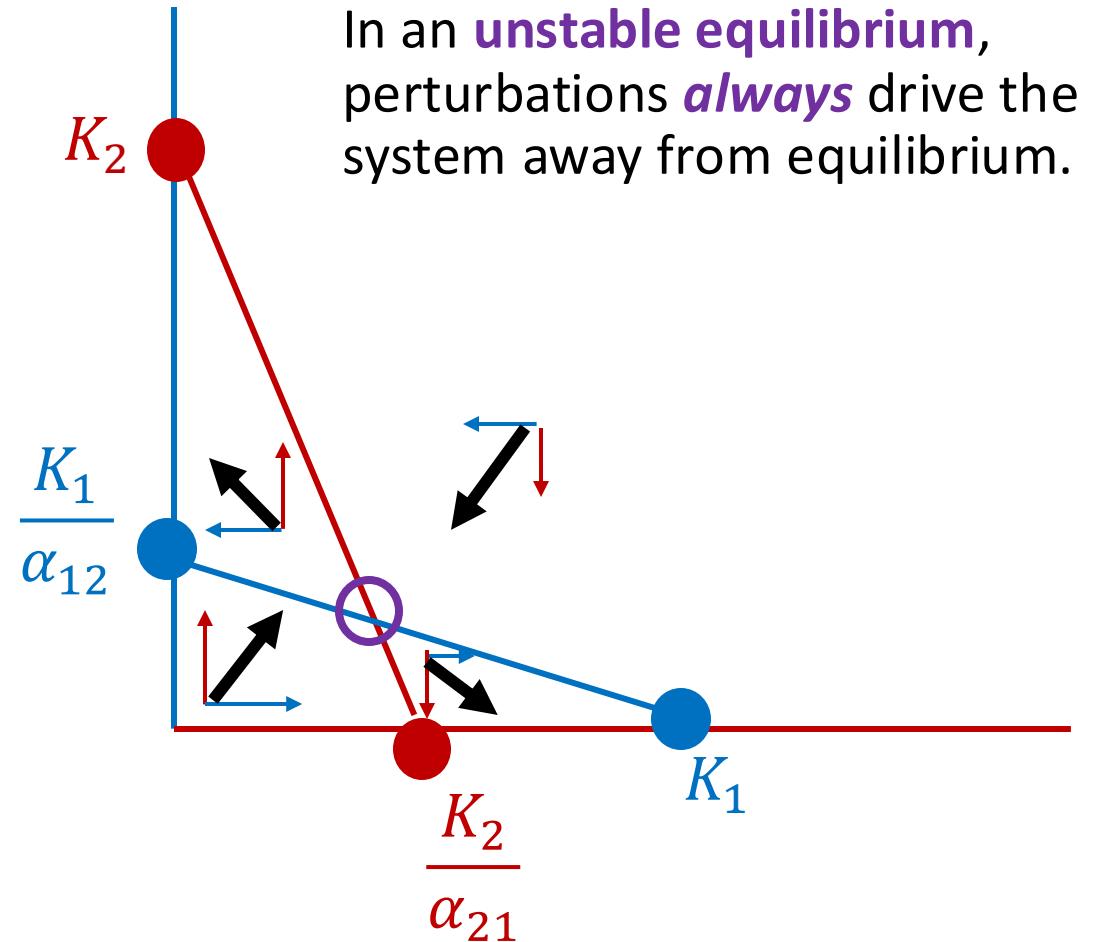
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

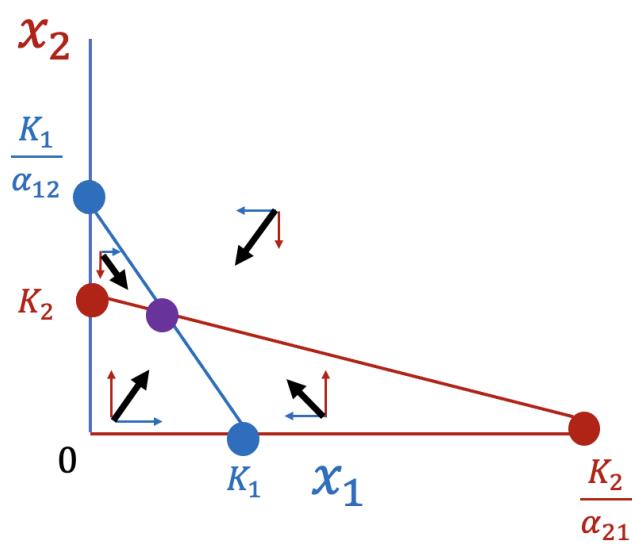
$$\frac{K_1}{\alpha_{12}} < K_2 \text{ & } \frac{K_2}{\alpha_{21}} < K_1$$

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

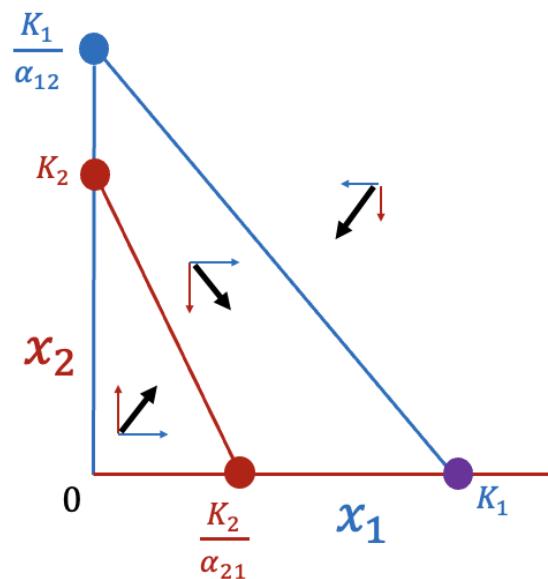


Phase plane analysis: graphical determination of the behavior of the state variables in a dynamical system (here, populations of animals)

