Fundamentals of Ecology

Week 7, Ecology Lecture 4

Cara Brook

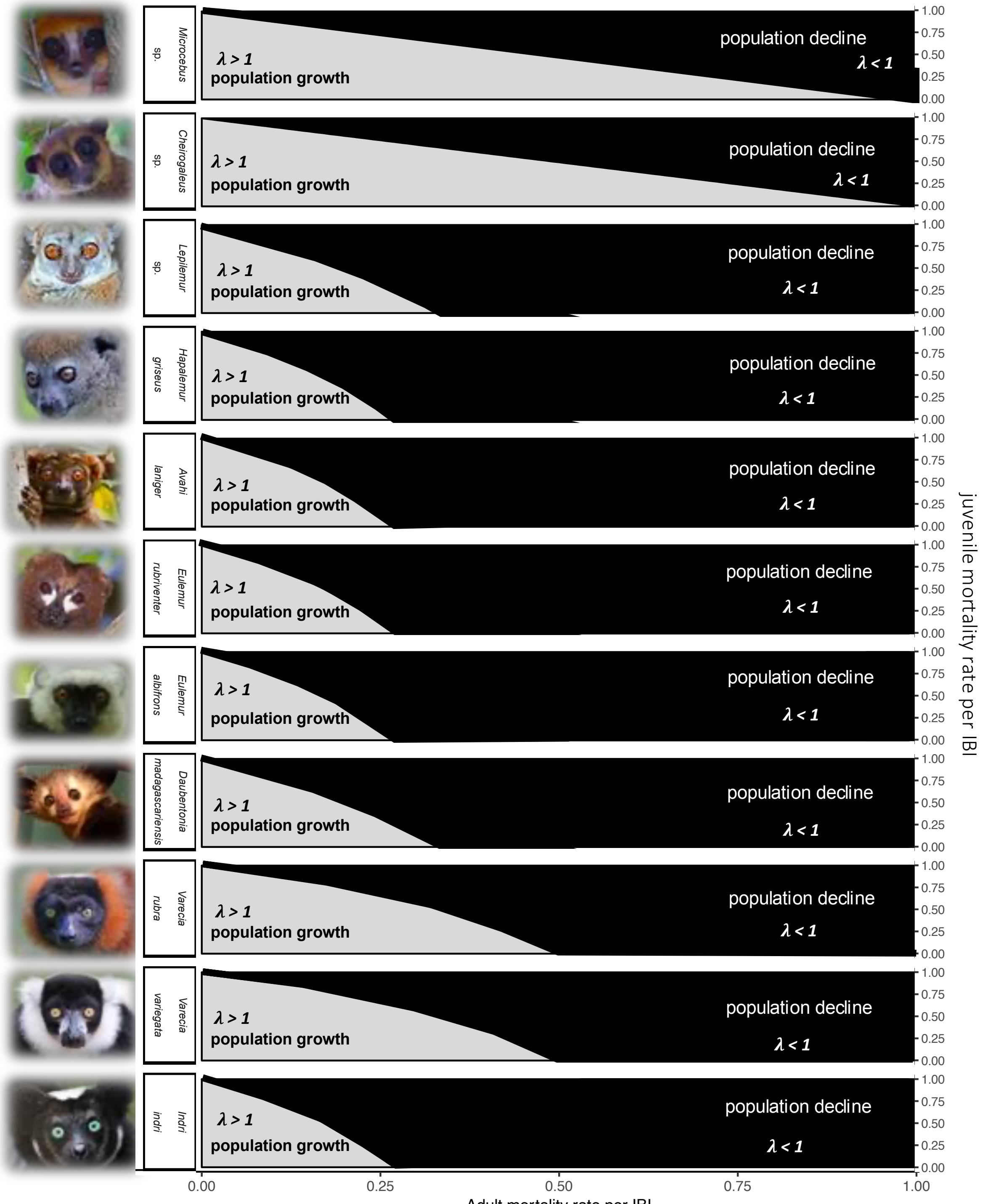
February 18, 2025

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**.

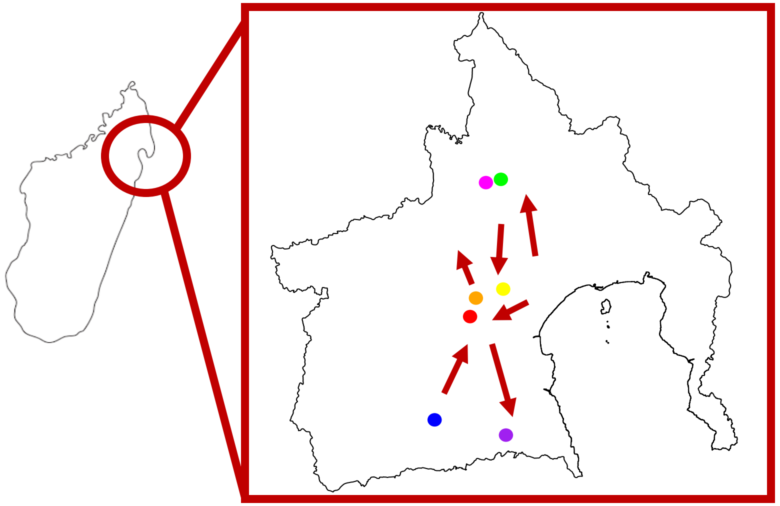
Bigger lemurs with **slower life histories** are particularly **vulnerable**.

Brook et al. 2018. *Conservation Biology.*

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

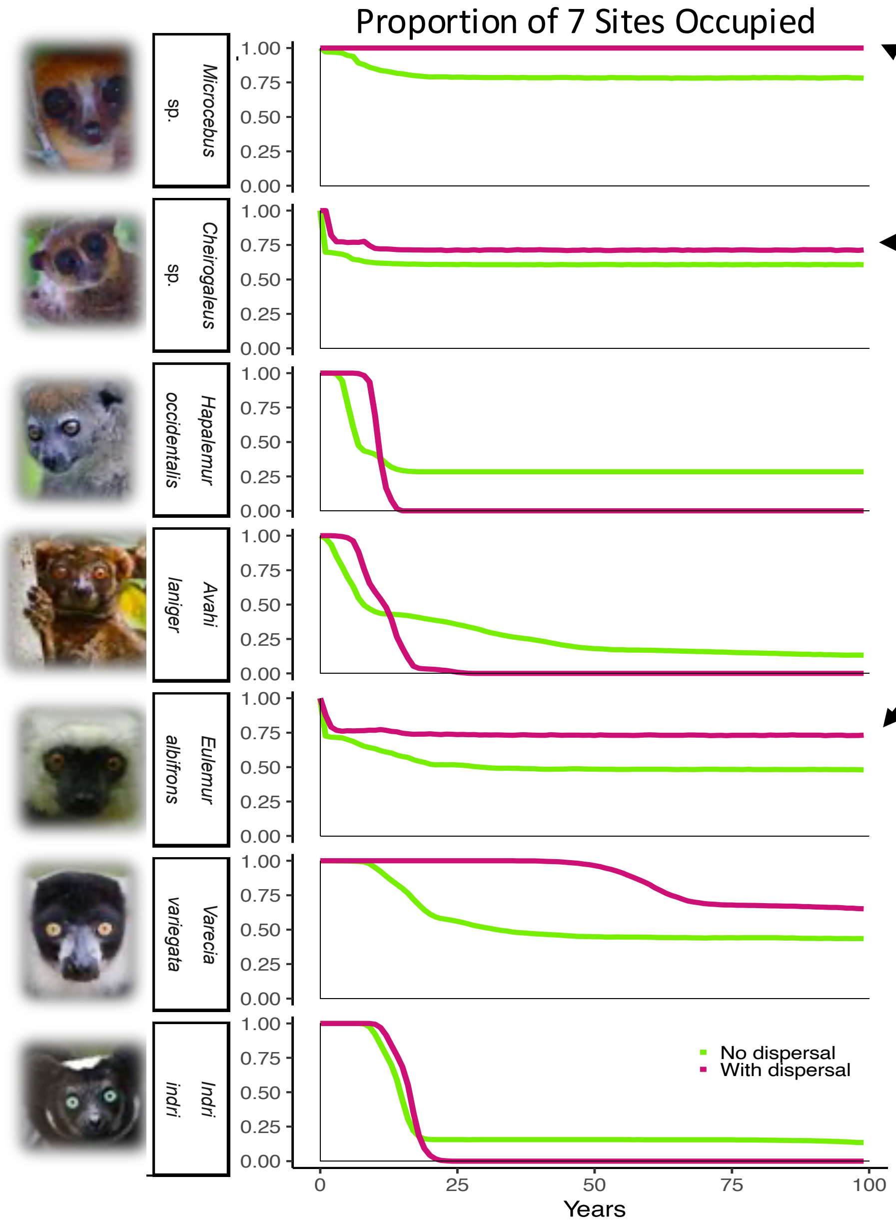
Assumptions:

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

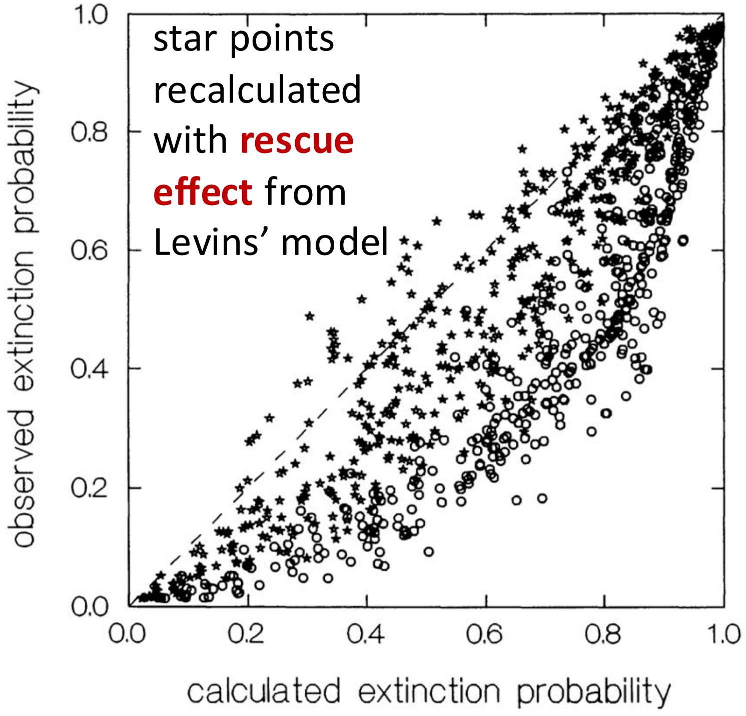


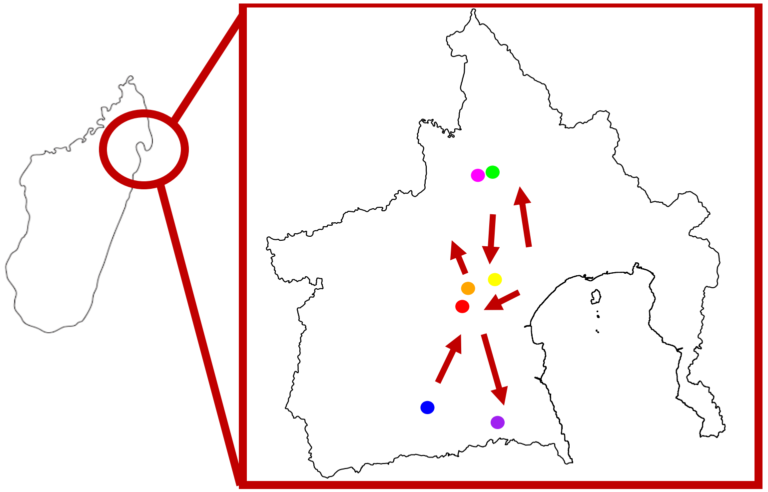
Brook et al. 2018. *Conservation Biology.*

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



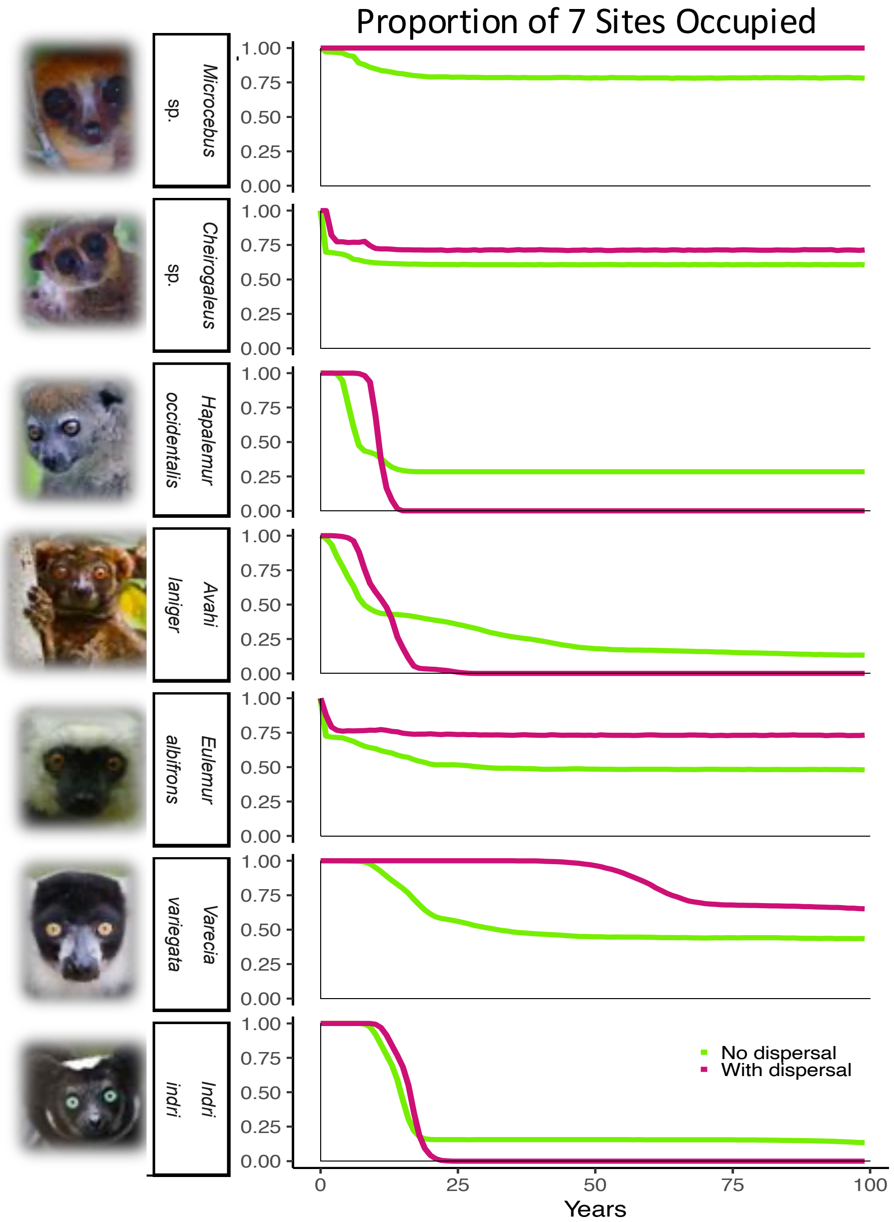
Metapopulation dynamics can promote more lemurs at more sites across the landscape!





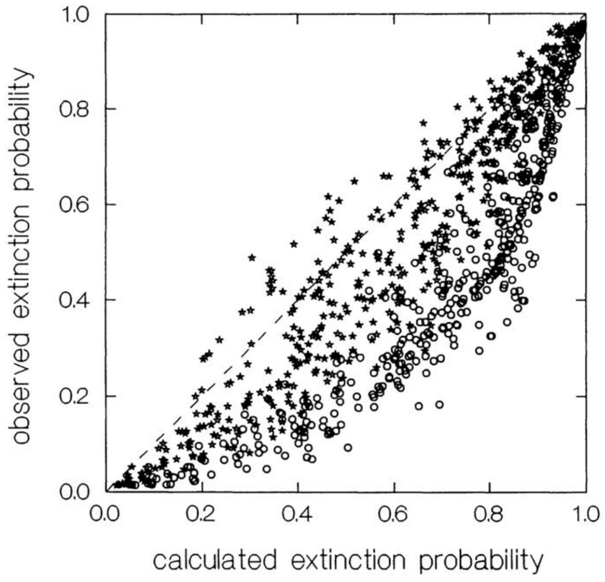
Brook et al. 2018. *Conservation Biology.*

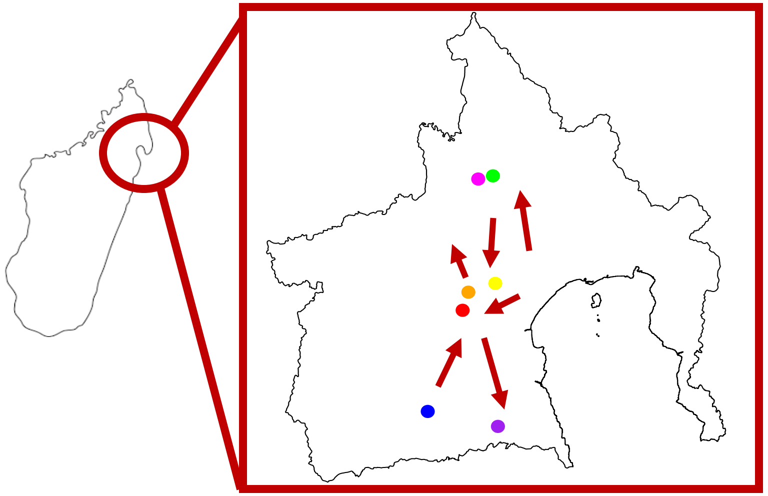
Dispersal can drive **regional extirpation** if the majority of local sites function as **population sinks**.



Metapopulation dynamics can drive regional declines in other cases!

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

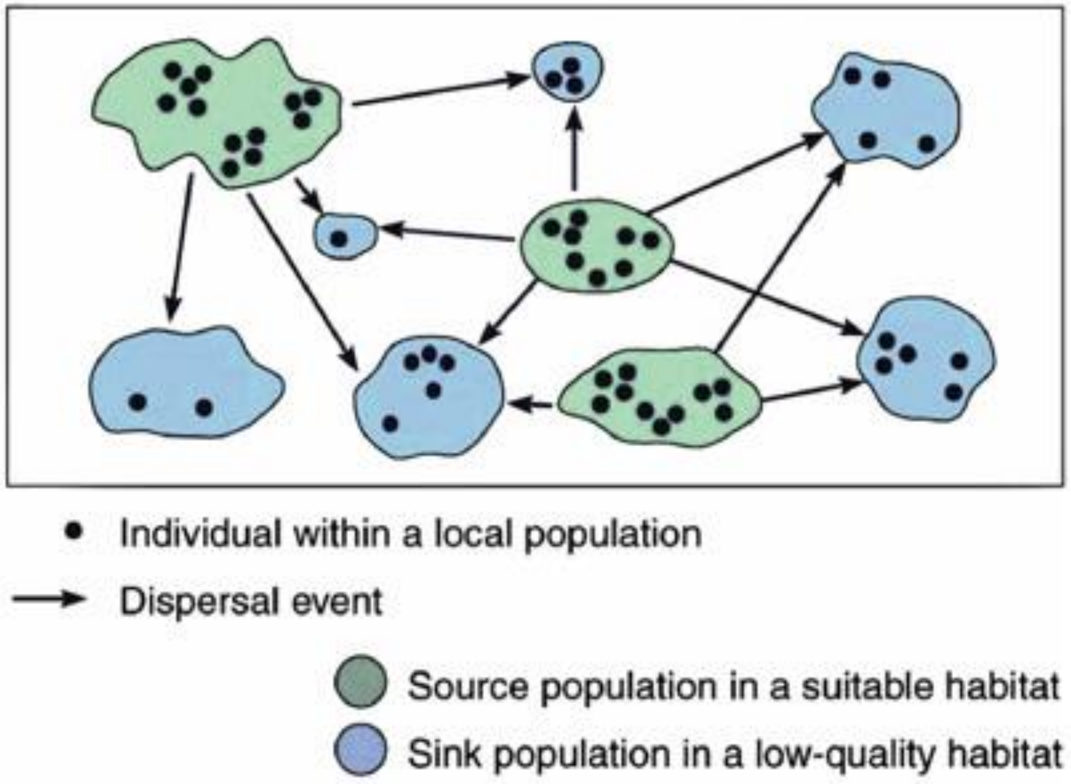




Brook et al. 2018. *Conservation Biology.*

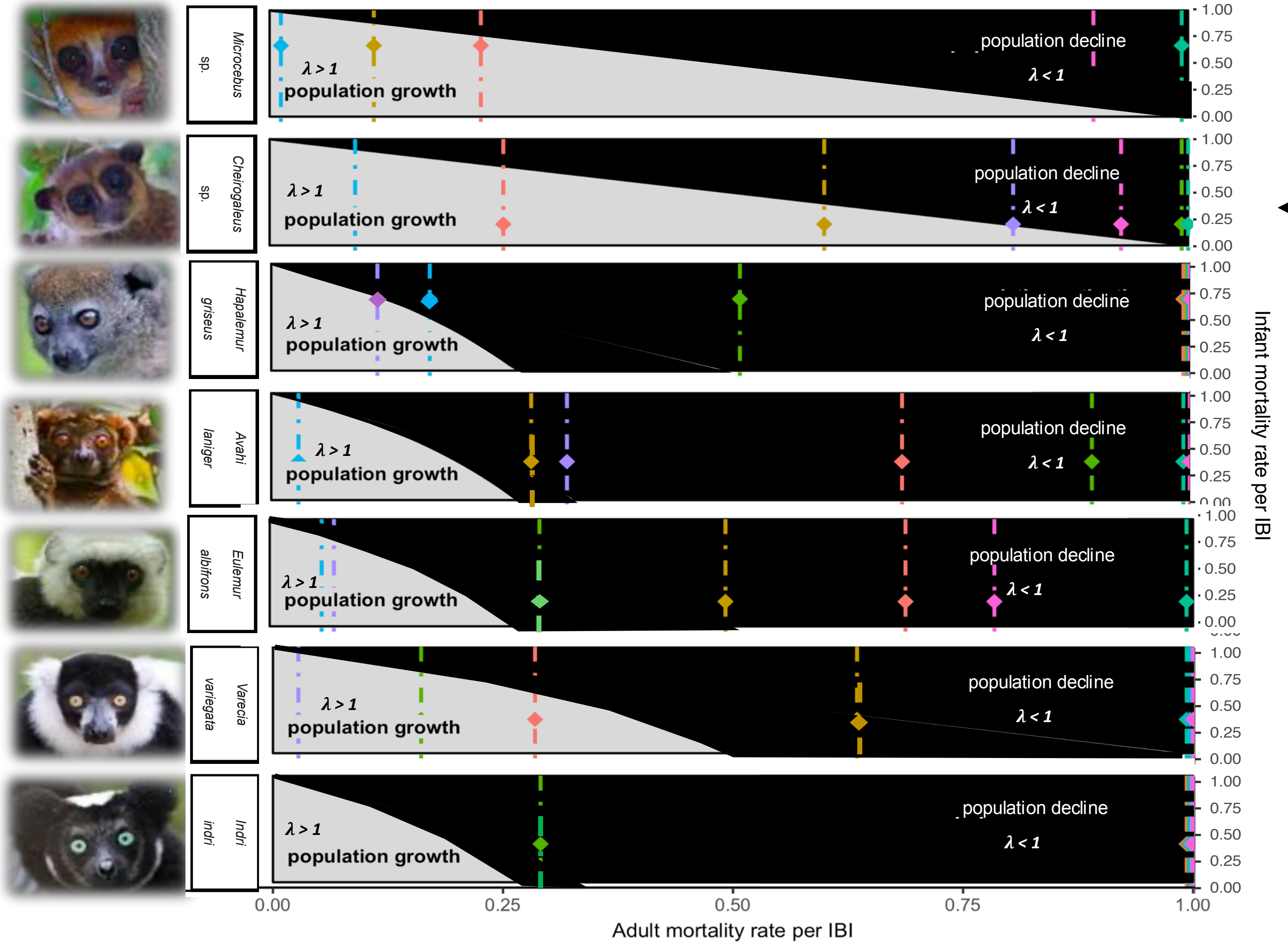
Source-sink theory describes how variation in habitat may affect population dynamics.