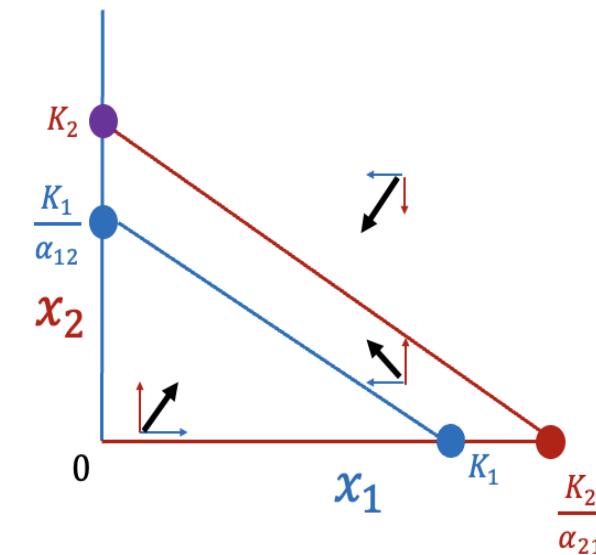
Case 1: Stable coexistence



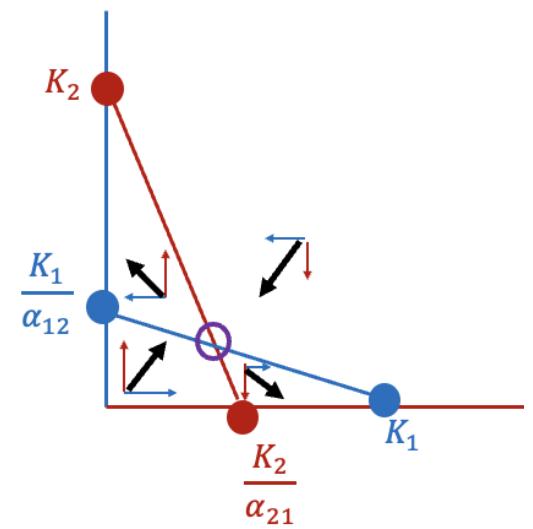
Case 2: Spp. 1 wins



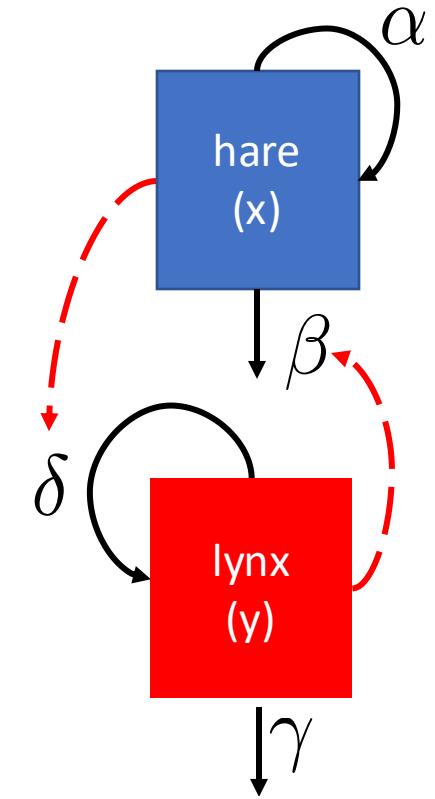
Case 3: Spp. 2 wins



Case 4: Precedence



Note the difference with a predator-prey model!

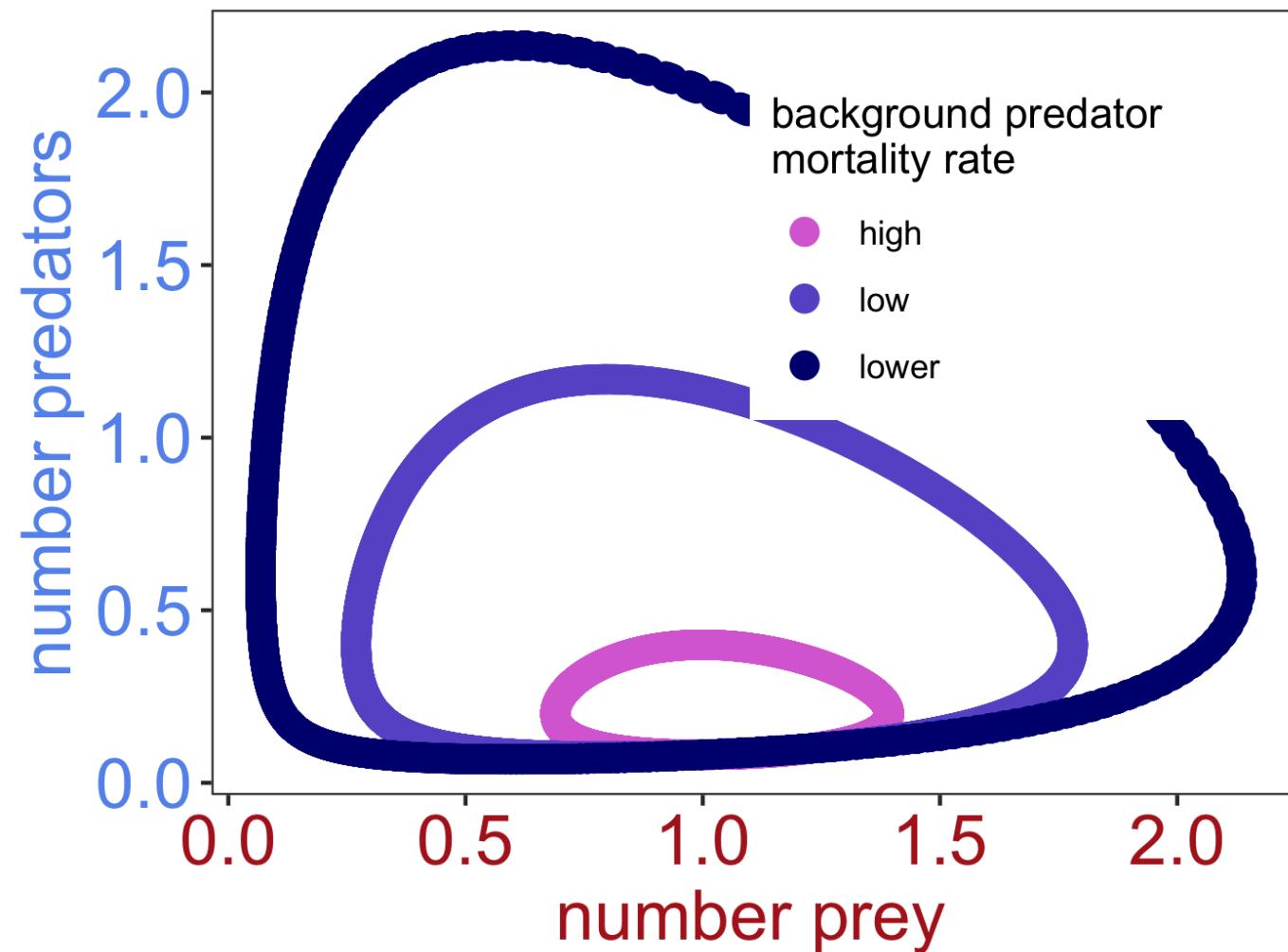


How does **hare** abundance **vary** with changes in **lynx** abundance?

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

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

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:



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:



“Neither can live while the other survives.”
- J.K. Rowling, 2003

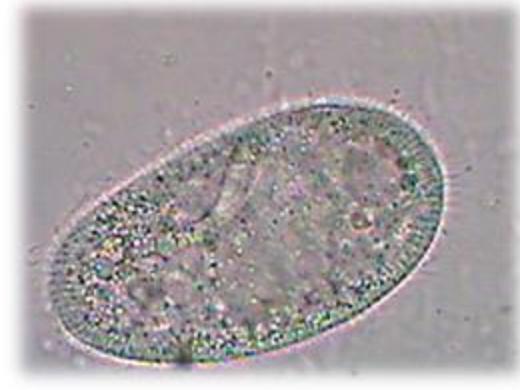
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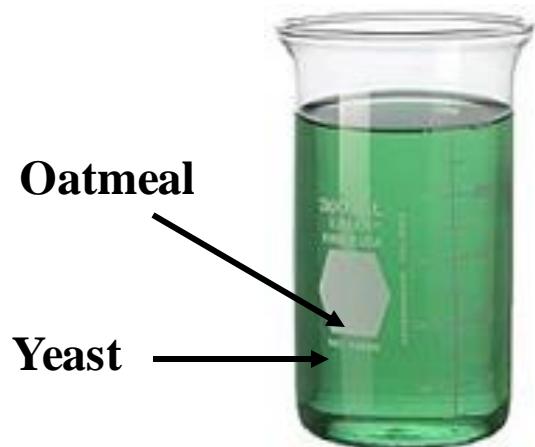
Paramecium aurelia



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



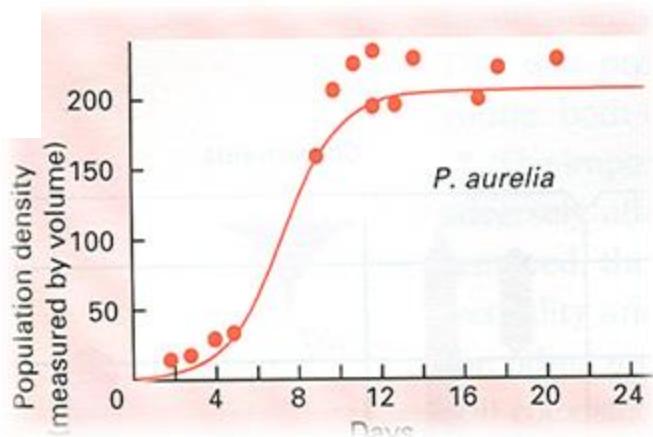
Gause 1934. *J Experimental Biology.*

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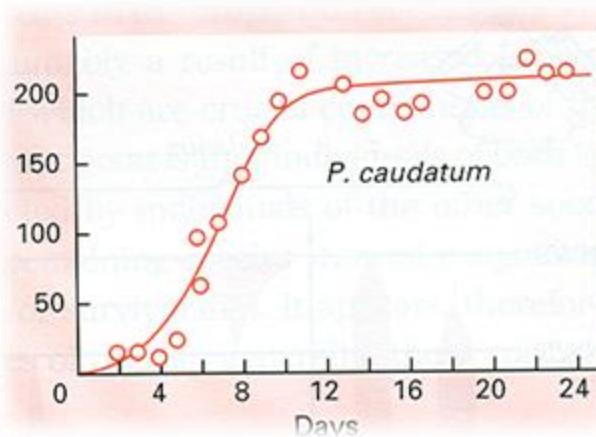
In isolation, each species grew logistically.