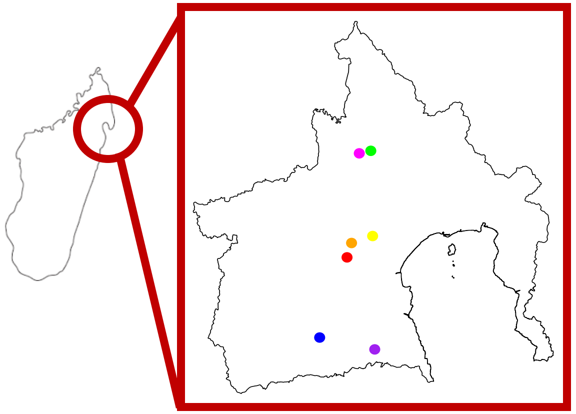
- Dispersal can drive **extinction** if the majority of sites function as **population sinks**.
- An **ecological trap** is an organism's preference for poor quality habitat
  - Ex: polarized light pollution & insect ovipositing



Pulliam 1988. *The American Naturalist.*

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



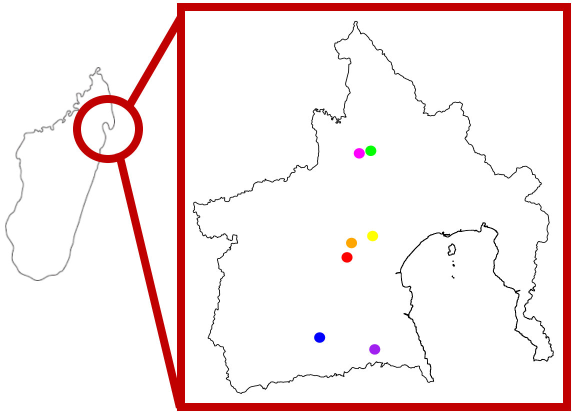


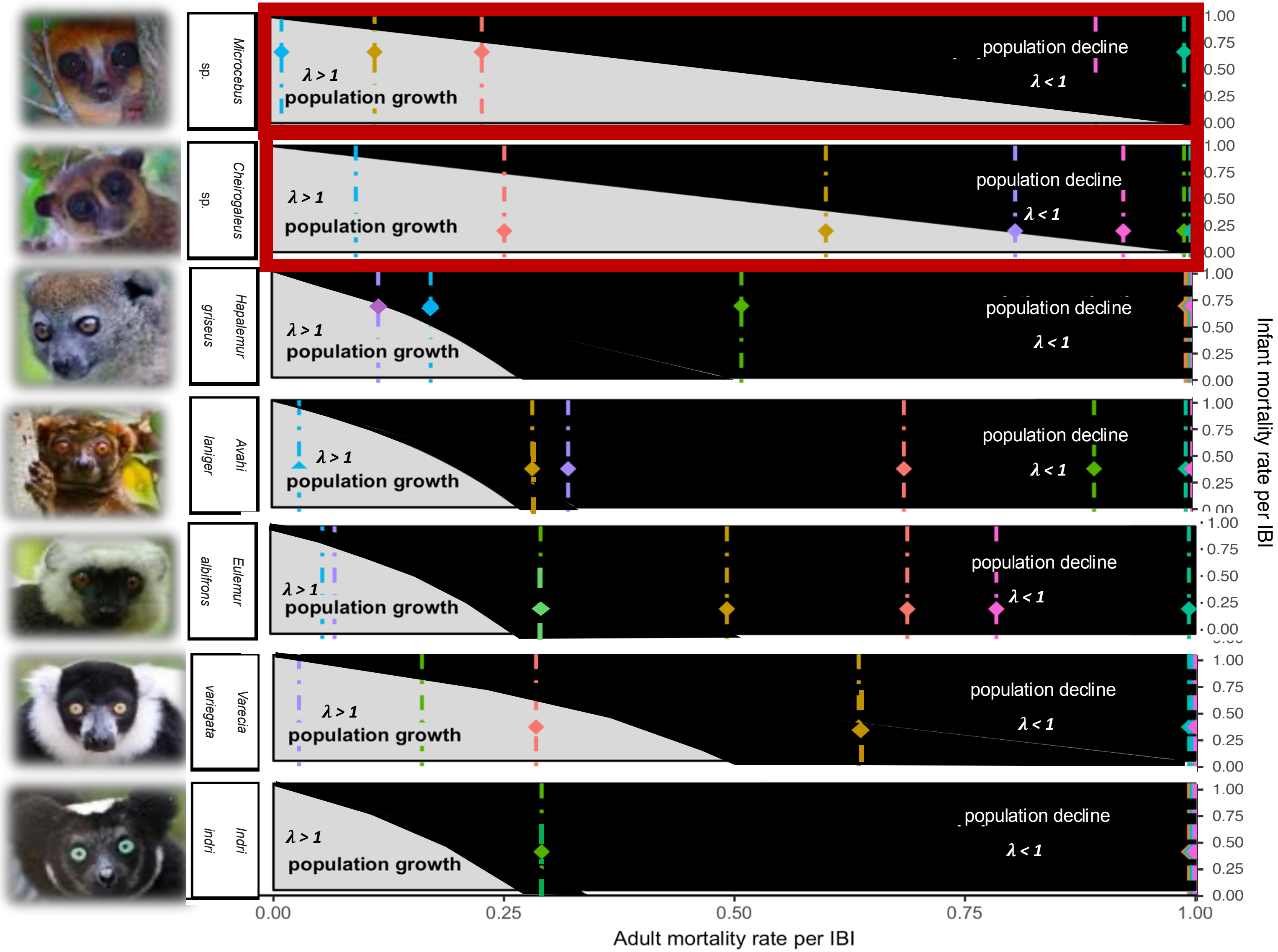
Colored vertical lines give **site-specific hunting rates** for adult lemurs.

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

Brook et al. 2018. *Conservation Biology.*

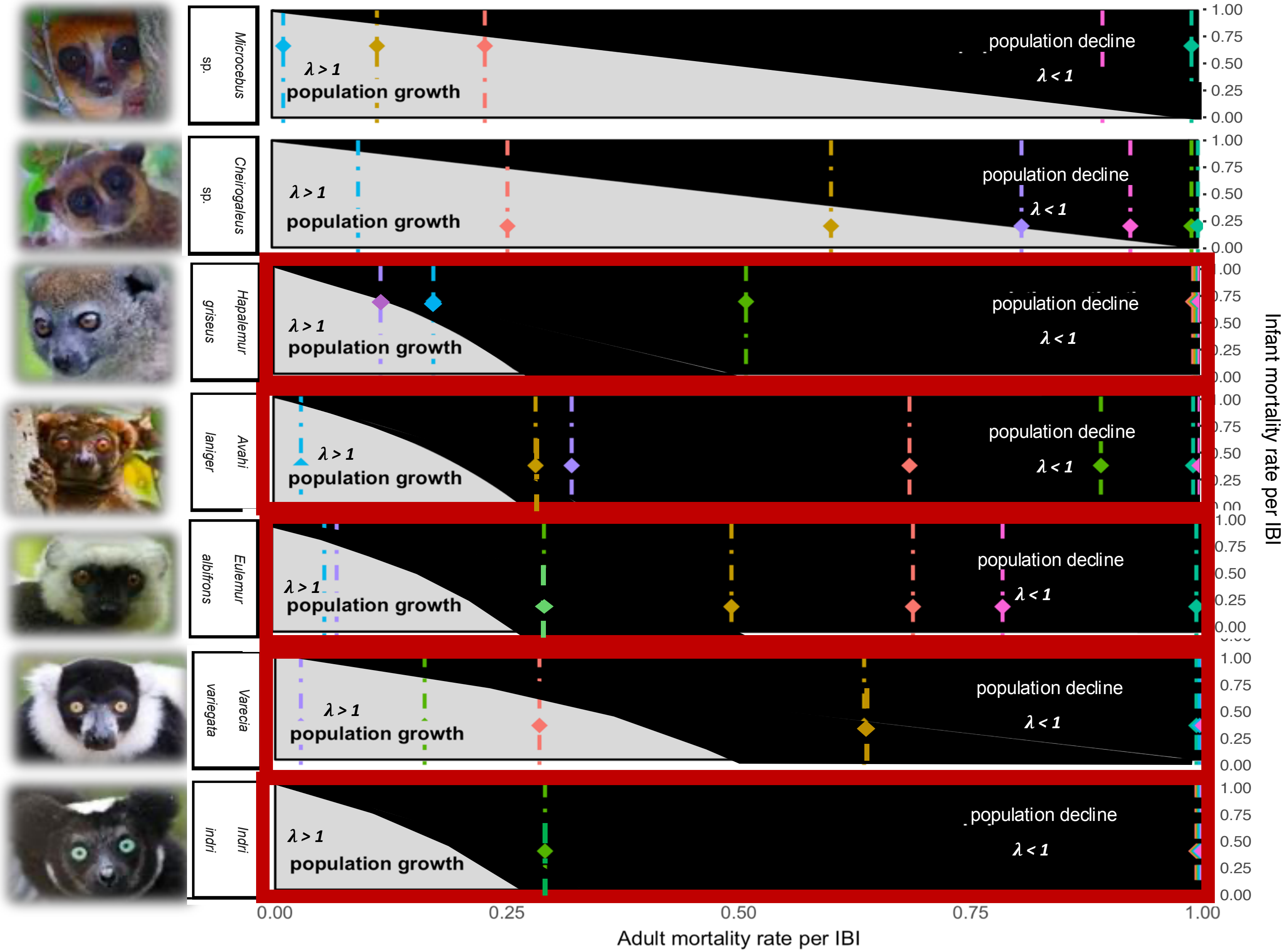
Small-bodied lemurs are largely **harvested at sustainable rates** on the Makira-Masoala peninsula.

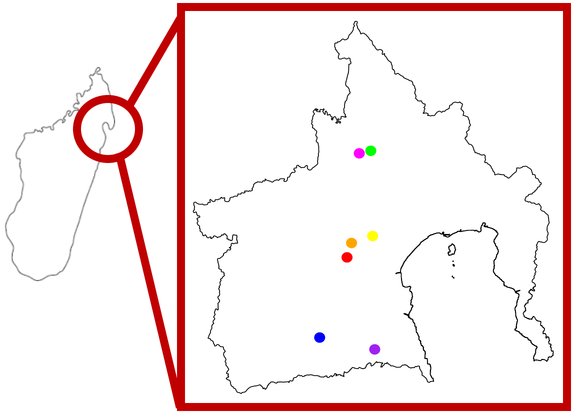




Brook et al. 2018. *Conservation Biology.*

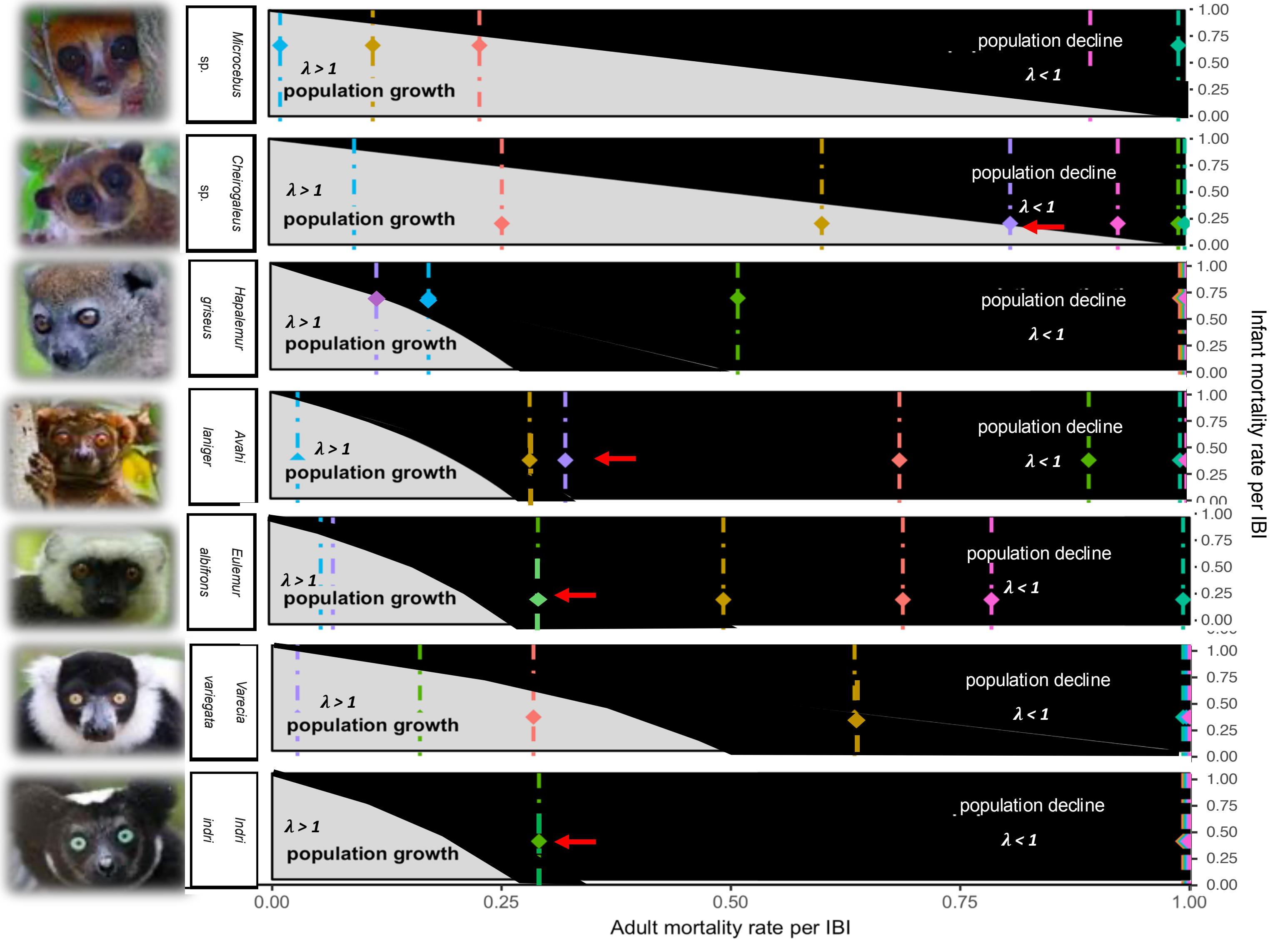
By contrast, **larger-bodied lemurs** are severely **threatened**.

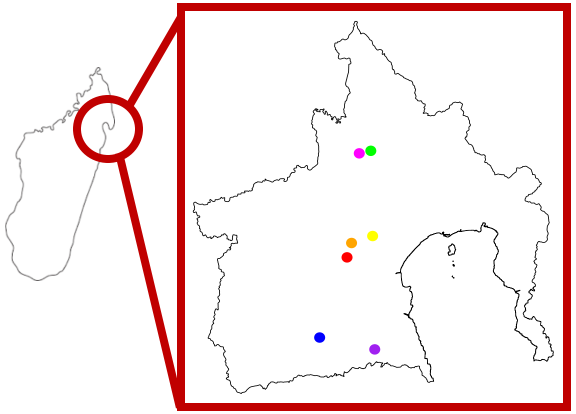




Brook et al. 2018. *Conservation Biology.*

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**

Brook et al. 2018. *Conservation Biology.*

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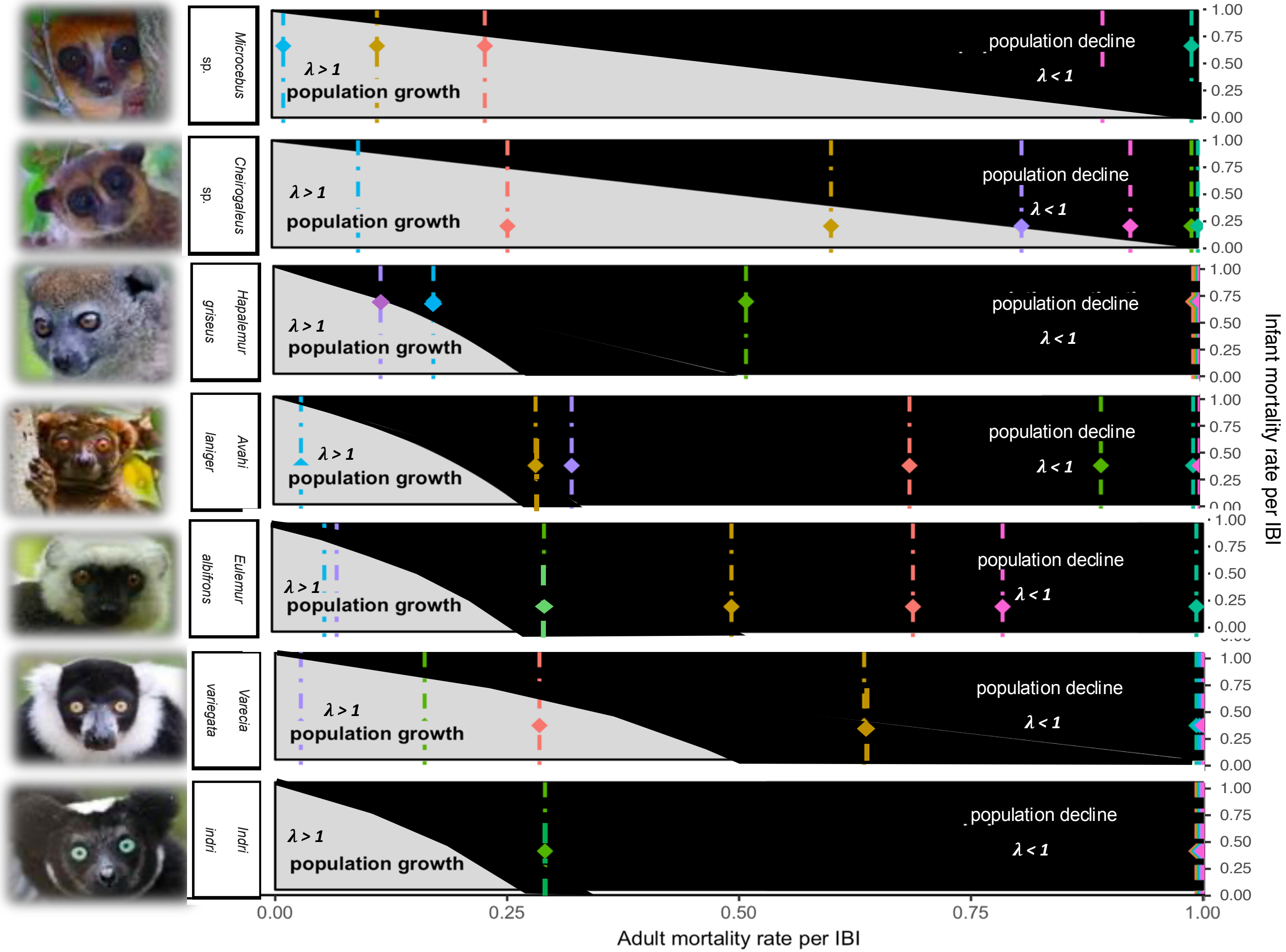
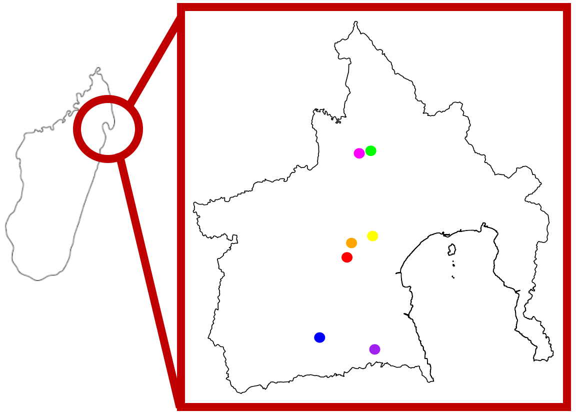


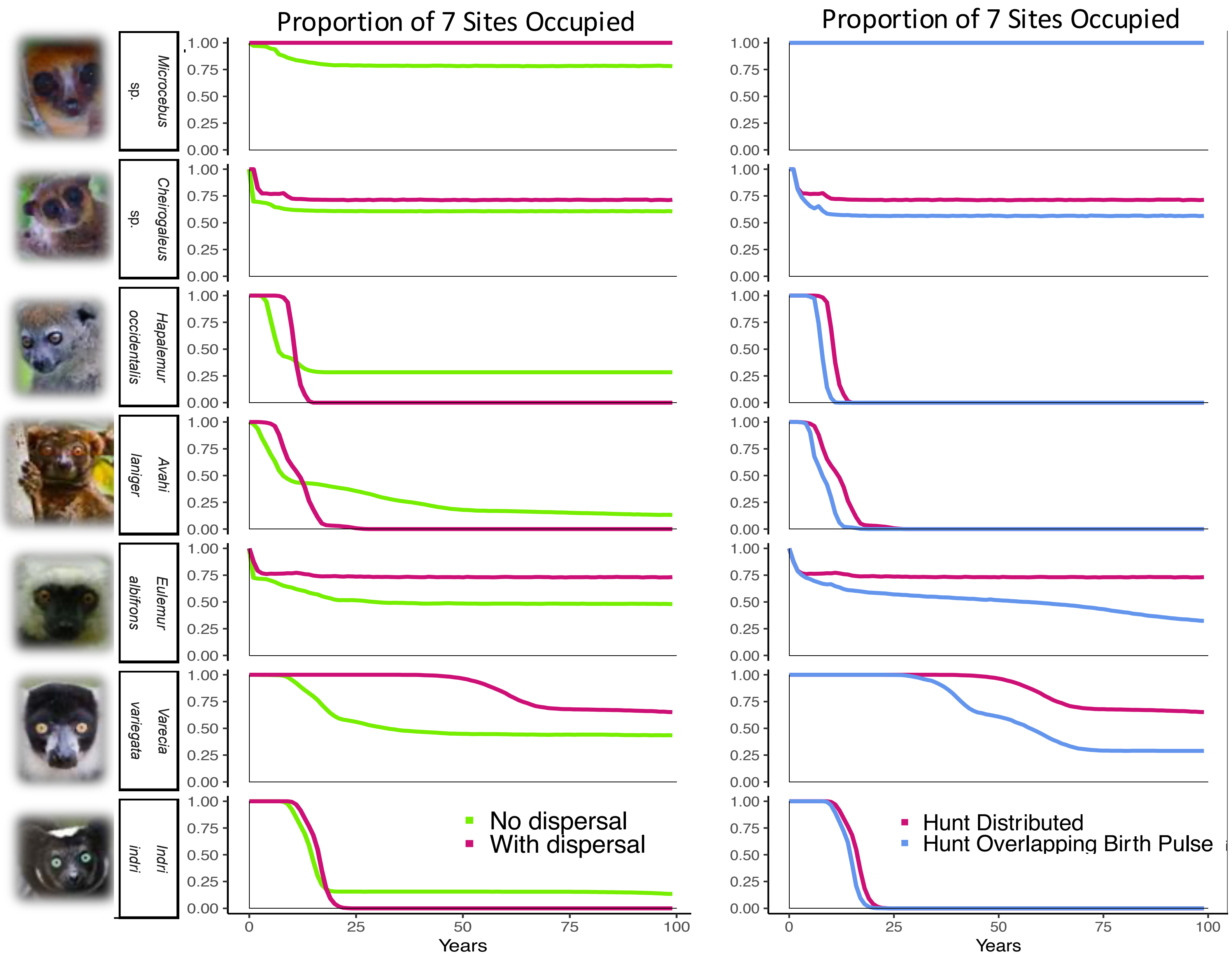


The **'Allee effect'** describes the correlation between population size and population 'fitness', often measured by the population rate of increase, λ.

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

Brook et al. 2018. *Conservation Biology.*

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



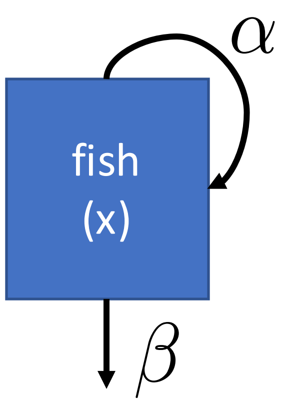
Our lemur model highlights some of the earlier challenges discussed with modeling '**maximum sustainable yield**' in fisheries!

Simplest representations of MSY:

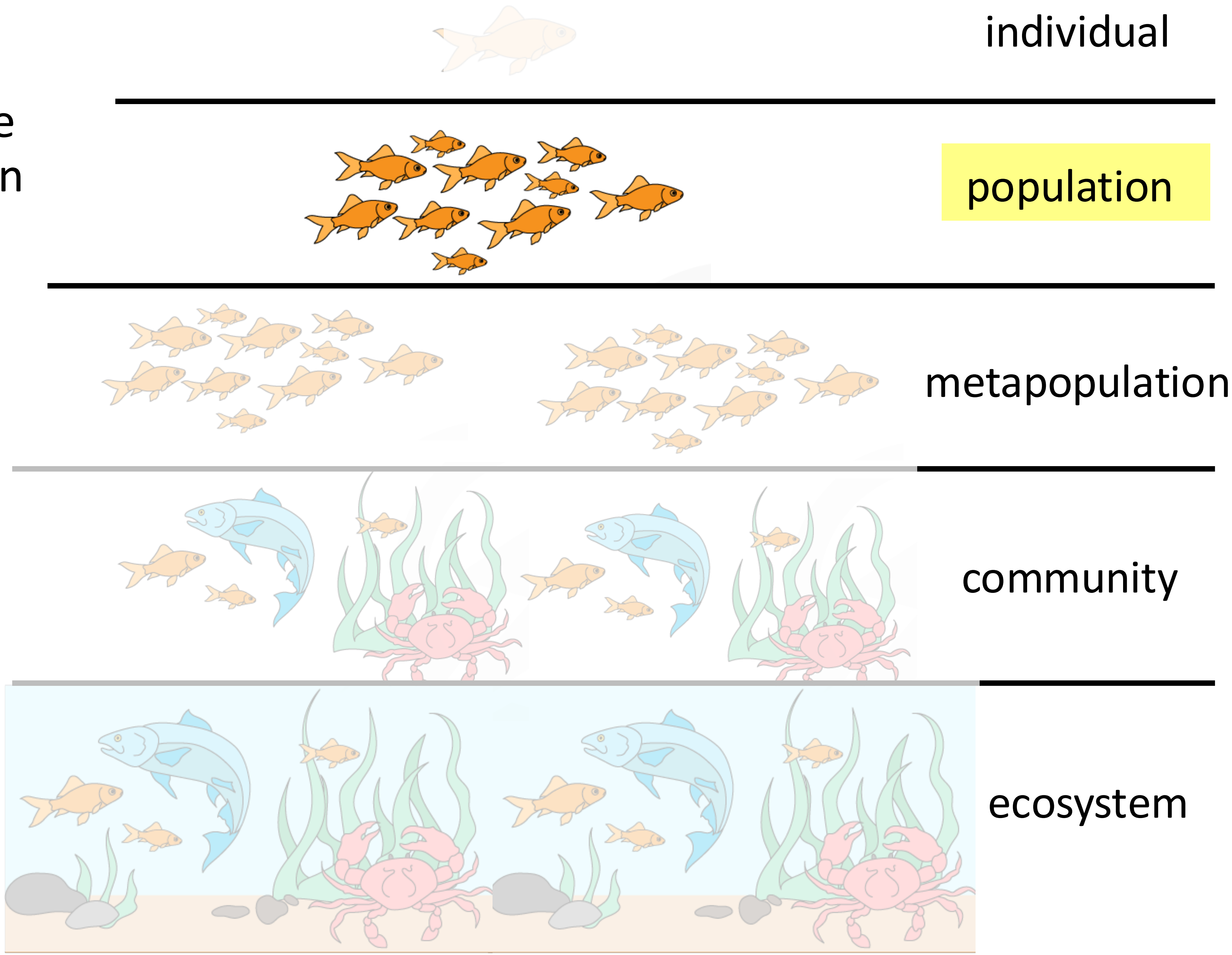
- Neglect population structure.
- Assume constant harvest.
- Ignore environmental and demographic stochasticity

Brook et al. 2018. *Conservation Biology.*

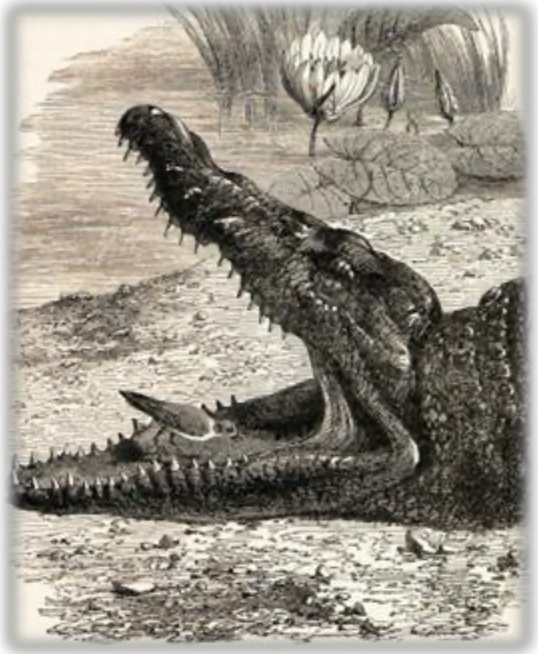
Population = multiple individuals of the same species (**conspecifics**) in the same habitat



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

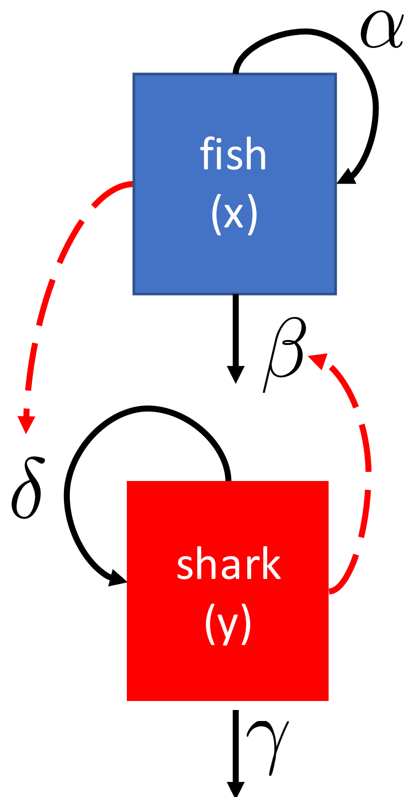


The logistic growth equation offers an explanation for population self-regulation, an example of **intraspecific competition**.

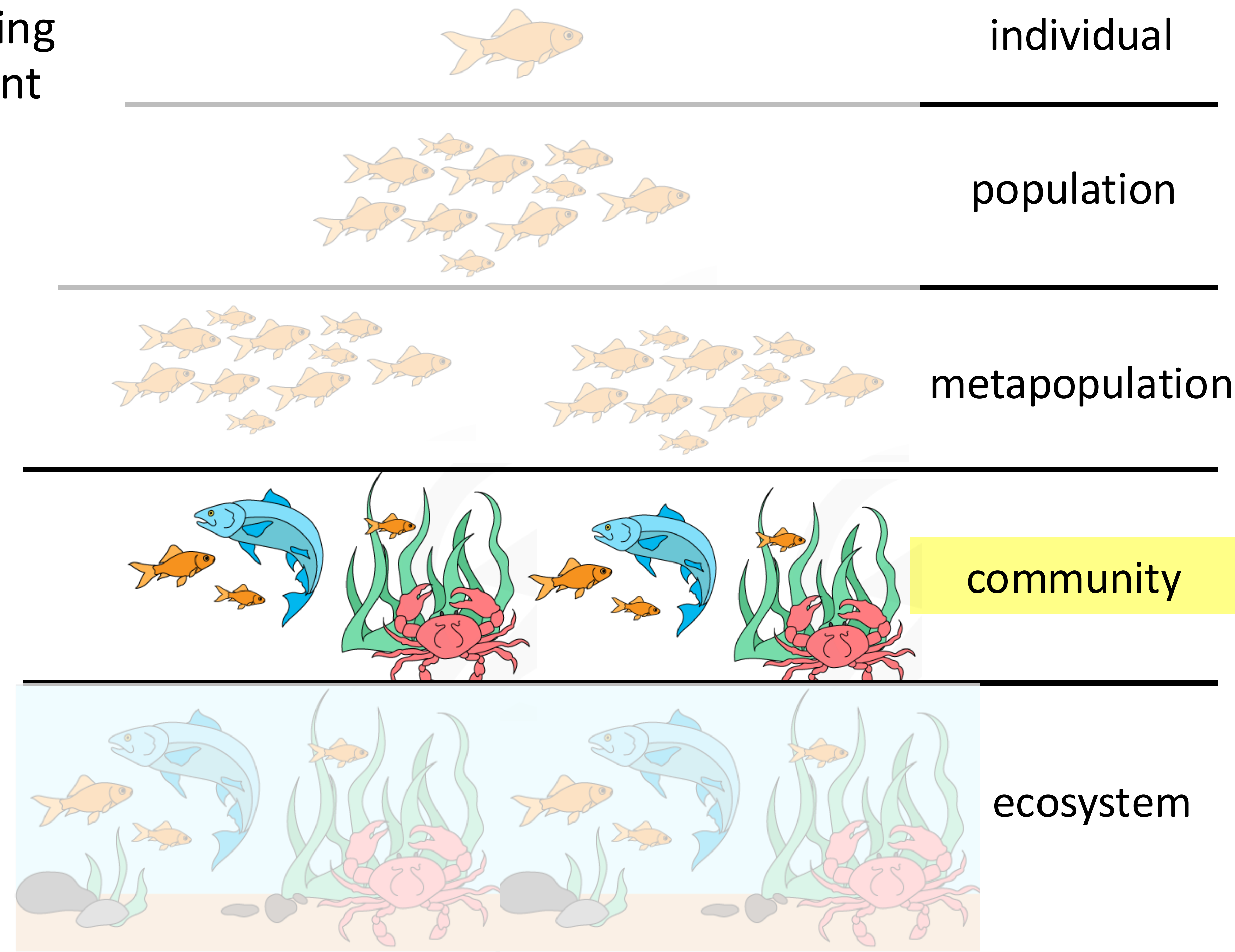


But ecology is the study of the **interactions** of organisms with each other and their environment, and in some cases, **interspecific interactions** are essential to understanding ecological systems.

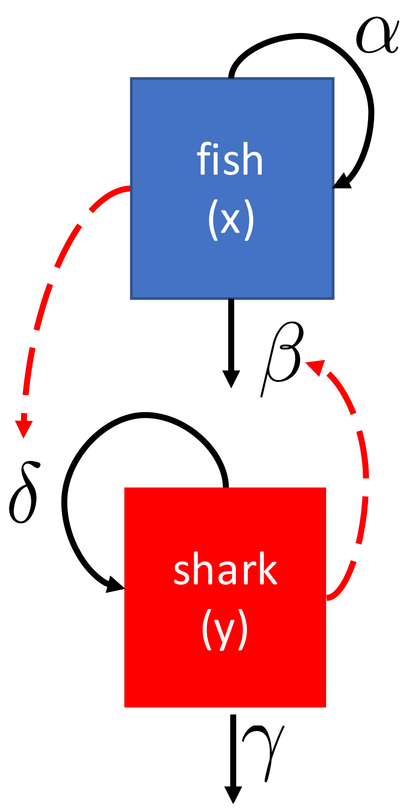
Community = interacting populations of different species



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



The Lotka-Volterra predator-prey model



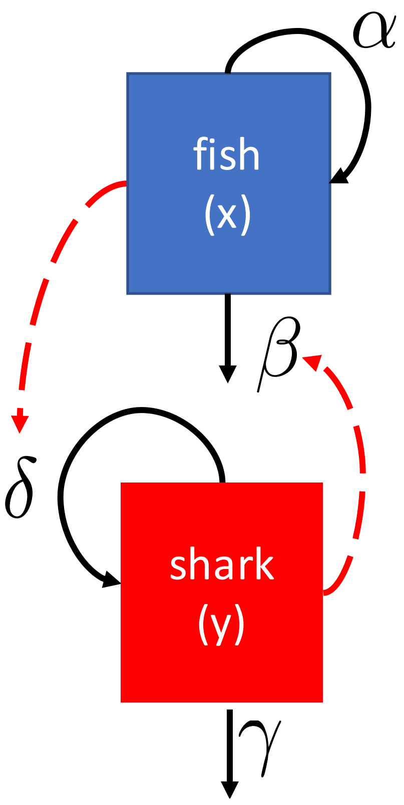
*How does **fish** abundance **vary** with **changes** in **shark** abundance?*

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

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

- First proposed by Polish-born American mathematician & chemist, Alfred J. Lotka, in 1920 to explain autocatalytic chemical reactions.
- Lotka worked with Soviet mathematician Andrey Kolmogorov to extend the model to “organic systems”, originally studying plant-herbivore interactions.
- In 1926, Italian mathematician Vito Volterra independently developed the same model to explain the dynamics of predatory fish catches which increased immediately following WWI after years of low fishing.
- Idea that **interspecies interactions** regulate populations

The Lotka-Volterra predator-prey model



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

growth rate of prey, independent of predator

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

death rate of prey, depends on abundance of predator

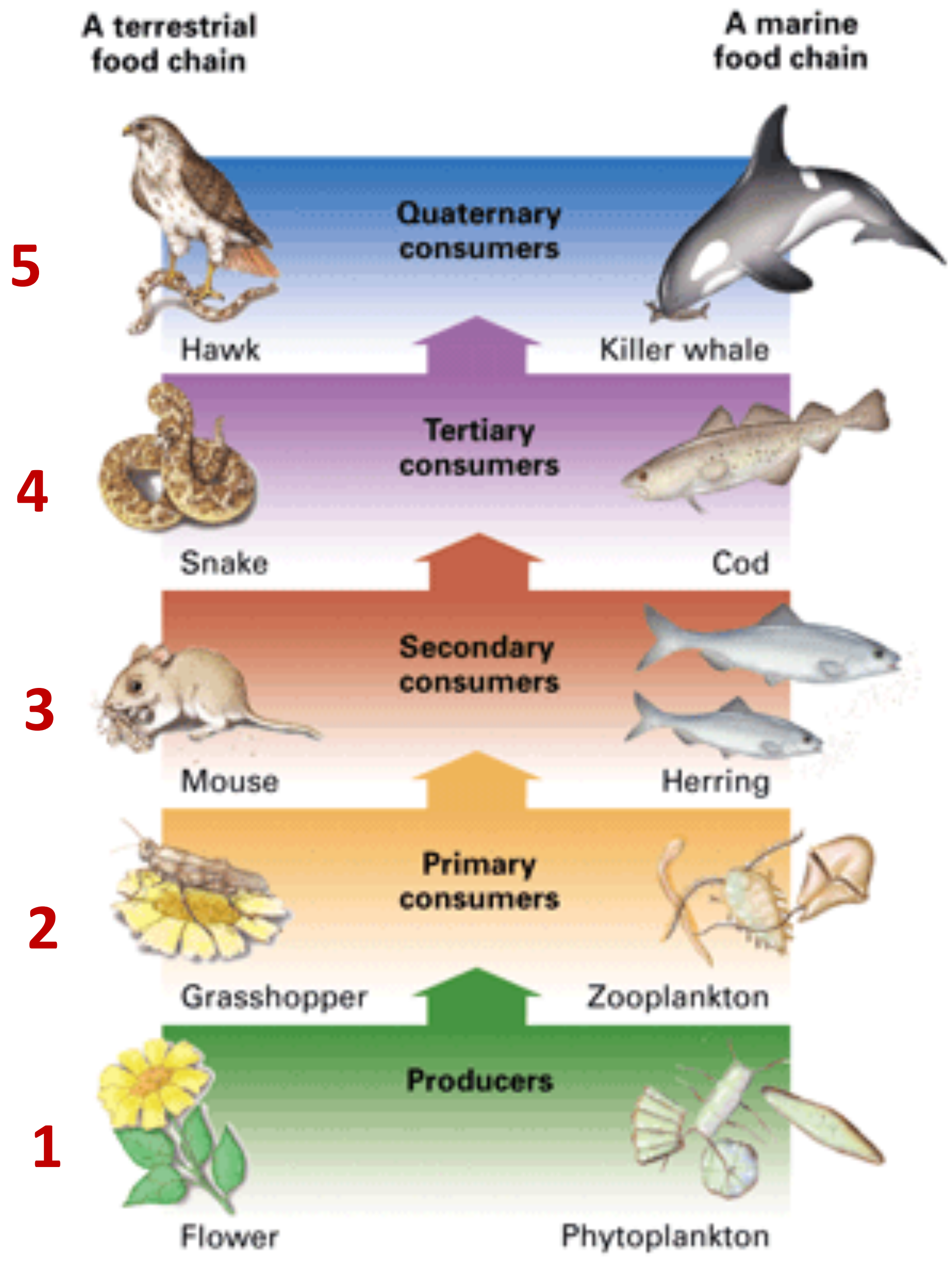
$$\frac{dy}{dt} = \delta xy - \gamma y$$

death rate of predator, independent of prey

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

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

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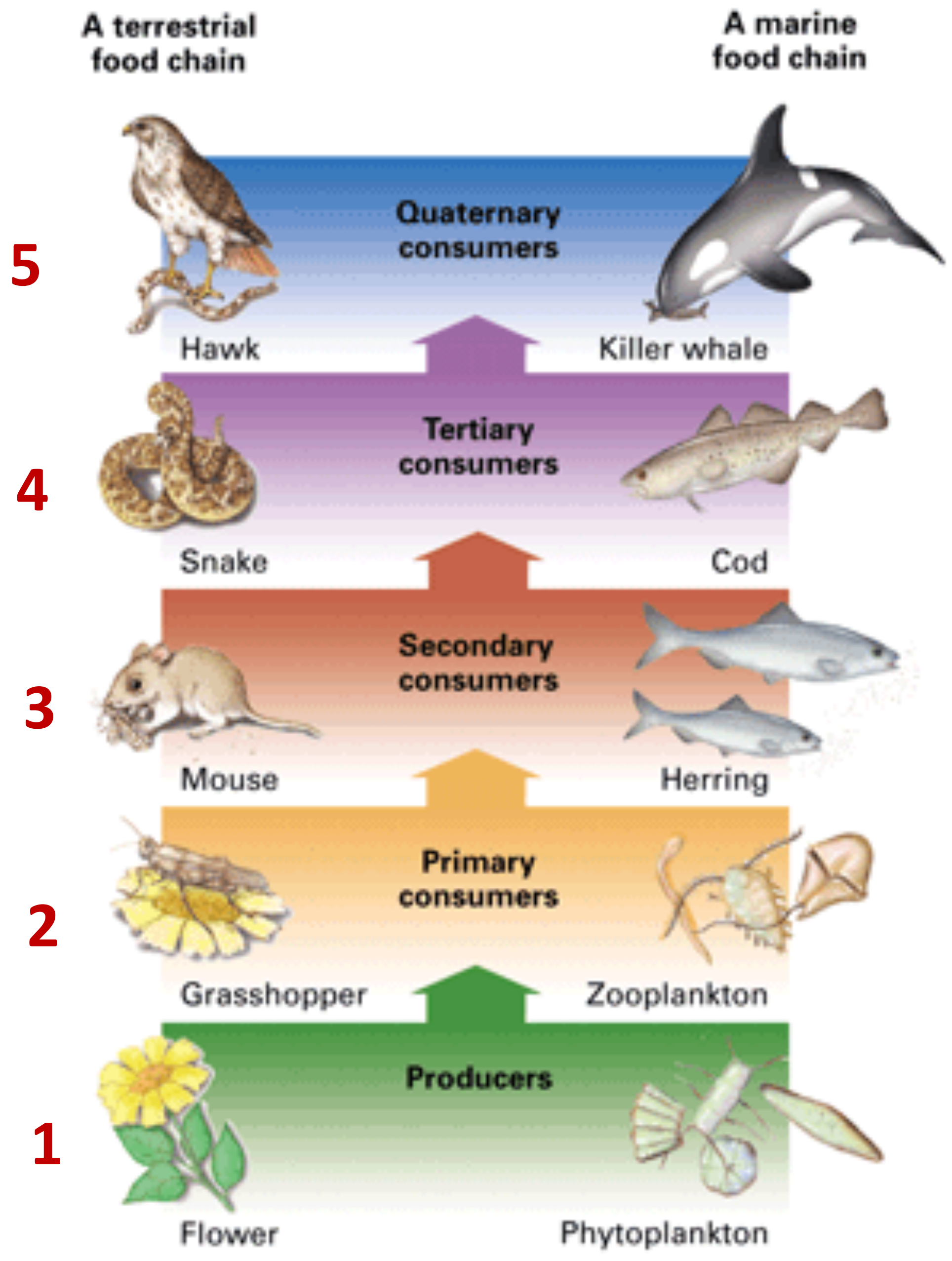
Energy efficiency is the term used to describe the transfer of energy moving up a trophic level.