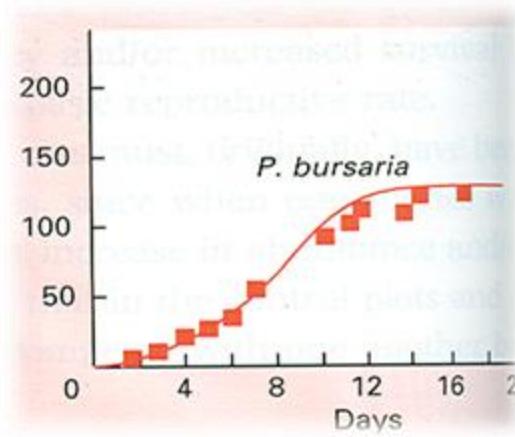
Paramecium aurelia



Paramecium caudatum



Paramecium bursaria



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Gause 1935. *Science.*

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



Paramecium aurelia

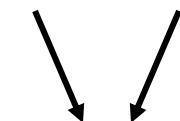
Paramecium caudatum



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Paramecium bursaria



Gause 1934. *J Experimental Biology.*

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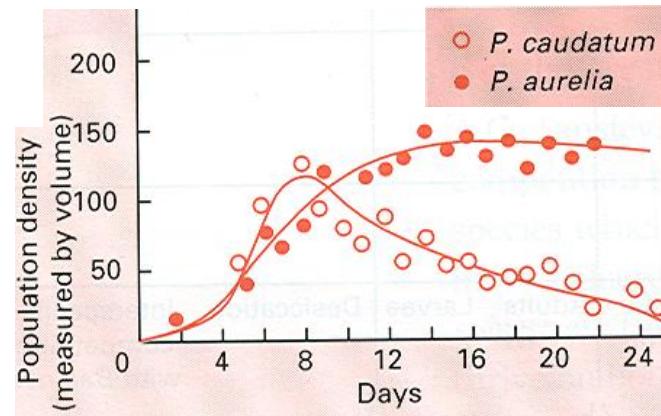
Competitive exclusion
was observed:



Paramecium aurelia



Paramecium caudatum



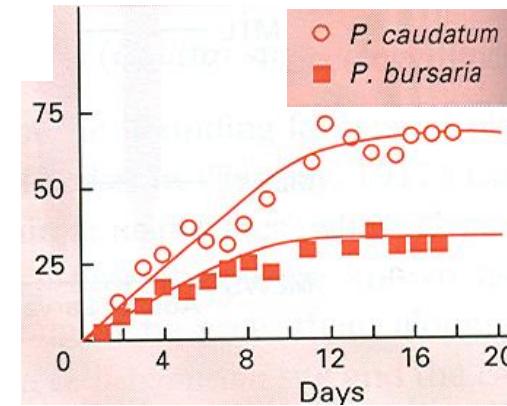
Coexistence was observed:



Paramecium caudatum



Paramecium bursaria



Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

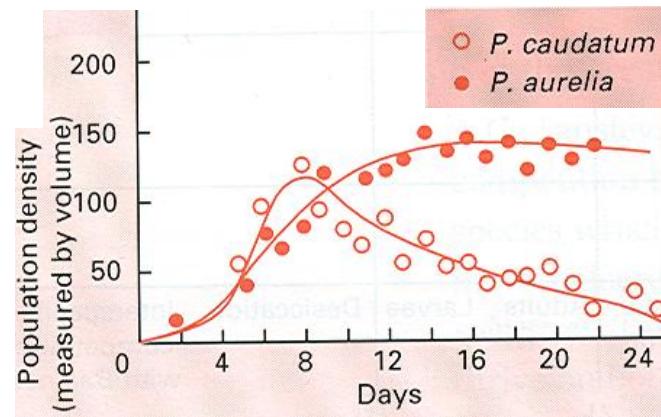
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Paramecium aurelia



Paramecium caudatum



Species coexisted below
each species' respective
individual carrying capacity.