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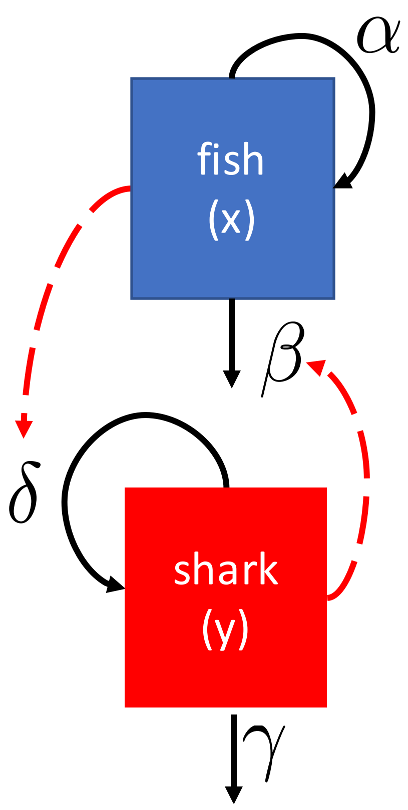

$$\frac{dx}{dt} = \alpha x - \beta xy$$

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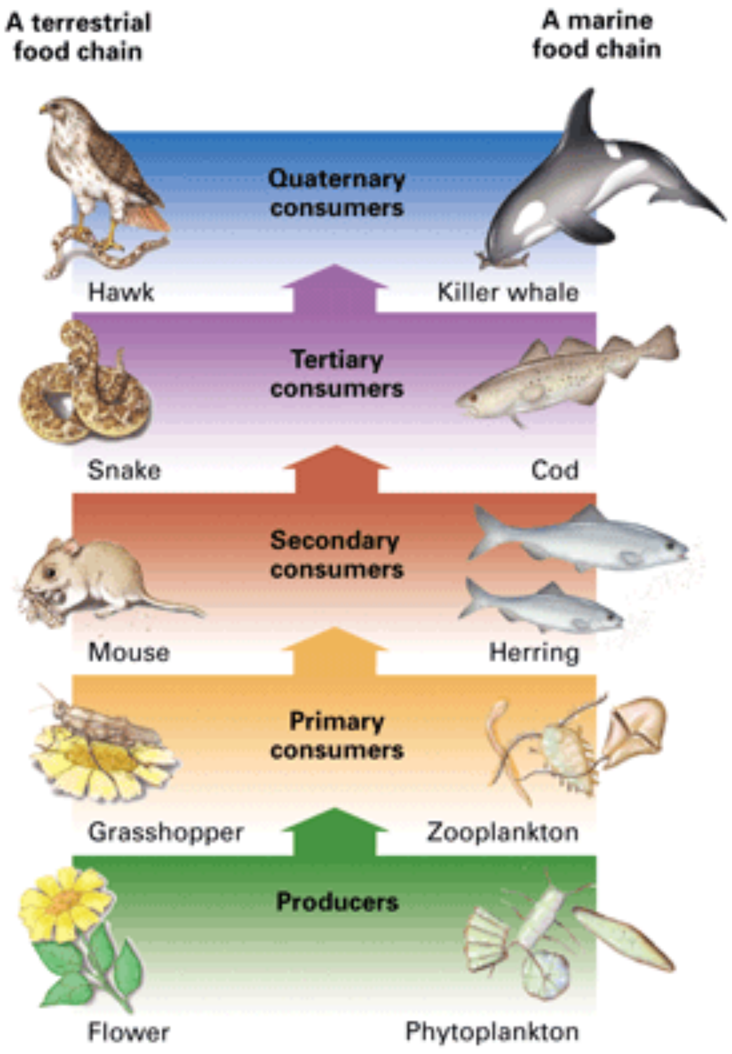
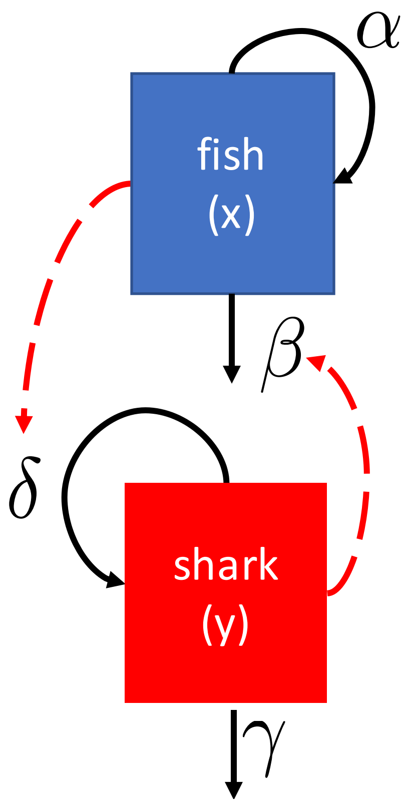
*How does **fish** abundance **vary** with **changes** in **shark** abundance?*

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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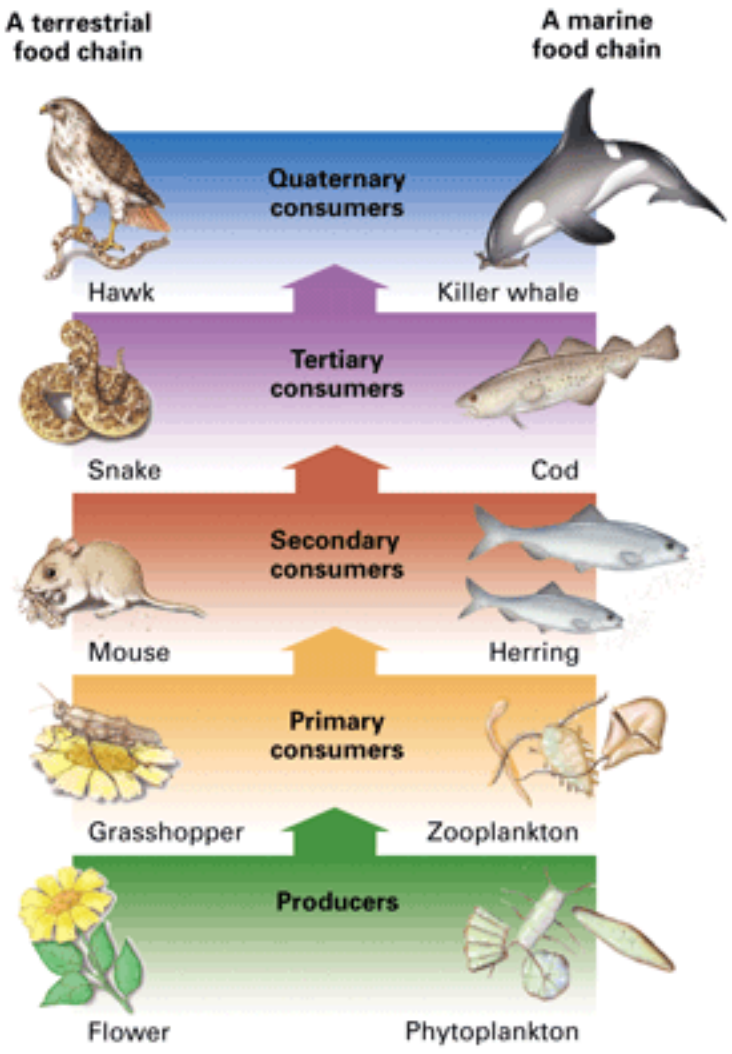
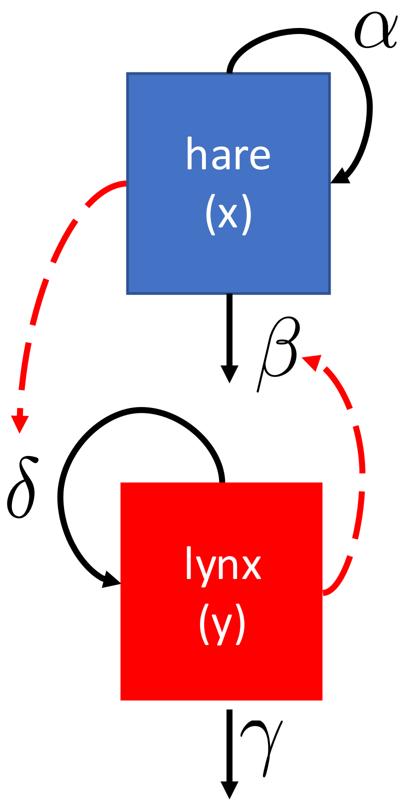


Lotka-Volterra predator-prey models with data



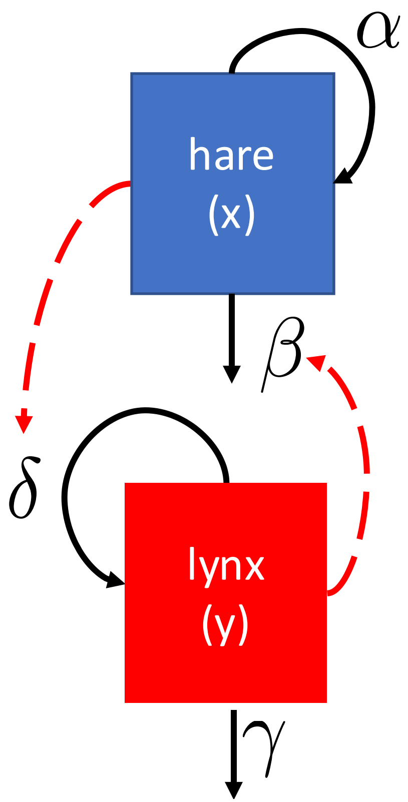
*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*

PRO PELLE CUTEM

HUDSON'S BAY

INCORPORATED 2 MAY 1670

Lotka-Volterra predator-prey models with data



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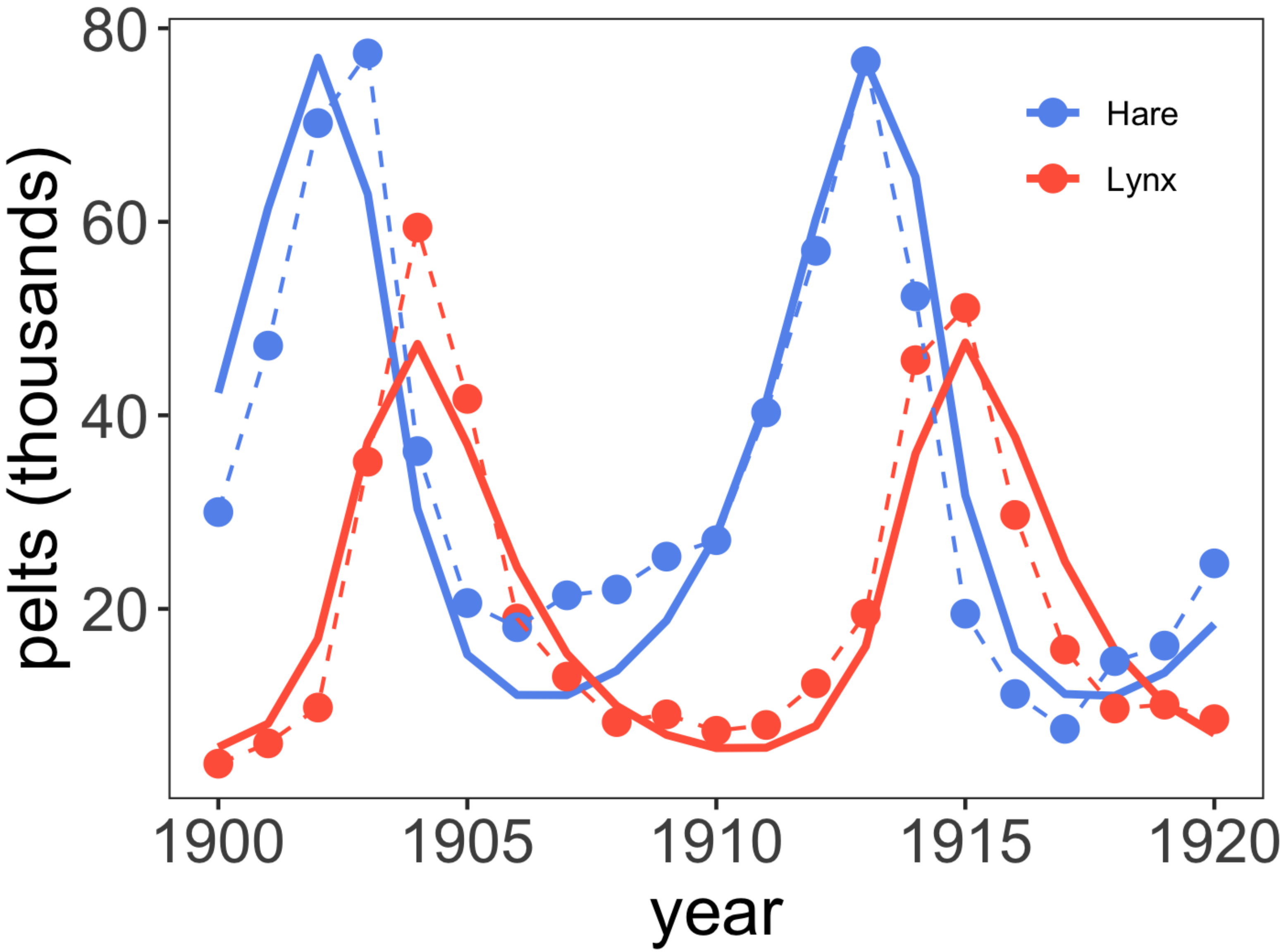

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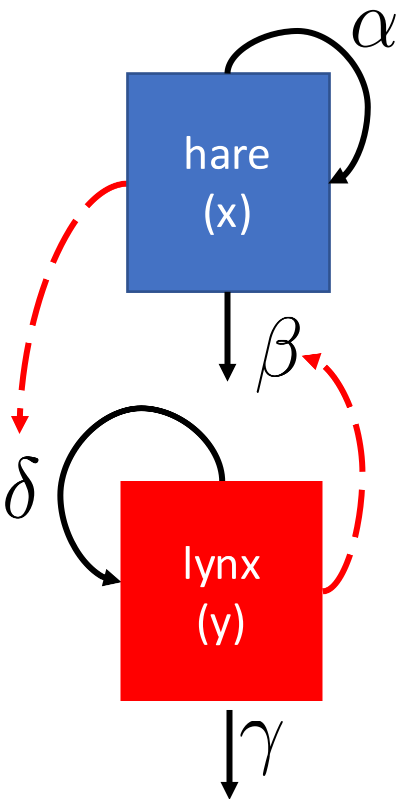
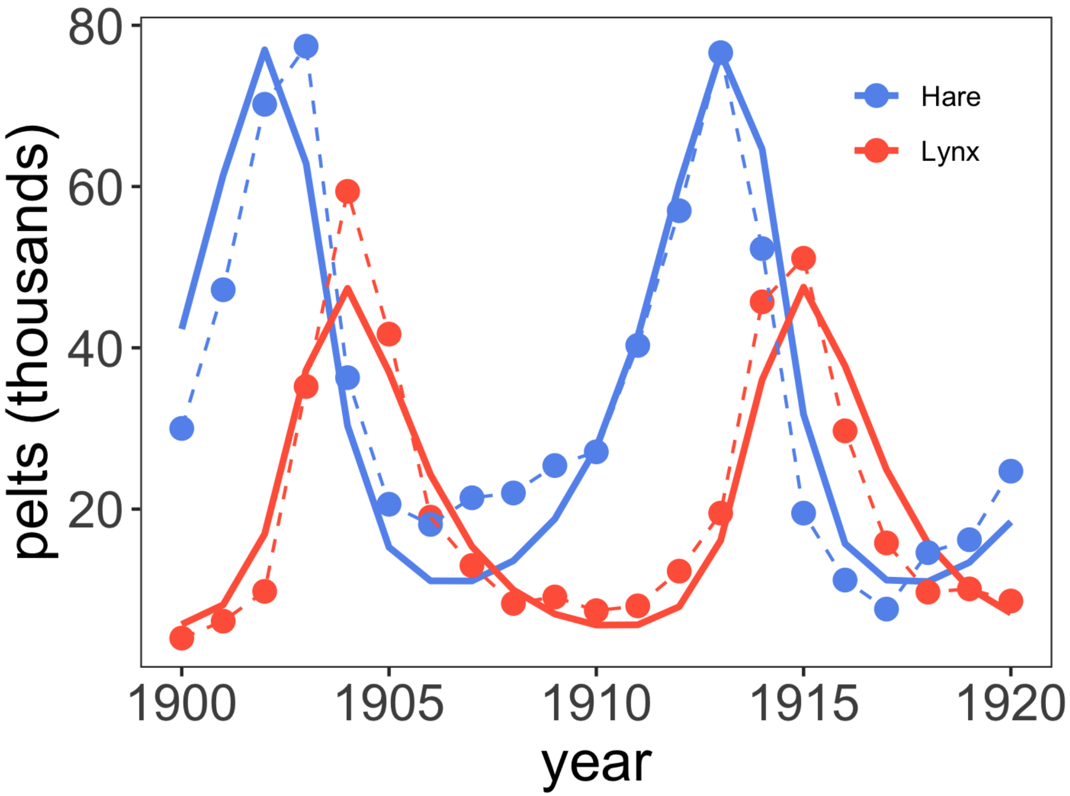




- Fitting a model to data allows us to estimate parameters – remember those growth rates from the human population models!
- Here, we can explore the growth rate of the prey under exponential growth (α), the efficiency of kill (β) and digestion (δ) by the predator, and the natural death rate of the predator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

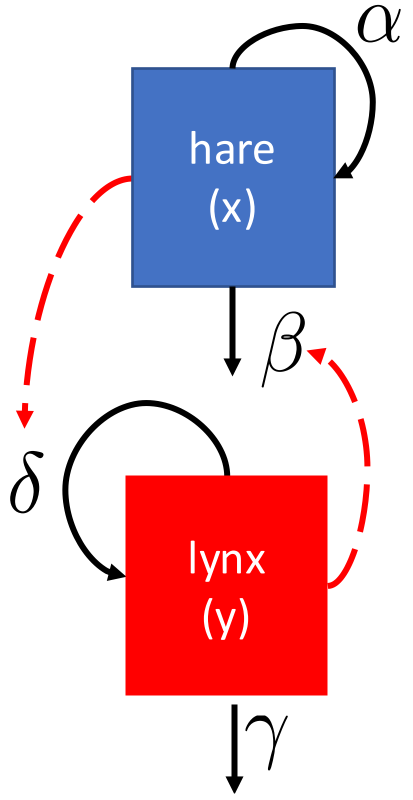
*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*

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

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

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

Lotka-Volterra predator-prey **isoclines**



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

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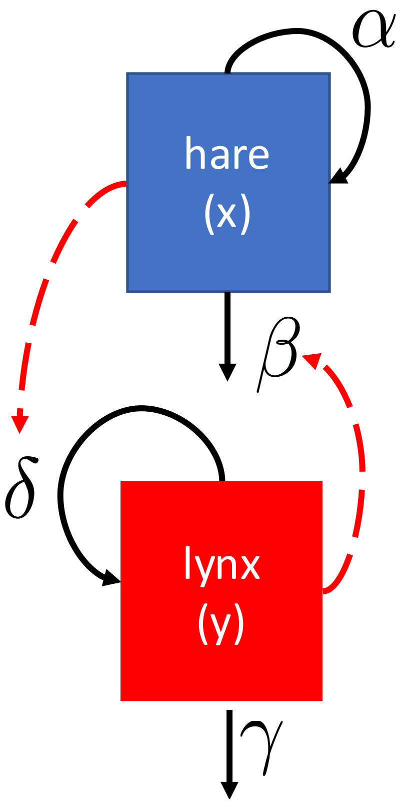
*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*

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**



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

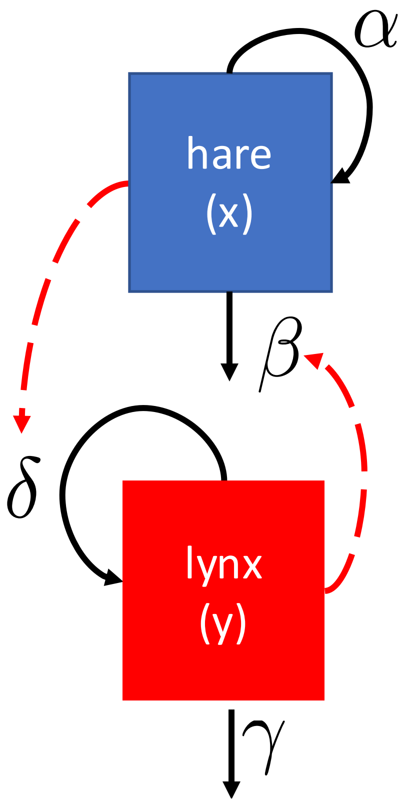
$$\frac{dy}{dt} = \delta xy - \gamma y$$

*What are the **prey** isoclines?*

(hint: this means the prey 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 **prey** isoclines?*

$$0 = \alpha x - \beta xy$$

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

$isoclines\ at$:

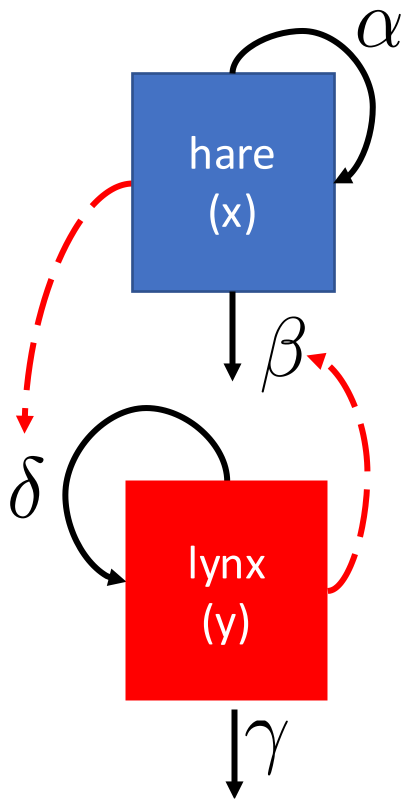
$$x = 0$$

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

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**



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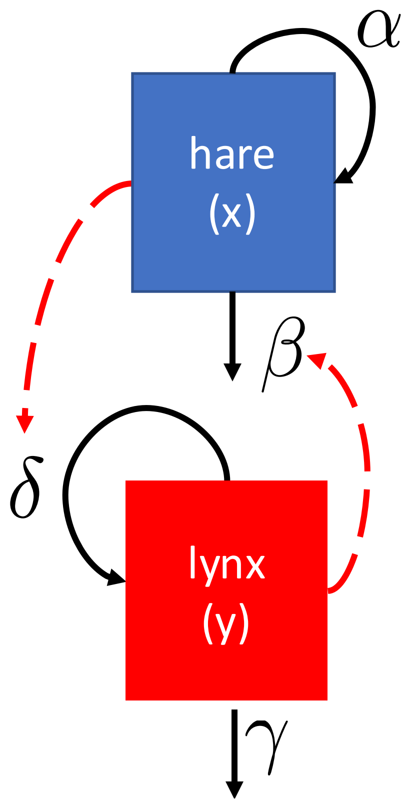
*What are the **predator** isoclines?*

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

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

Lotka-Volterra predator-prey **isoclines**



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

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

*What are the **predator** isoclines?*

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

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

$$isoclines \ at:$$

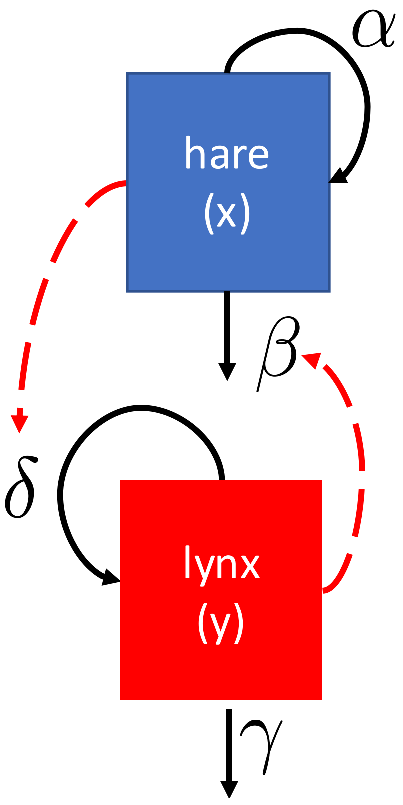
$$y = 0$$

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

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**



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

prey isoclines:

$$x = 0$$

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

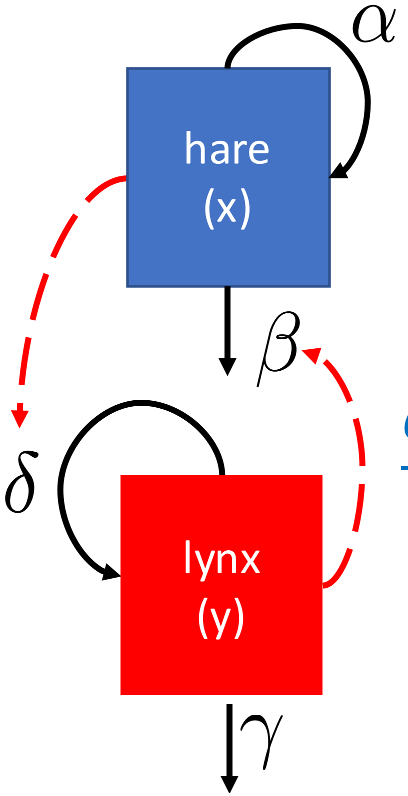
predator isoclines:

$$y = 0$$

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

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

Lotka-Volterra predator-prey **isoclines**



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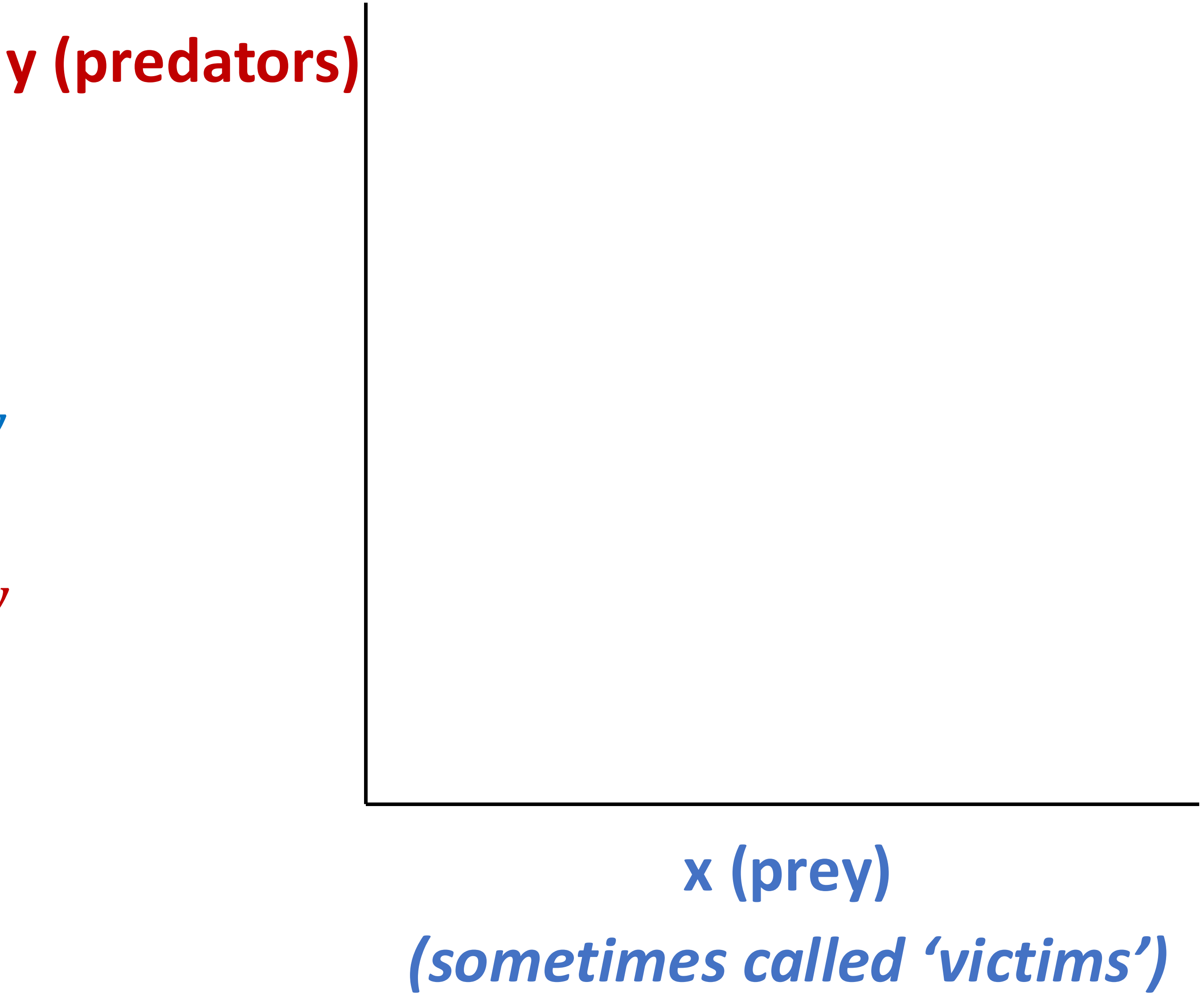
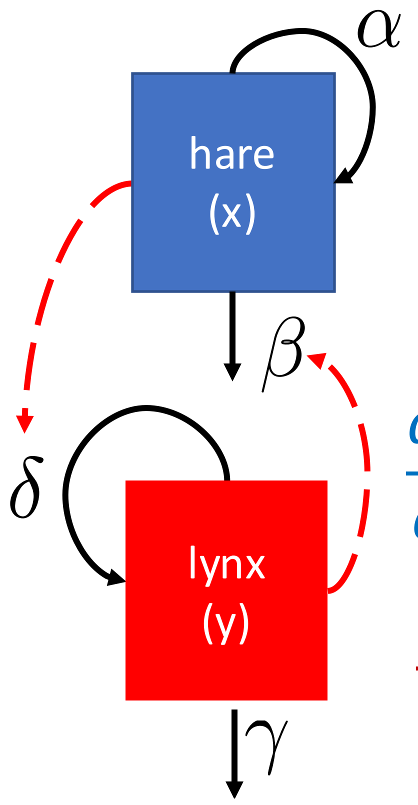


Lotka-Volterra predator-prey isoclines



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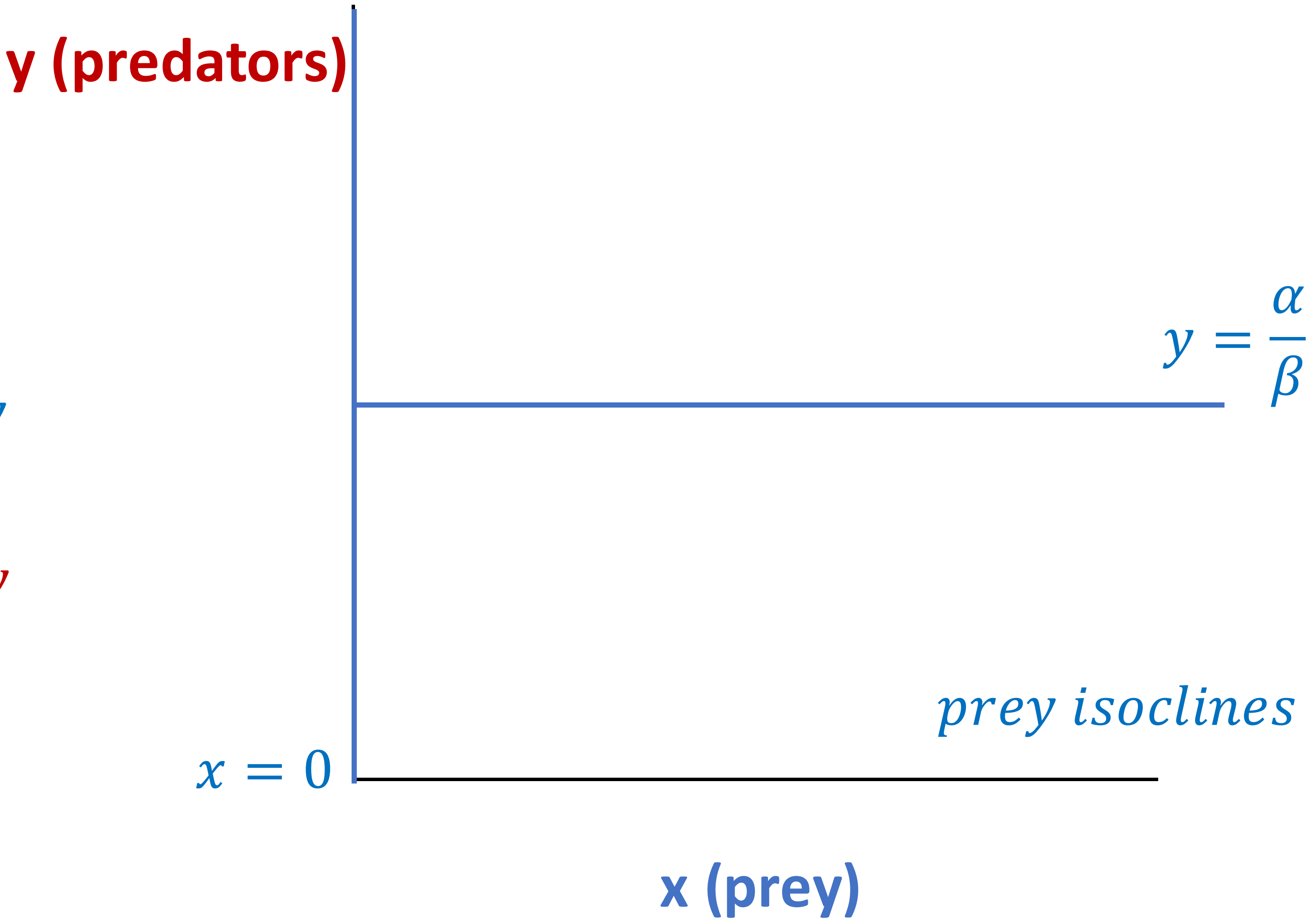
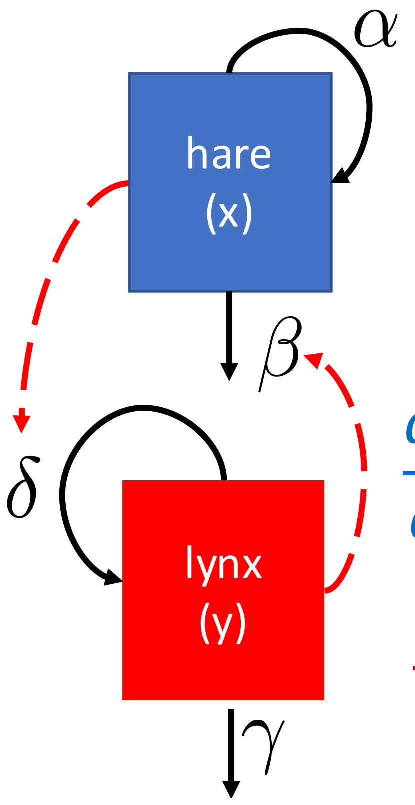


Lotka-Volterra predator-prey isoclines

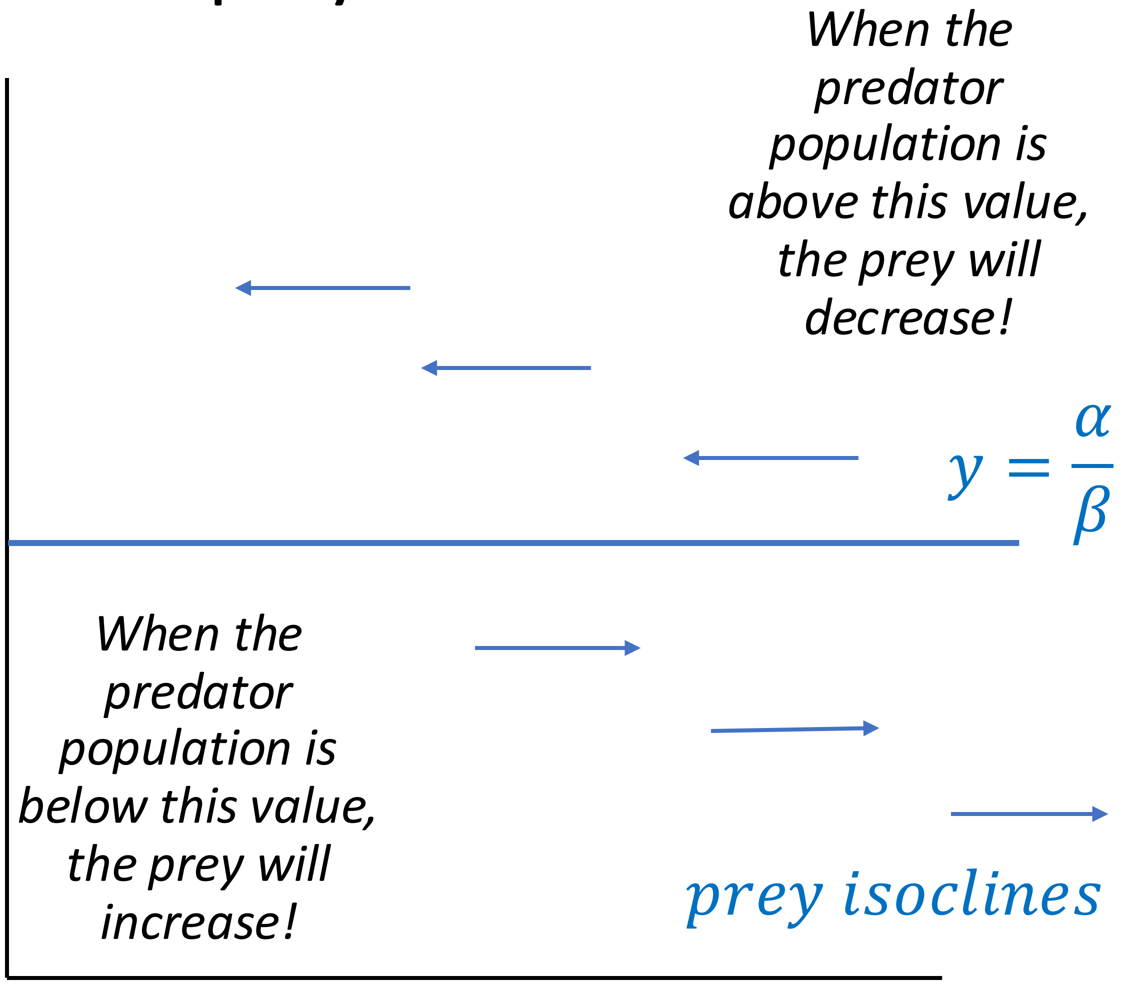


$$\frac{dx}{dt} = \alpha x - \beta xy$$

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

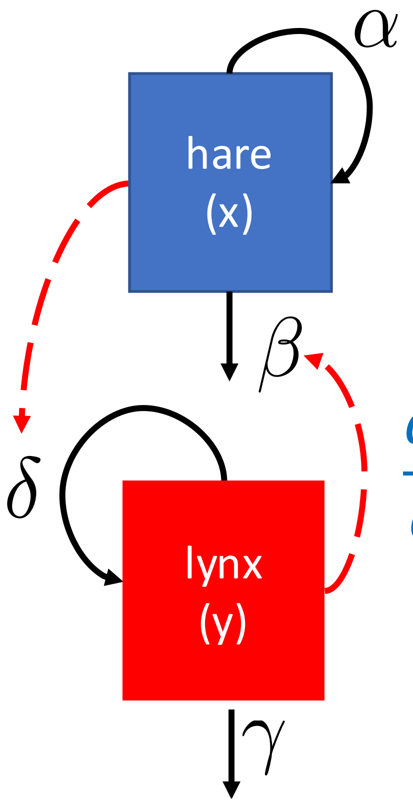
*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*

y (predators)



x (prey)

Lotka-Volterra predator-prey **isoclines**



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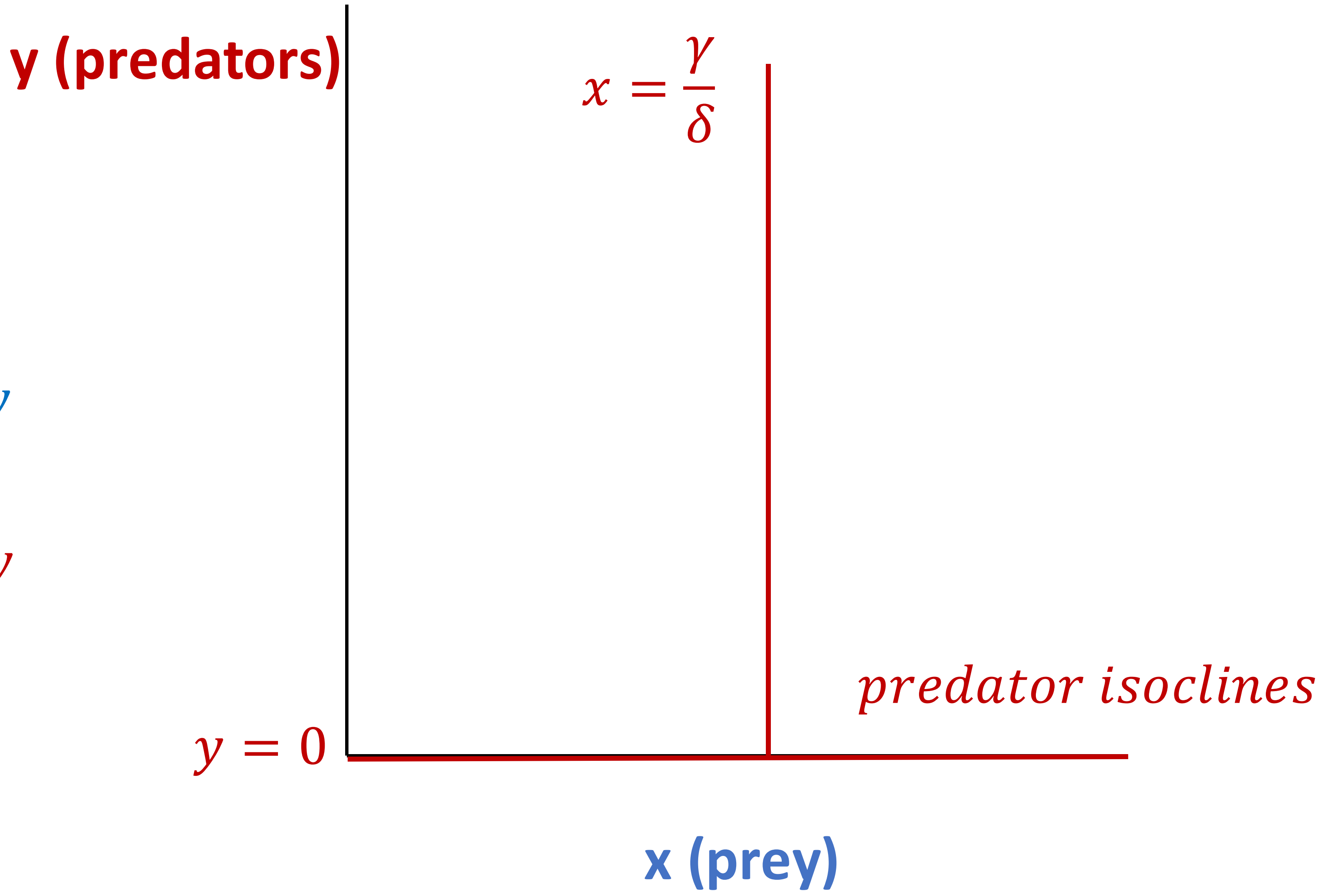

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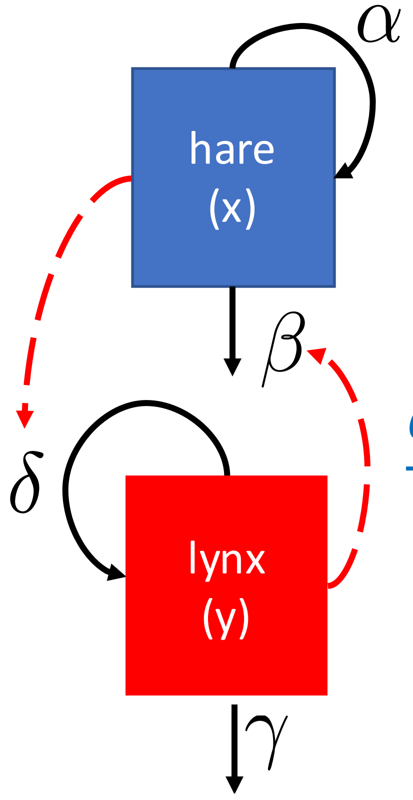

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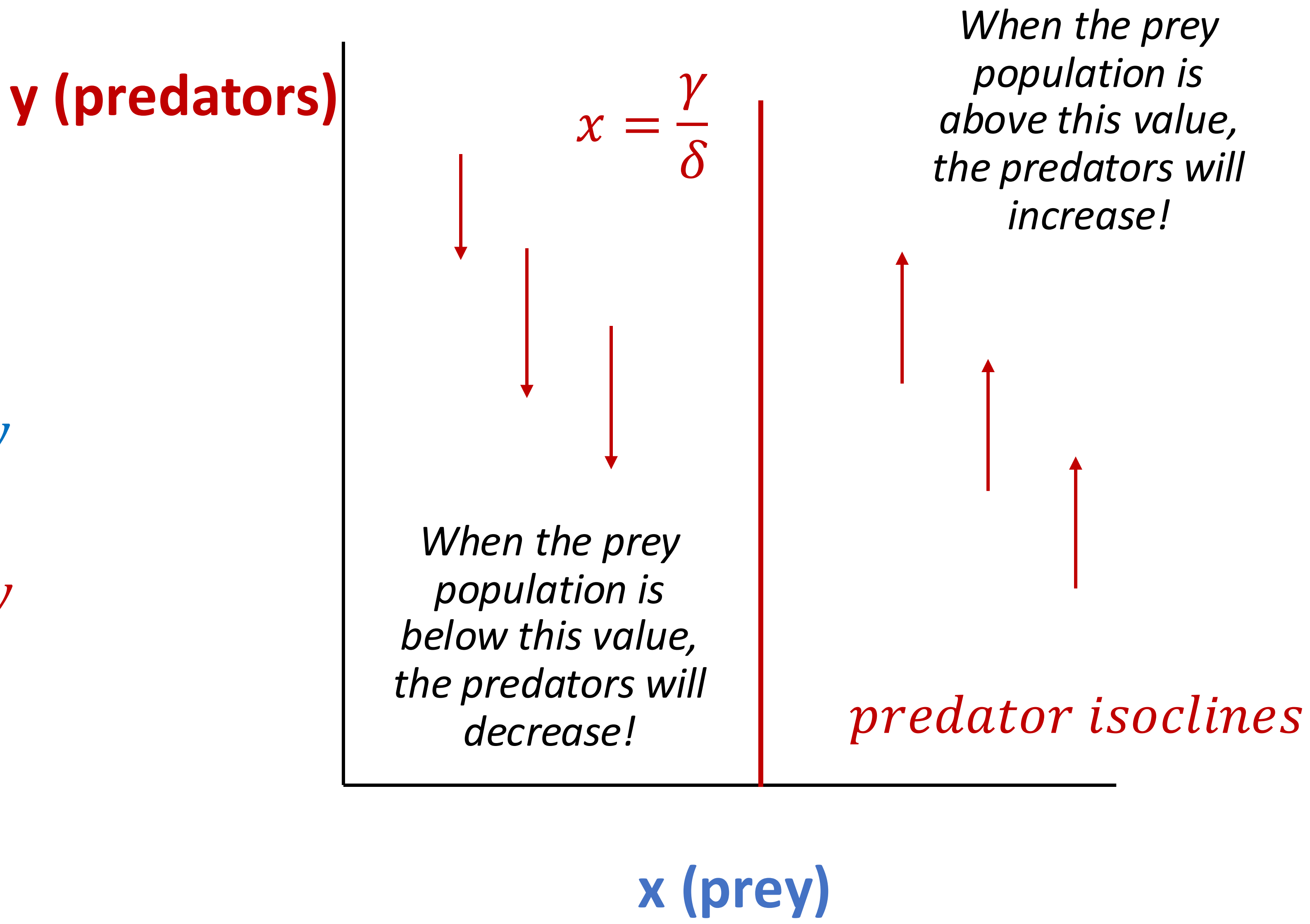