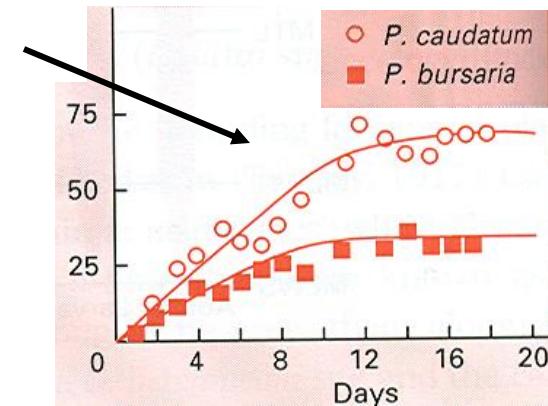
Coexistence was observed:



Paramecium caudatum



Paramecium bursaria



Gause 1934. *J Experimental Biology.*

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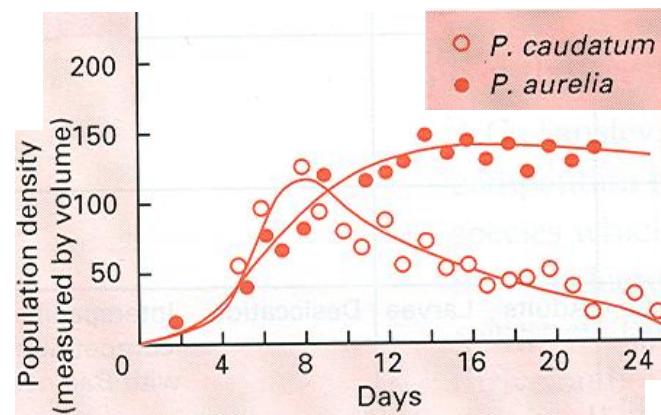
Competitive exclusion
was observed:



Paramecium aurelia



Paramecium caudatum



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.

Coexistence was observed:

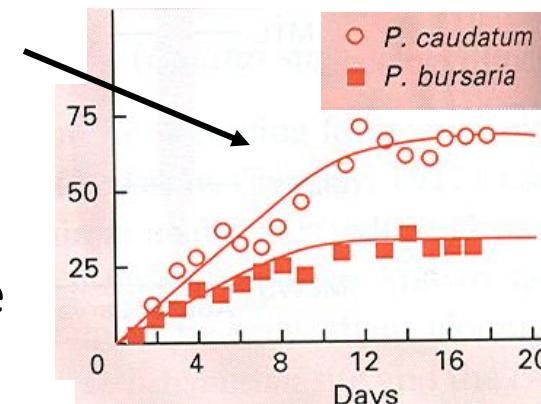


Paramecium caudatum



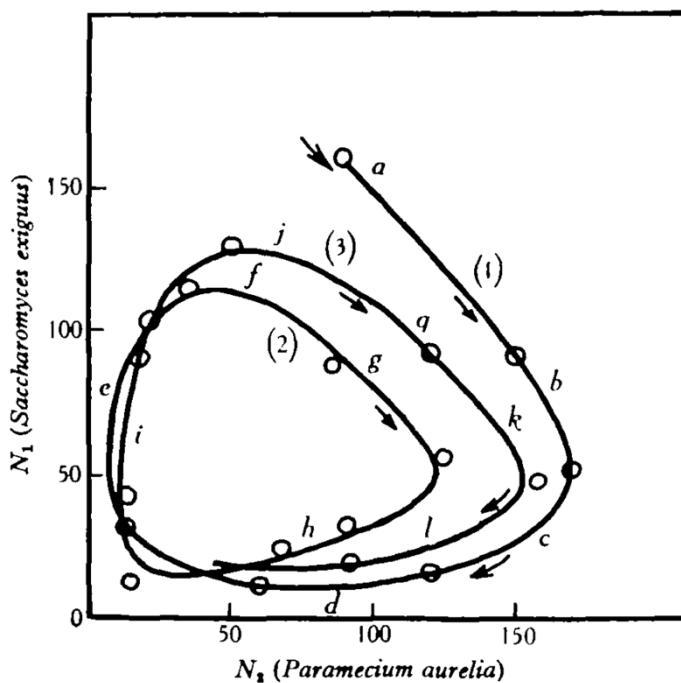
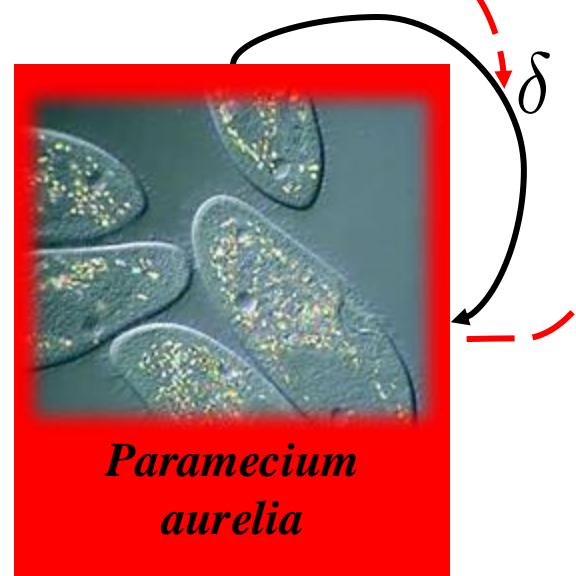
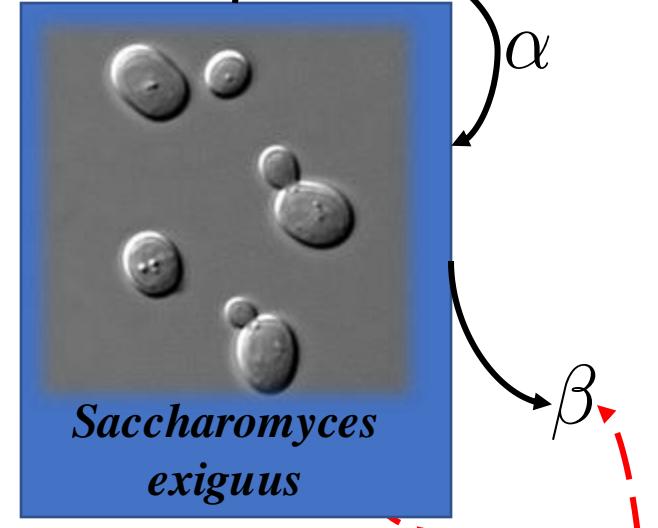
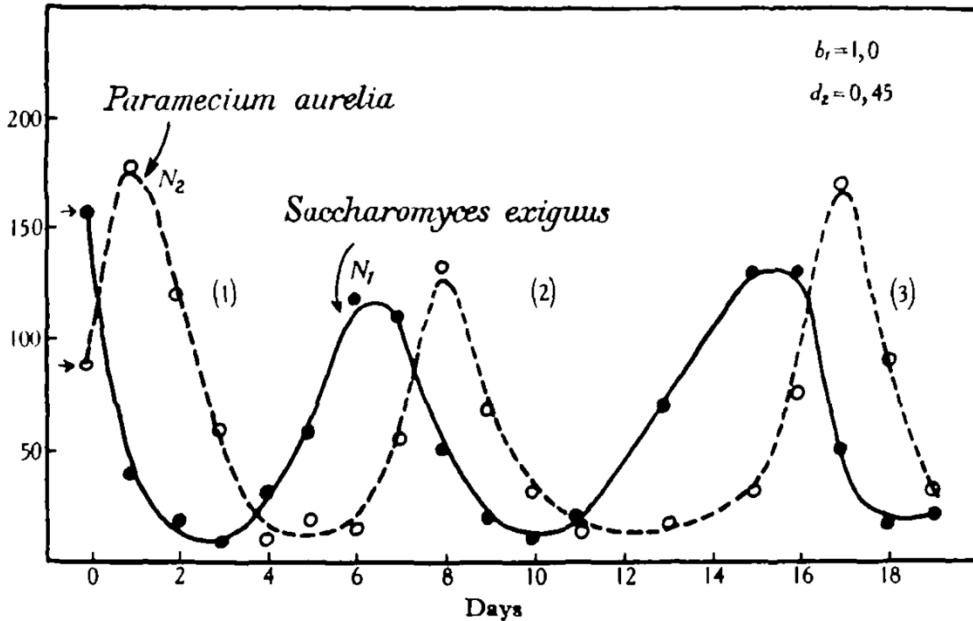
Paramecium bursaria