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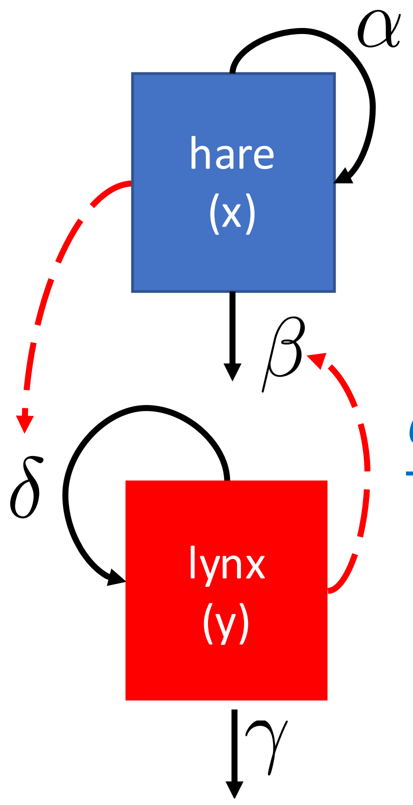

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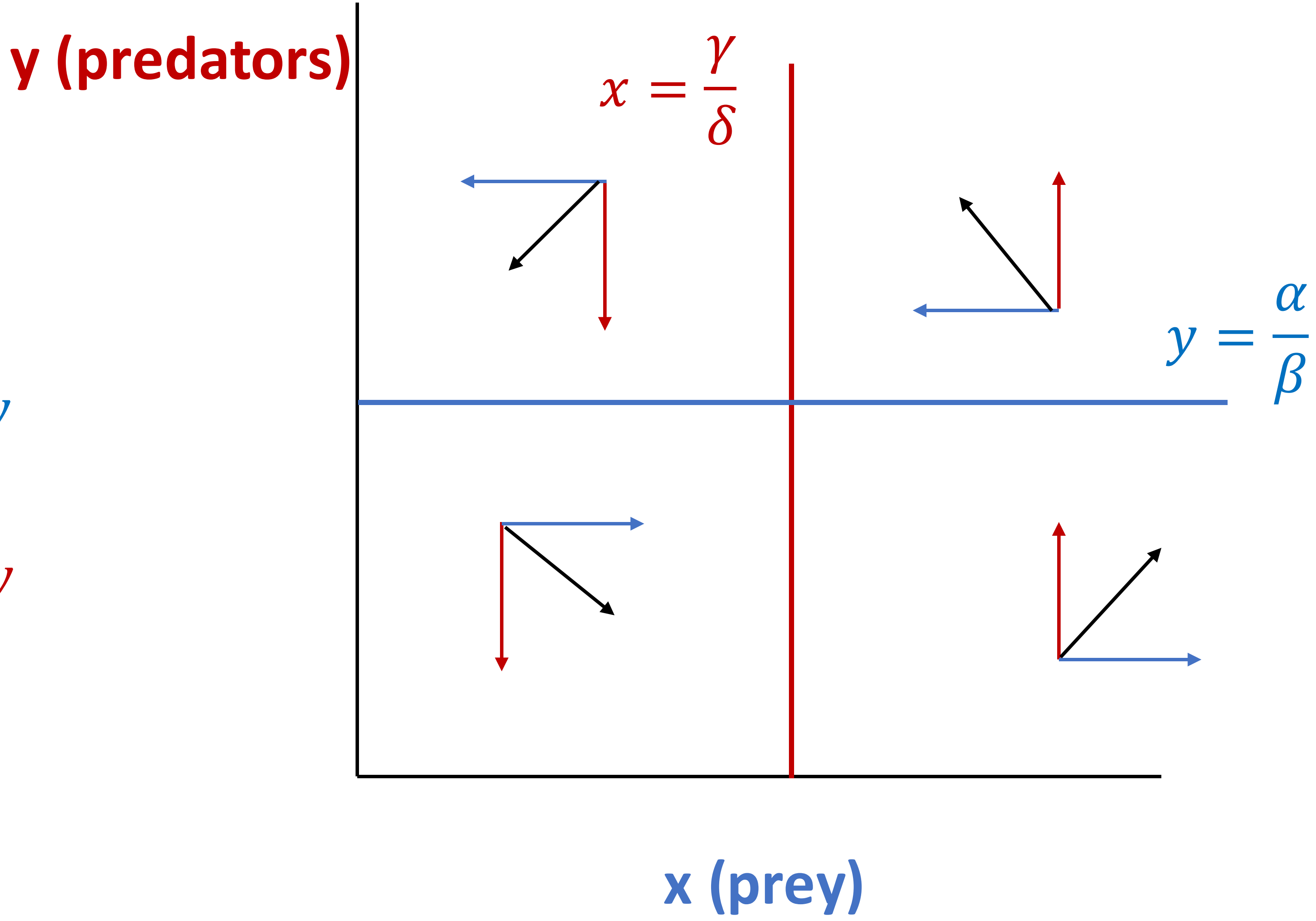

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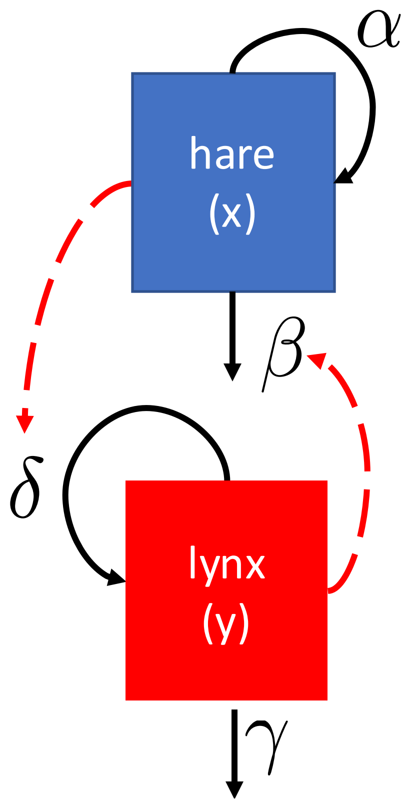

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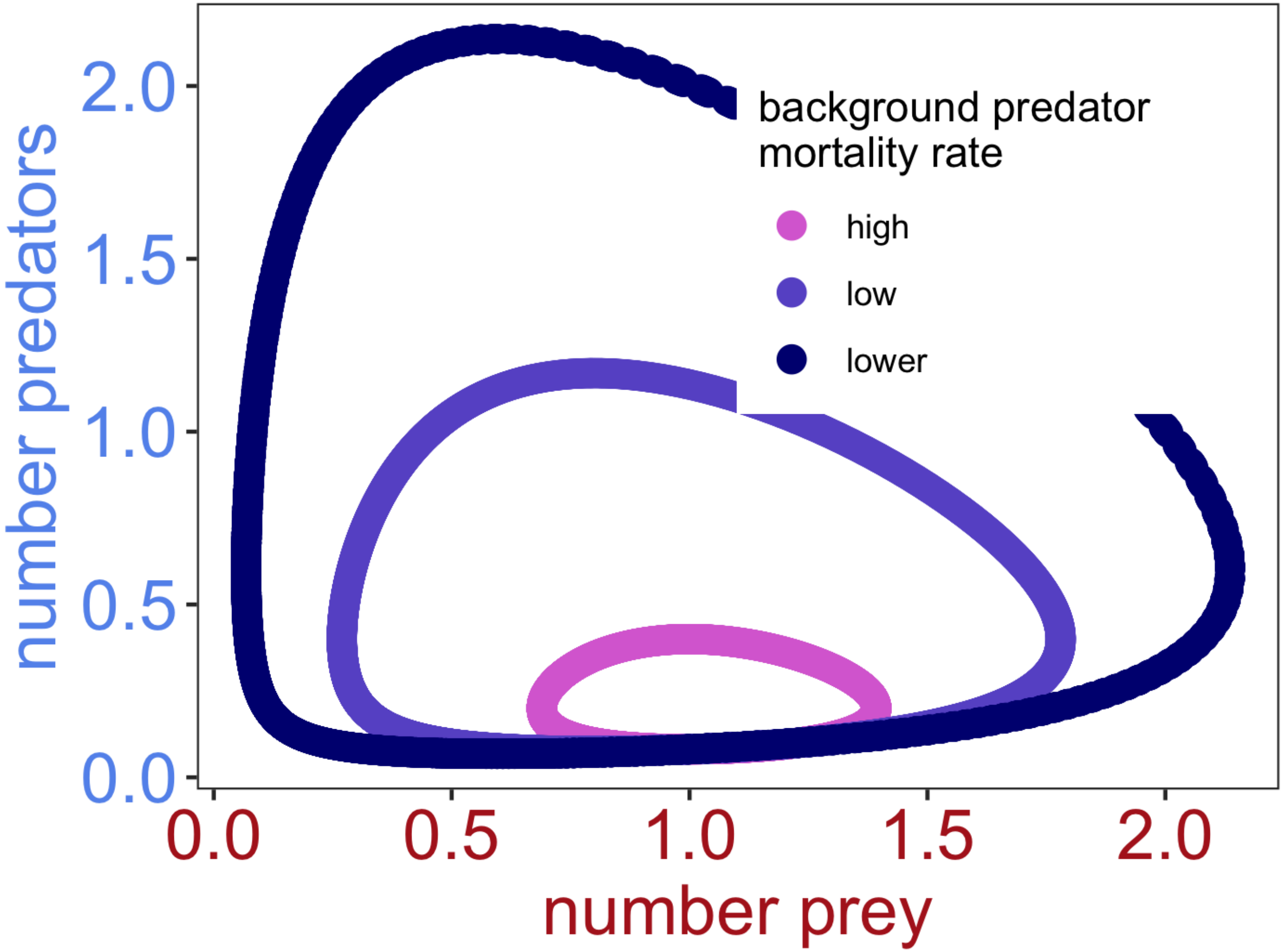
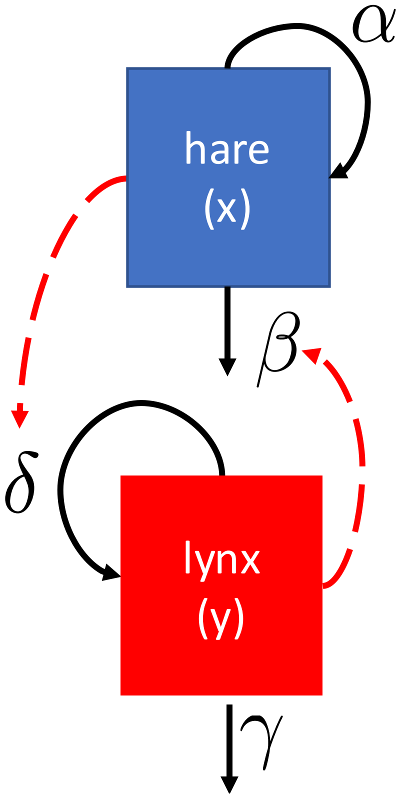
How does ***hare*** *abundance* ***vary*** *with* ***changes*** *in* ***lynx*** *abundance?*

Predator-prey cycles can be visualized as oscillations.



Lotka-Volterra predator-prey isoclines



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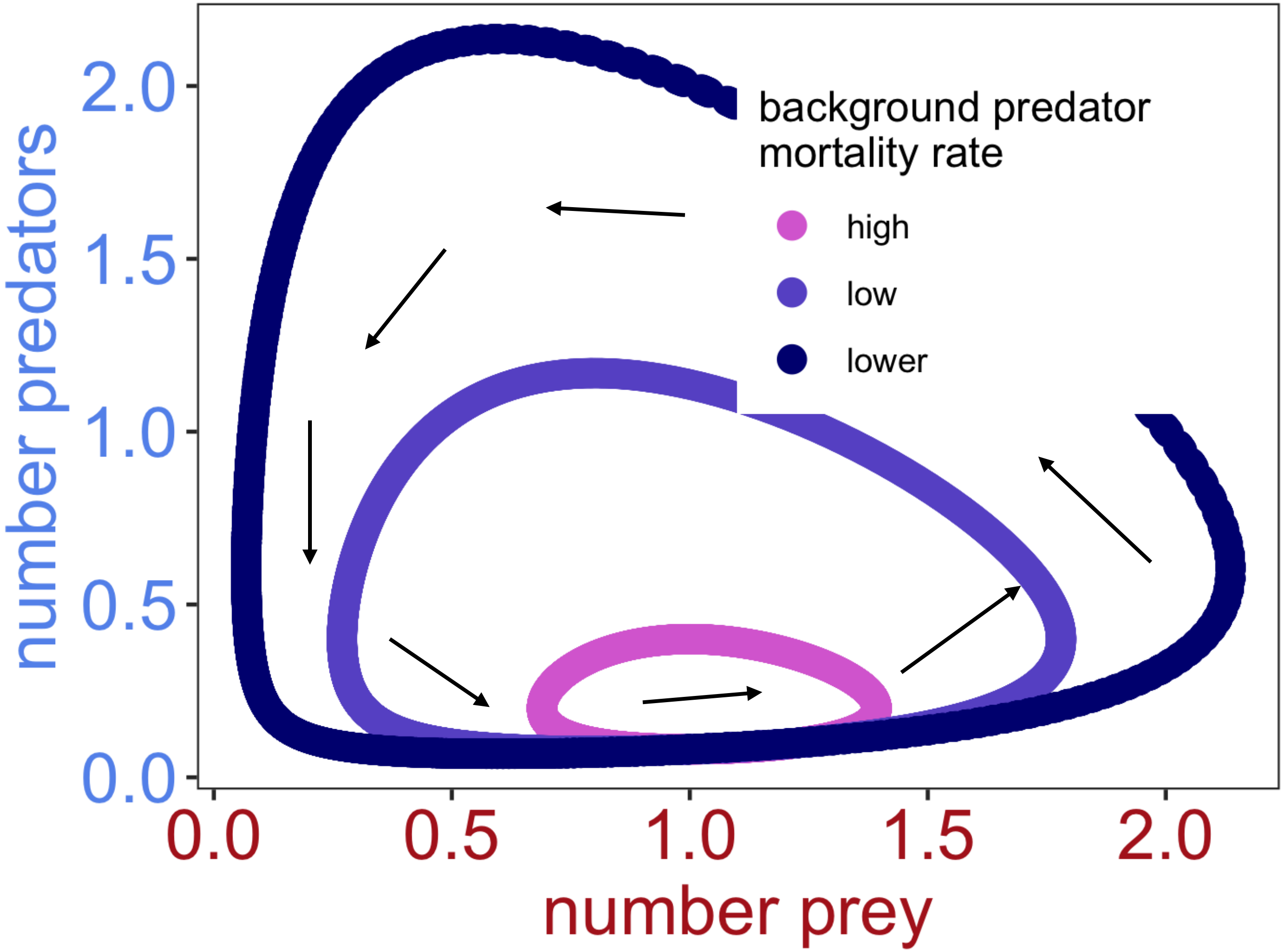
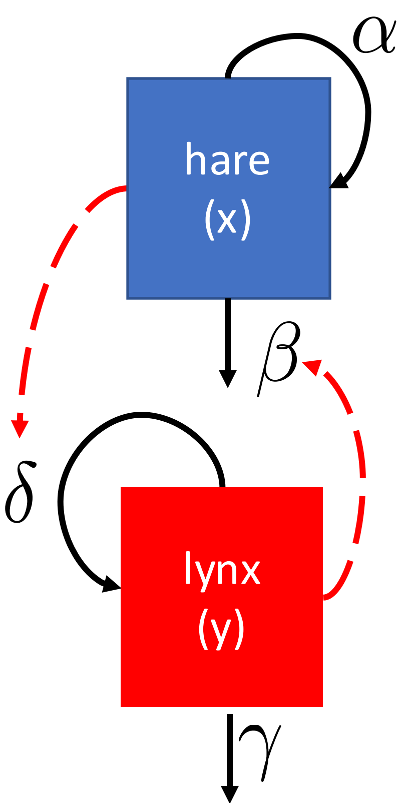


These oscillations are just another way of visualizing the time series!



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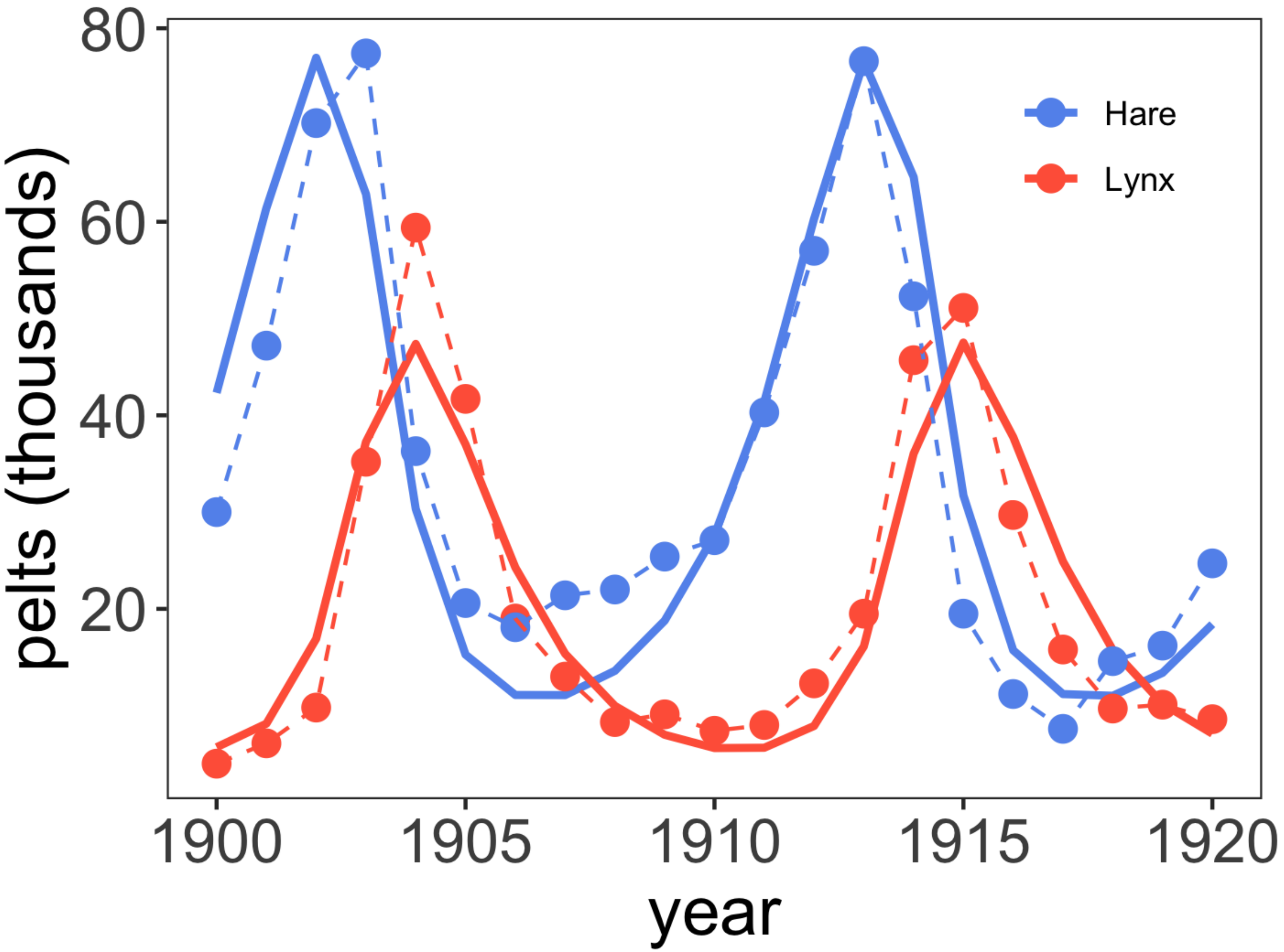
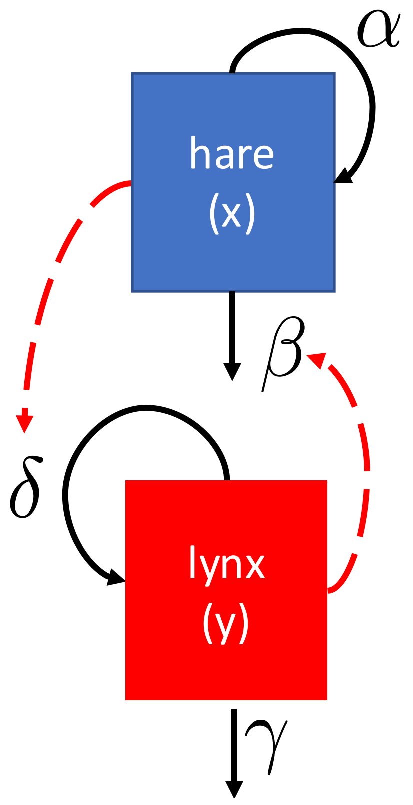


Lotka-Volterra predator-prey **isoclines** with data



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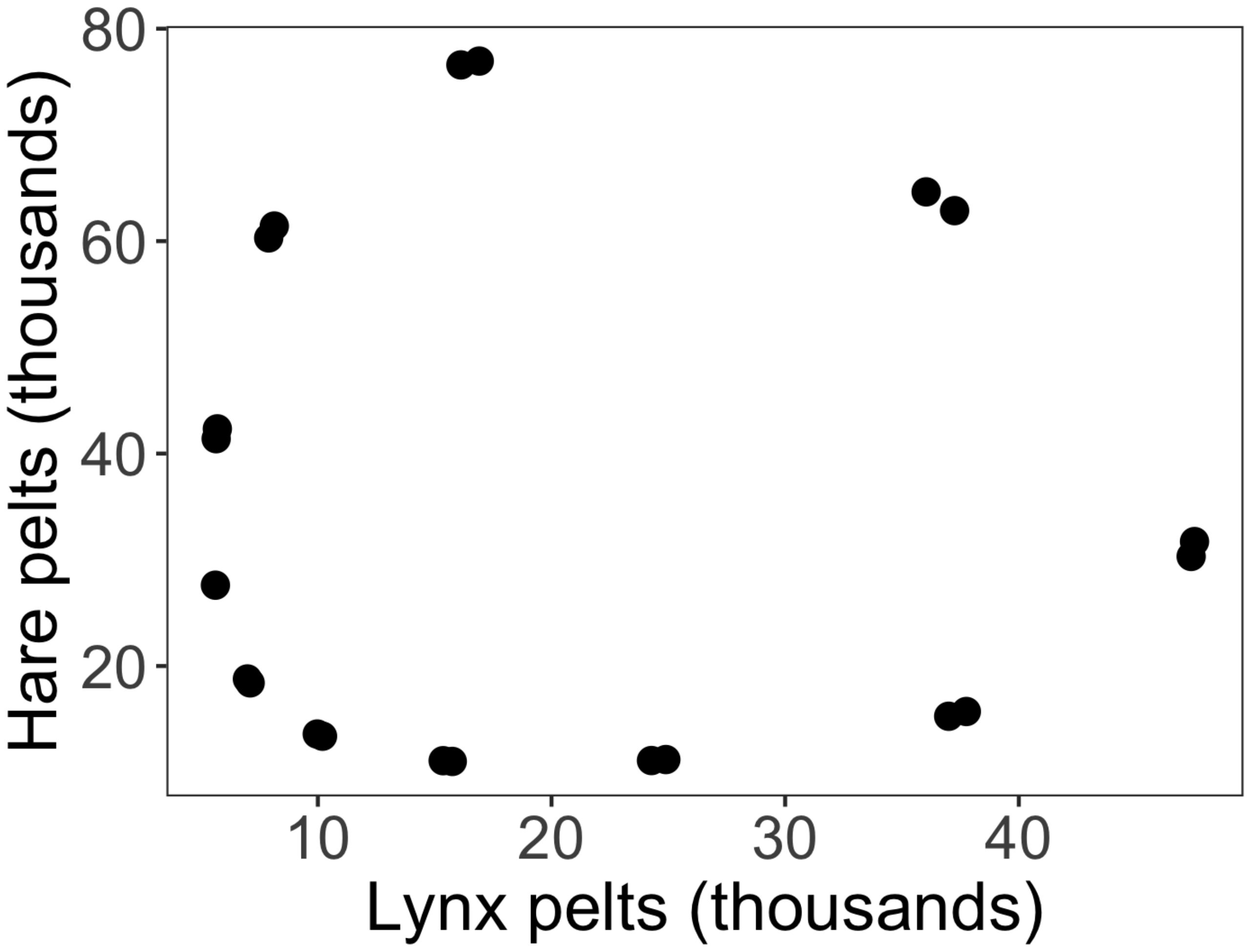

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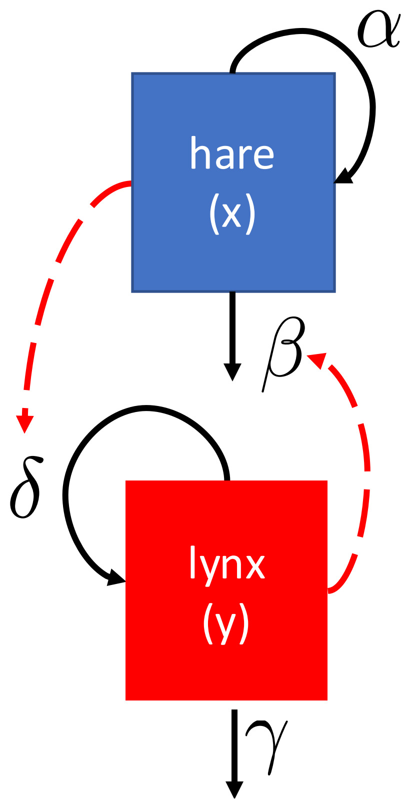

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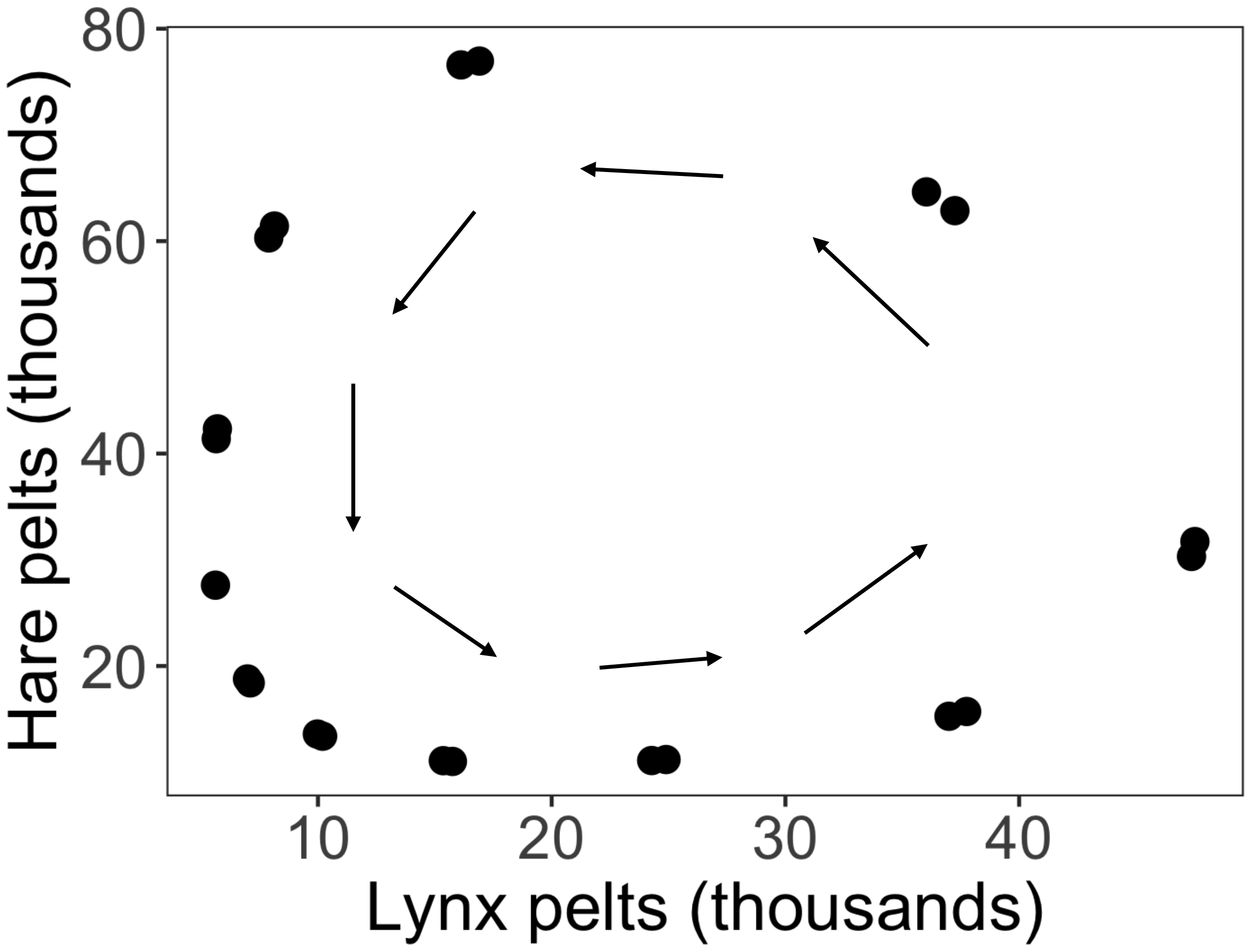
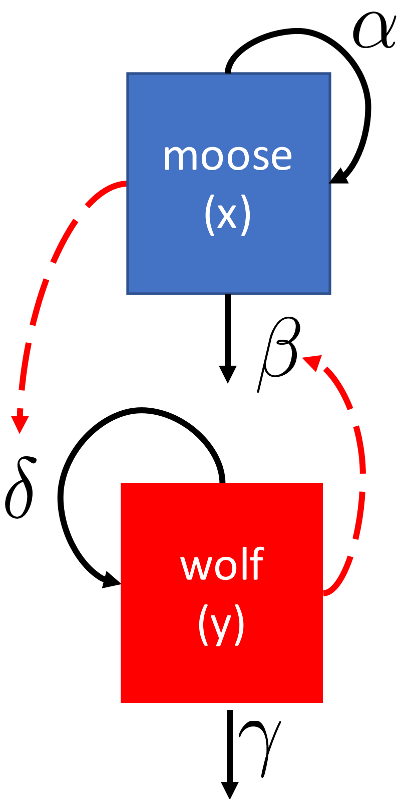


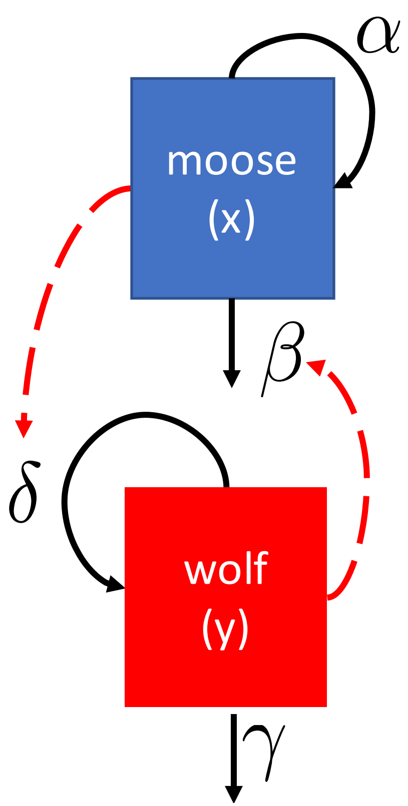
Another famous example: Wolf-Moose on Isle Royale

isleroyalewolf.org

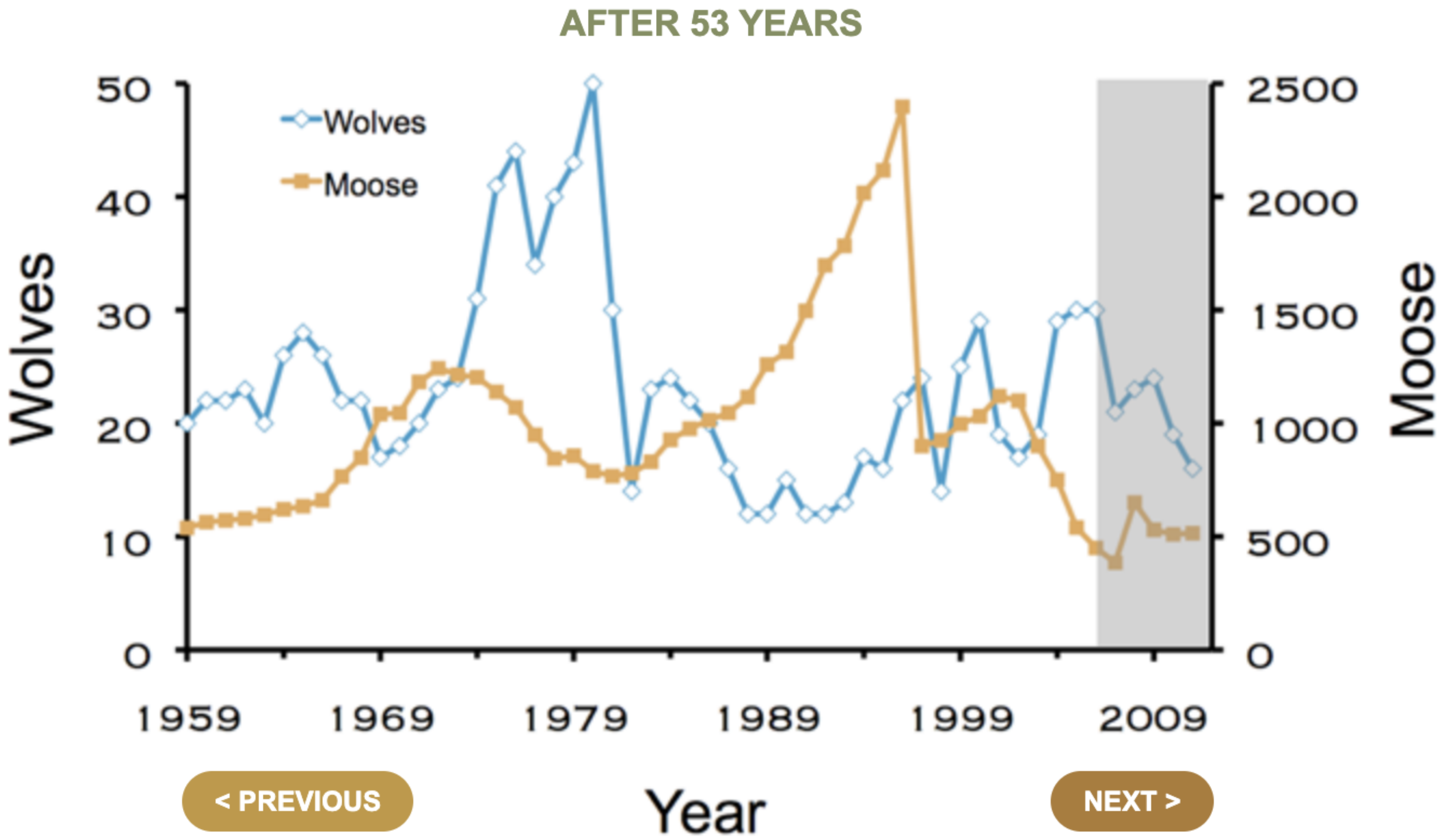


*How does **moose** abundance **vary** with **changes** in **wolf** abundance?*

Another famous example: Wolf-Moose on Isle Royale



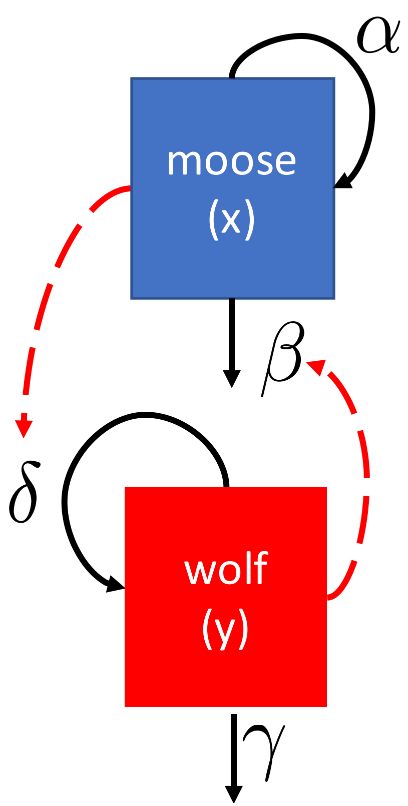
How does ***moose*** *abundance* ***vary*** *with* ***changes*** *in* ***wolf*** *abundance?*



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

isleroyalewolf.org

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.

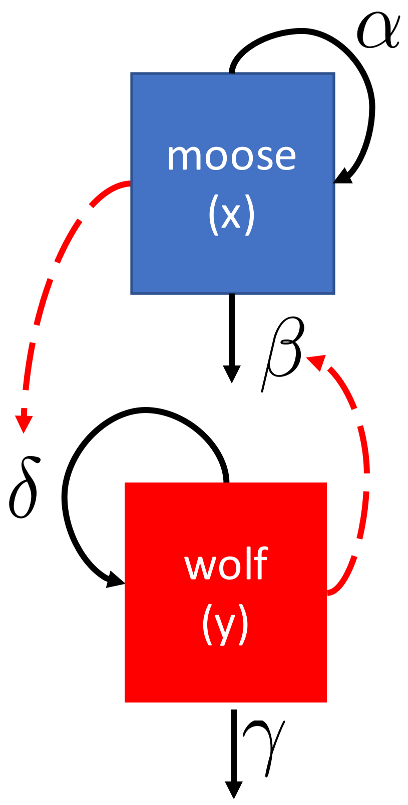
Duration: Approximately 4-5 weeks between early-May and mid-June.

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.

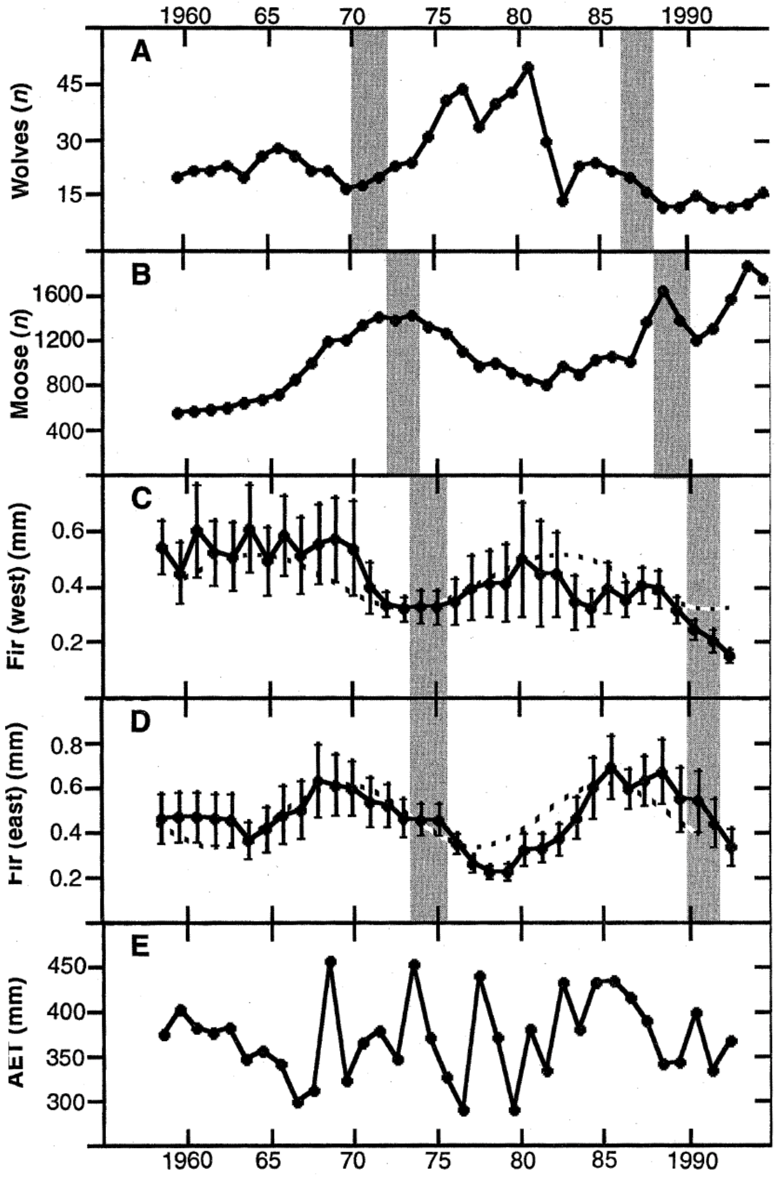
Work Schedule: Typically spend 6-8 days in the field followed by 1-2 days at base camp. Work schedule varies depending upon conditions, project needs and logistics.

isleroyalewolf.org

Another famous example: Wolf-Moose on Isle Royale



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



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

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

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

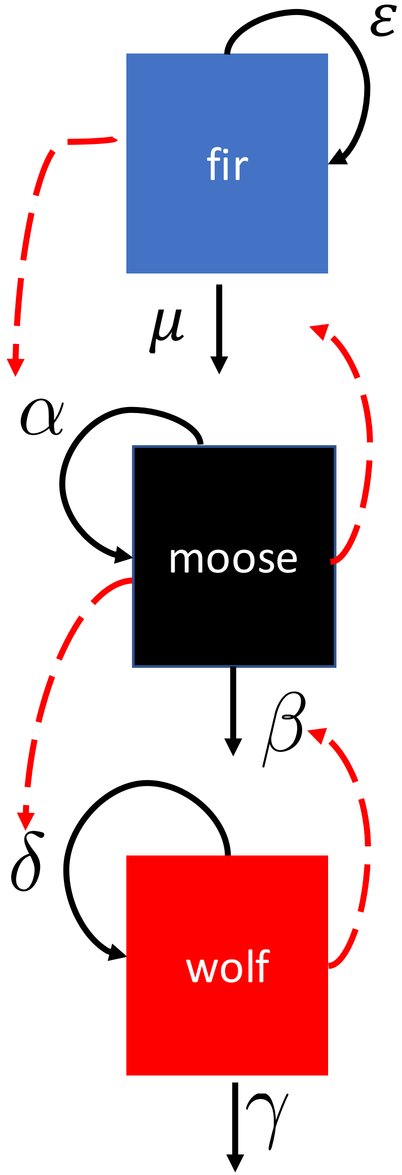
Wolves, Moose, and Tree Rings on Isle Royale