Species coexisted below each species' respective individual carrying capacity.



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

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



γ

Gause 1935. *Science.*

α

β

δ

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

i species

\swarrow \searrow

vector of intrinsic growth rates for i species

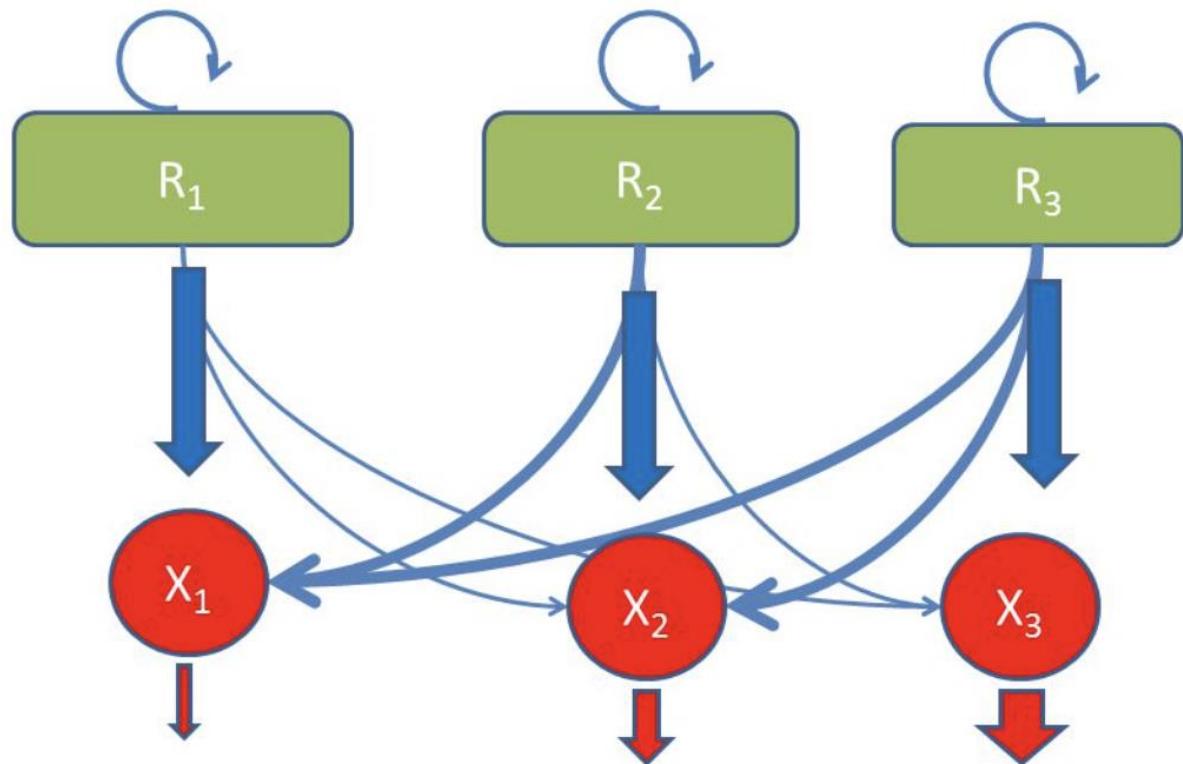
community matrix of interactions between species i and j

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.

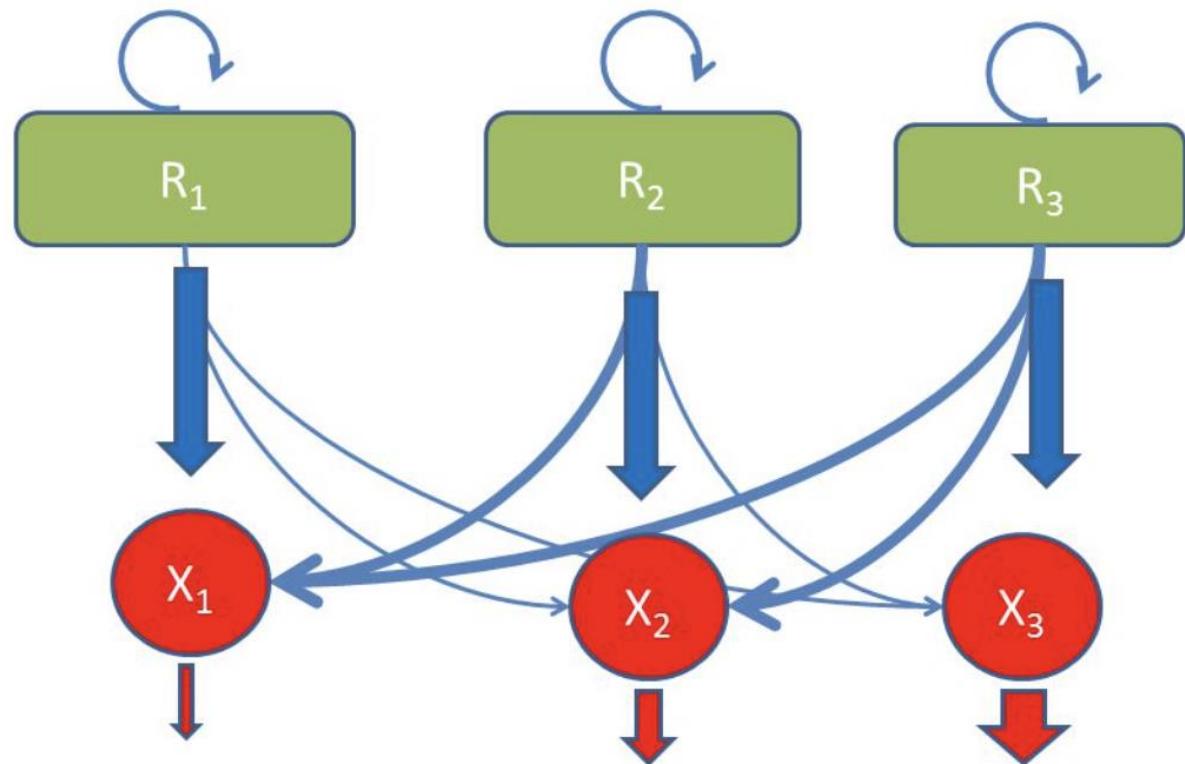
In later work, **consumer-resource models** added definition to competitive interactions



Fitness gradient: $X_1 > X_2 > X_3$

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

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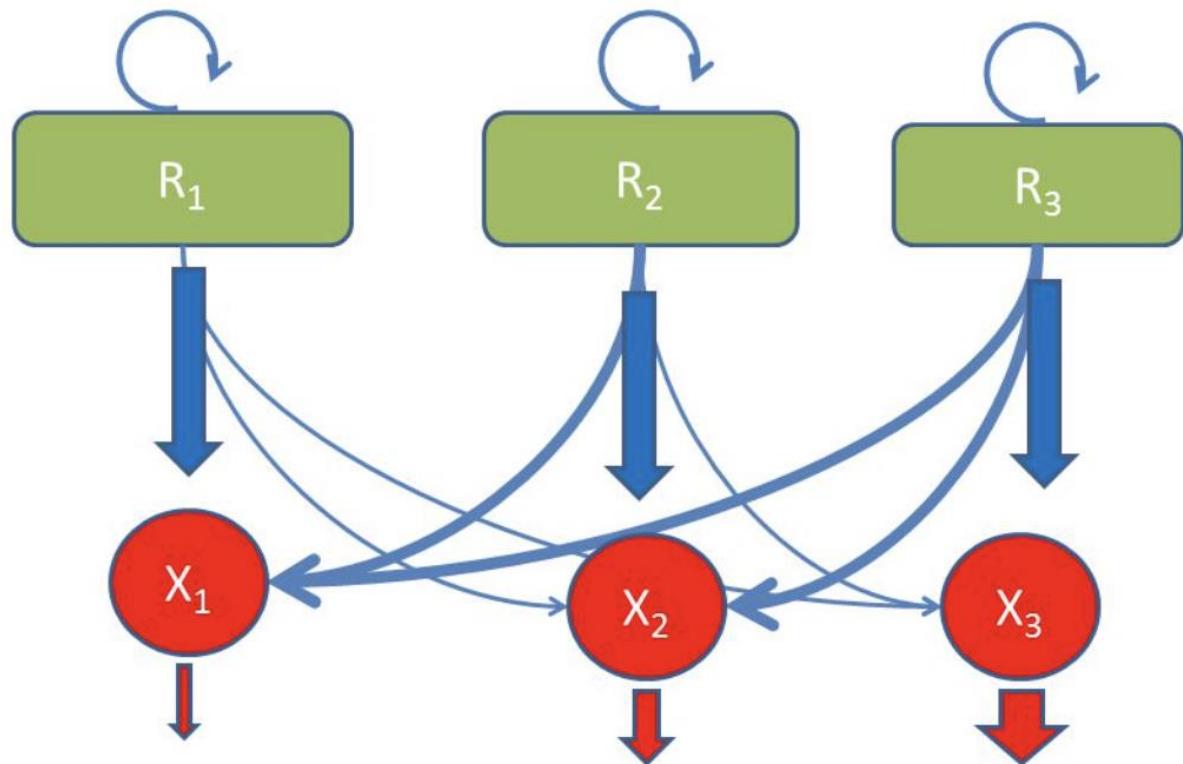


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Competitive exclusion still applies, as, theoretically, **complete competitors require unique resources to coexist.**

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.

Tilman modeled competition for limited resources, both theoretically and empirically

$$\frac{dN_j}{dt} = N_j(a_j R - d)$$

j species species resource consumption by species *j* *j* species mortality

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



Cedar Creek experiment from the University of Minnesota

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growth of resource in absence of consumption

consumption of resource by all interacting species



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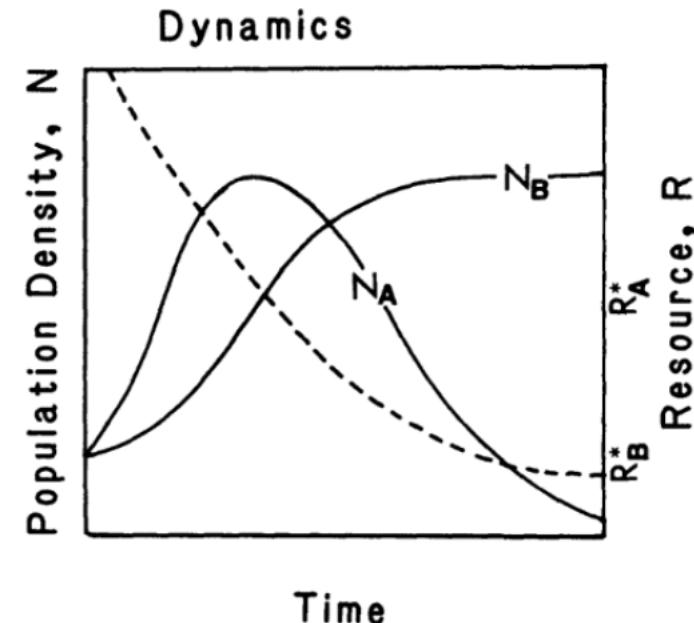
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r growth of resource in absence of consumption
 $a_j N_j$ consumption of resource by all interacting species

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

equilibrium resource density

Each consumer has a distinct R^* for each resource



Tilman modeled competition for limited resources, both theoretically and empirically

$$\frac{dN_j}{dt} = N_j(a_j R - d)$$

j species
species resource consumption by species j
 d
 N_j
 a_j
 R

d → species resource consumption by species j
 N_j → j species mortality

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

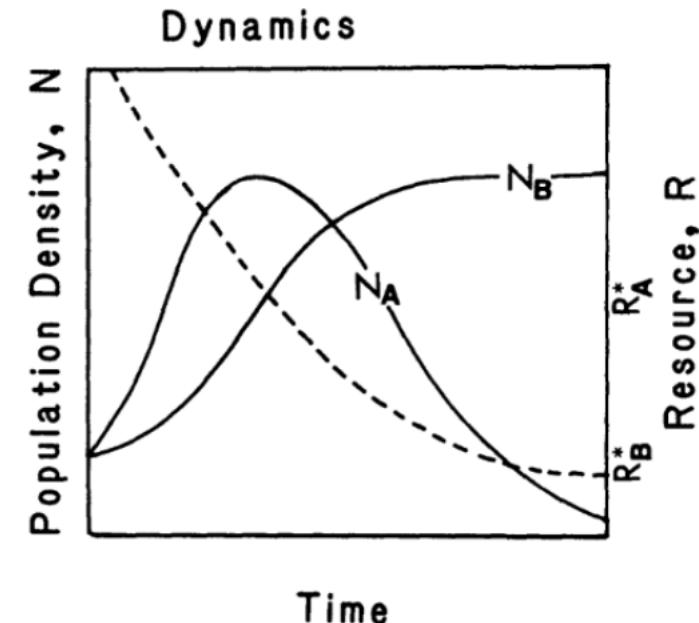
dR
 dt
 r
 R
 \sum
 j
 a_j
 N_j

growth of resource in absence of consumption
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.



Tilman modeled competition for limited resources, both theoretically and empirically

$$\frac{dN_j}{dt} = N_j(a_j R - d)$$

species resource consumption by species j

dN_j

$\frac{dN_j}{dt}$

j species

j species mortality

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

equilibrium resource density

Tilman reproduced these theoretical results empirically at Cedar Creek

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

growth of resource in absence of consumption

consumption of resource by all interacting species