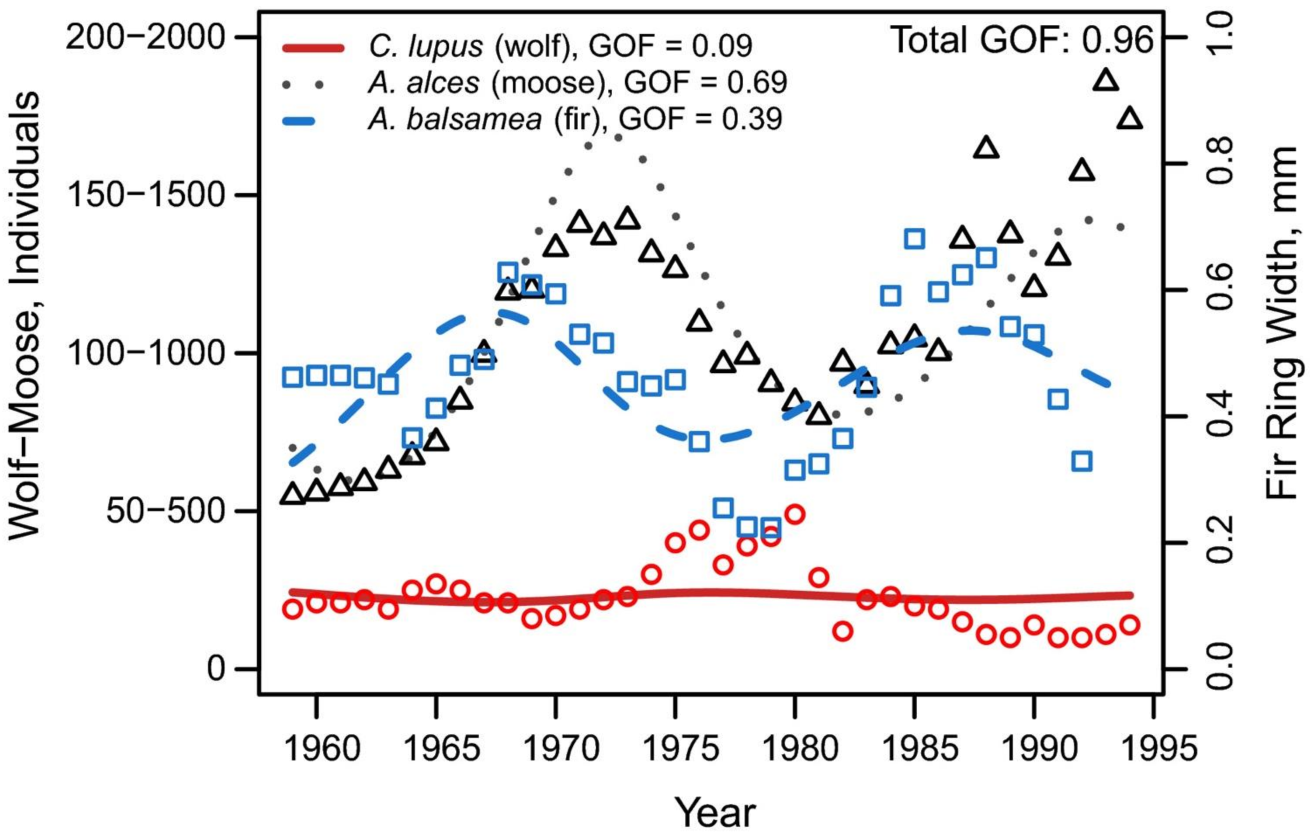
B. E. McLaren* and R. O. Peterson

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

SCIENCE • VOL. 266 • 2 DECEMBER 1994

Another famous example: Wolf-Moose on Isle Royale





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

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

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

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

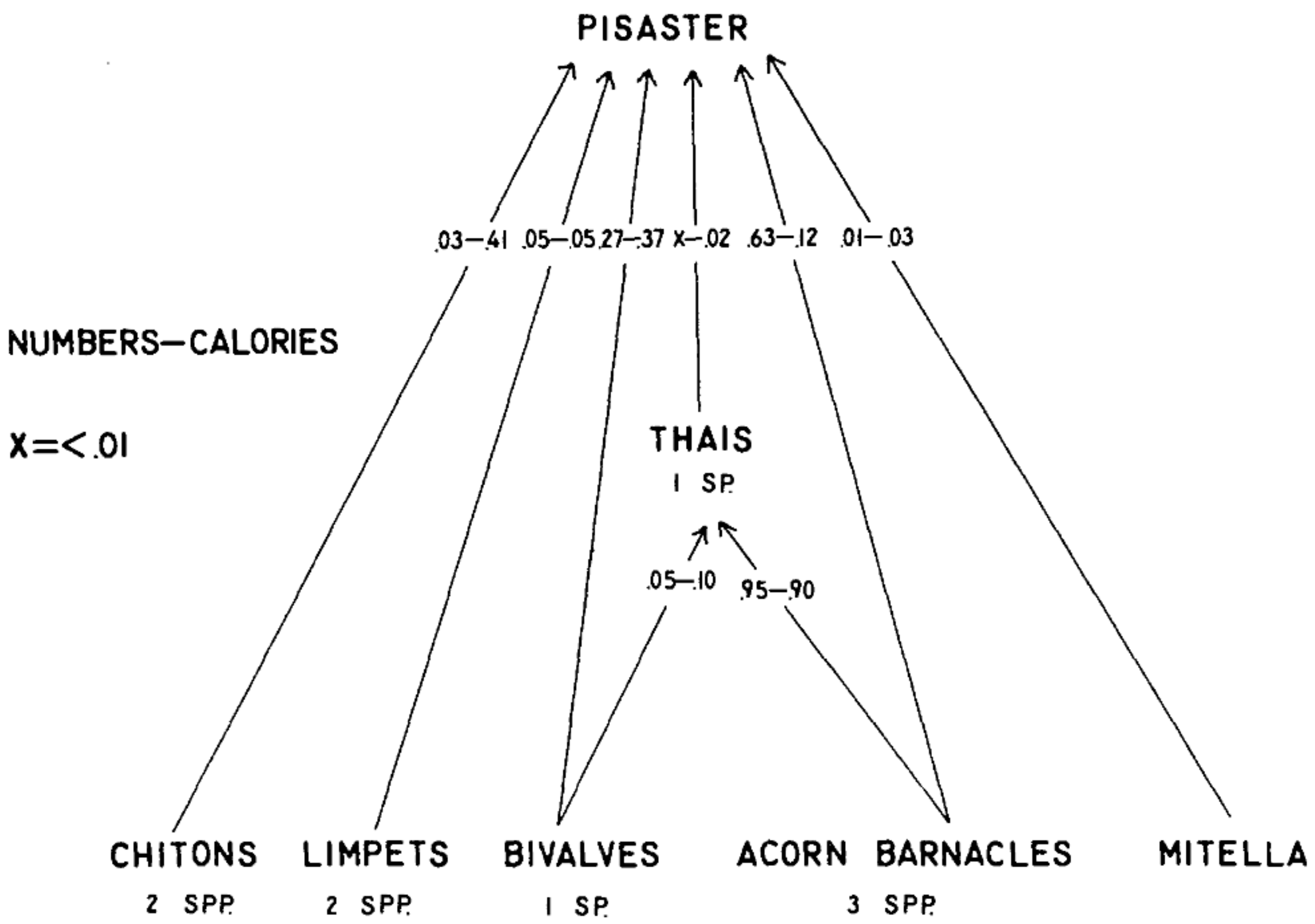
Vol. XCIV, No. 879 The American Naturalist November–December, 1960

COMMUNITY STRUCTURE, POPULATION CONTROL, AND COMPETITION

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

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

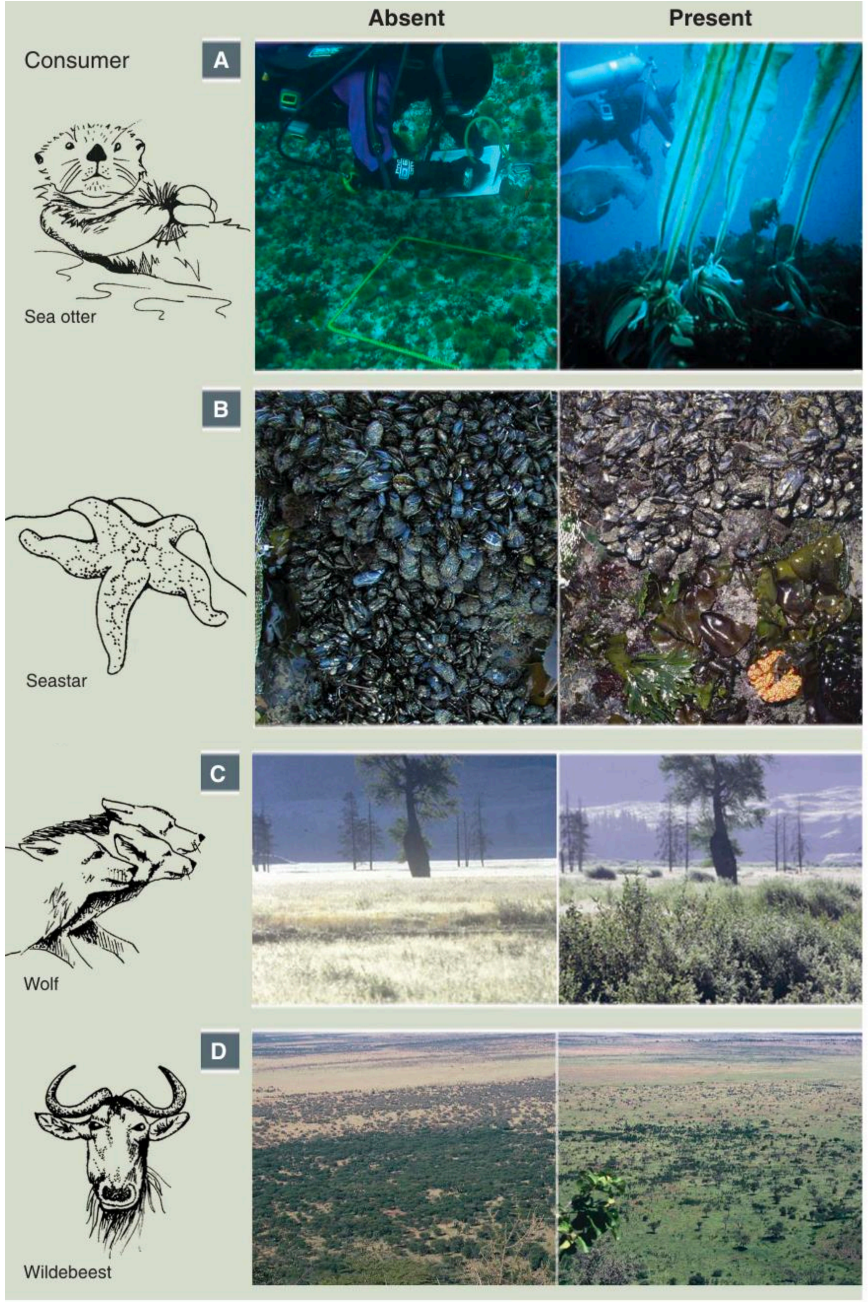
This work inspired empirical studies on **trophic cascades**: *Pisaster* removal on Tatoosh Island



Paine 1966. *The American Naturalist.*

Other famous **trophic cascades:**

Estes et al. 2011. *Science.*

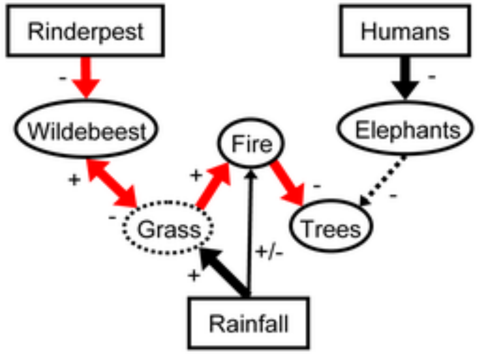


CA sea otters maintain kelp forest diversity by consuming herbivorous sea urchins. (Estes & Duggins 1995. *Ecological Monographs*)

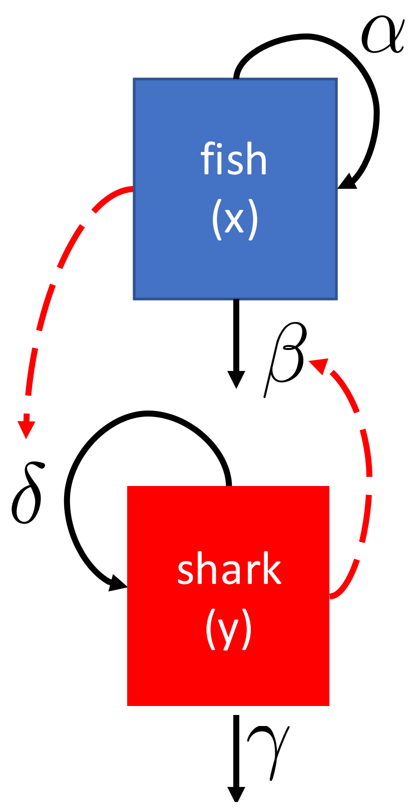
Starfish maintain diversity in Pacific intertidal by consuming space-dominating mussels. (Paine 1966 *The American* Naturalist)

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

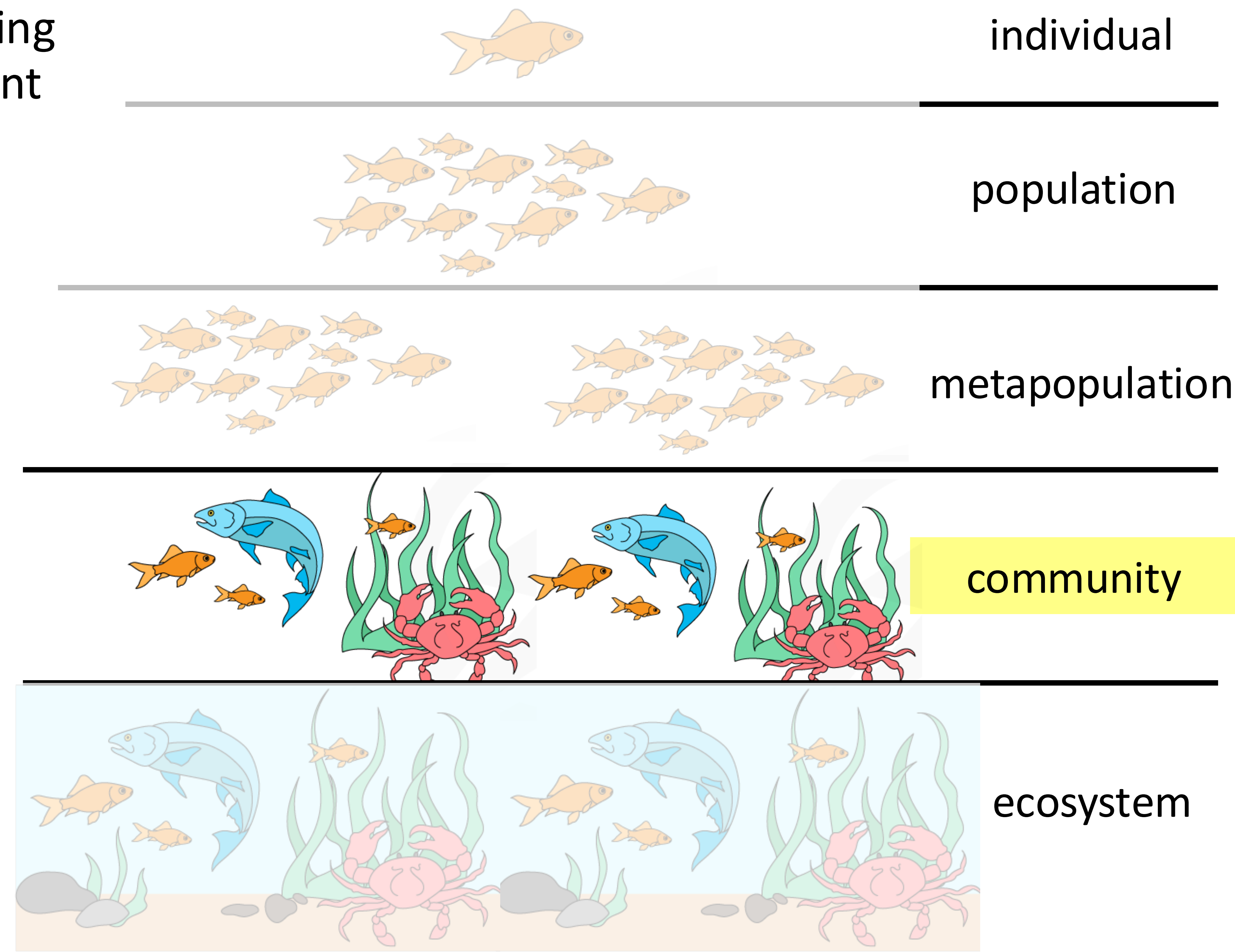
Rinderpest eradication releases wildebeest populations that control savanna, limit fire, and promote tree regrowth (Holdo et al. 2009. *PLoS Biology*)



Community = interacting populations of different species



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



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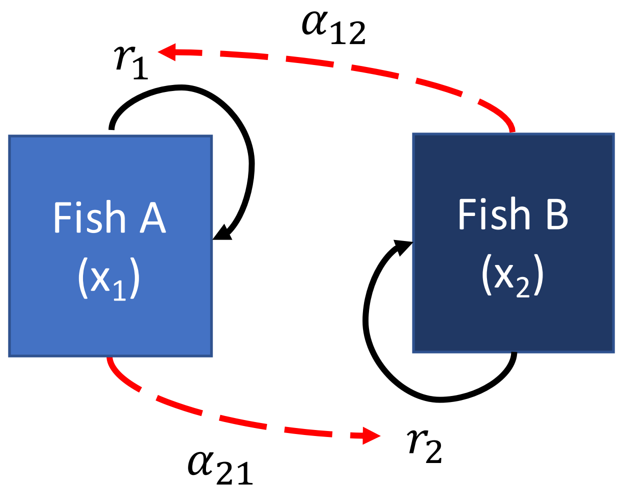
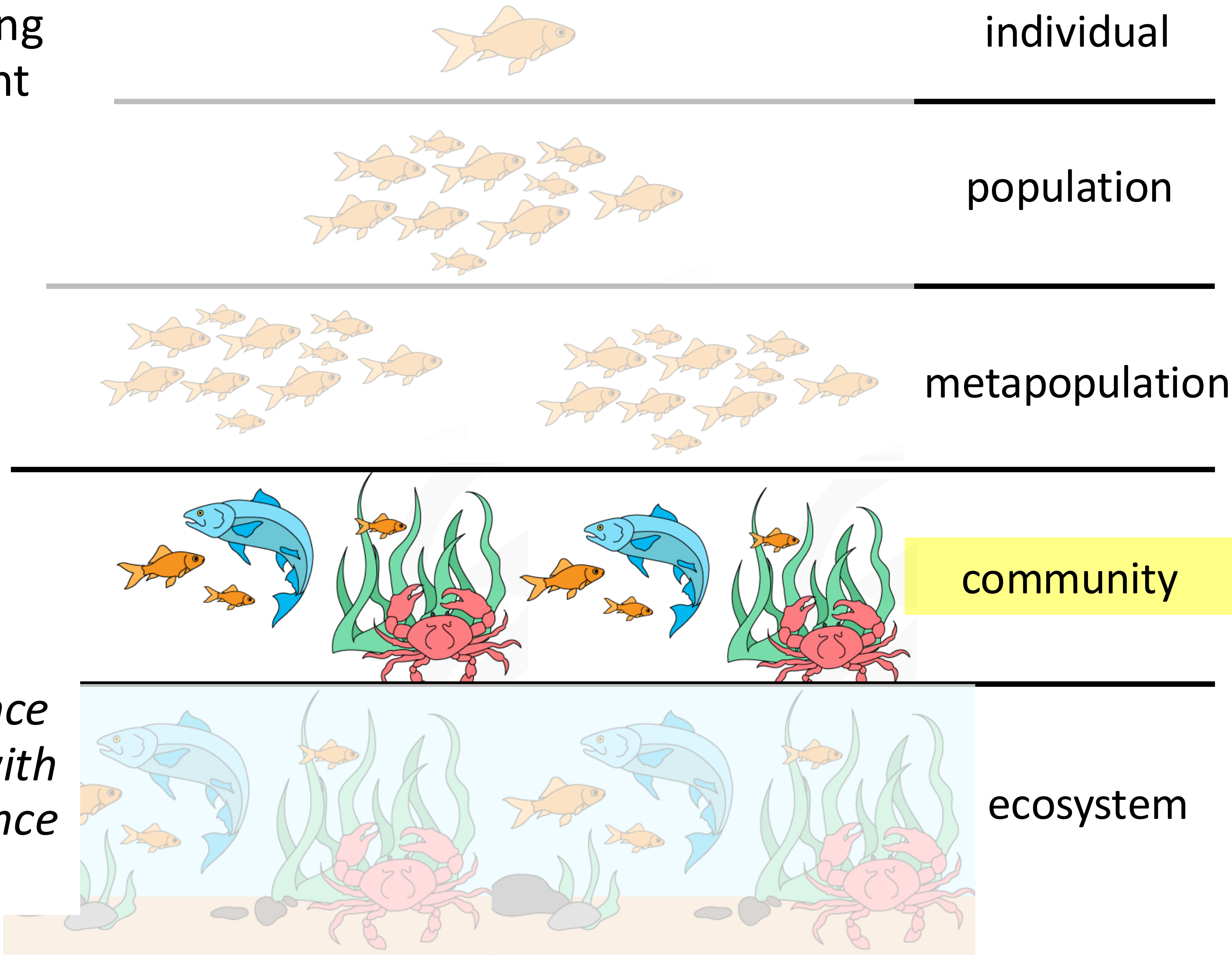


*How does the abundance of **fish species A** vary with changes in the abundance of **fish species B**?*



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

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

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

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

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

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

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

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

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

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

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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).

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

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

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

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!

$$0 = \frac{dx_1}{dt} = r_1x_1 - \frac{r_1(x_1)^2}{K_1} - \frac{r_1x_1x_2\alpha_{12}}{K_1}$$

$$0 = \frac{dx_2}{dt} = r_2x_2 - \frac{r_2(x_2)^2}{K_2} - \frac{r_2x_2x_1\alpha_{21}}{K_2}$$

Four equilibria at:

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

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Four equilibria at:

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$x_1^* = 0\,;\, x_2^* = K_2$ Species 1 extinct. Species 2 at carrying capacity.

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Four equilibria at:

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

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

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

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

Coexistence.

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

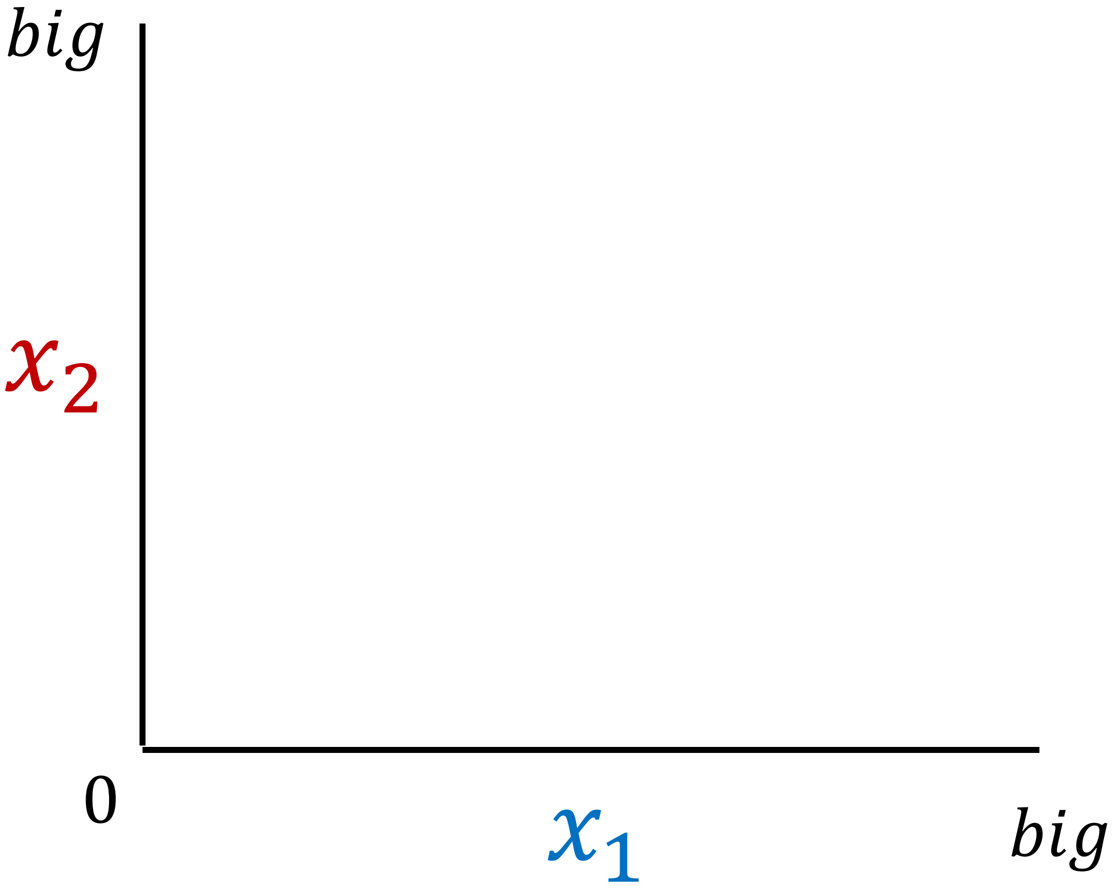
These are the lines that correspond to the conditions when the rate of change for **one species** is not changing!

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

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

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

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



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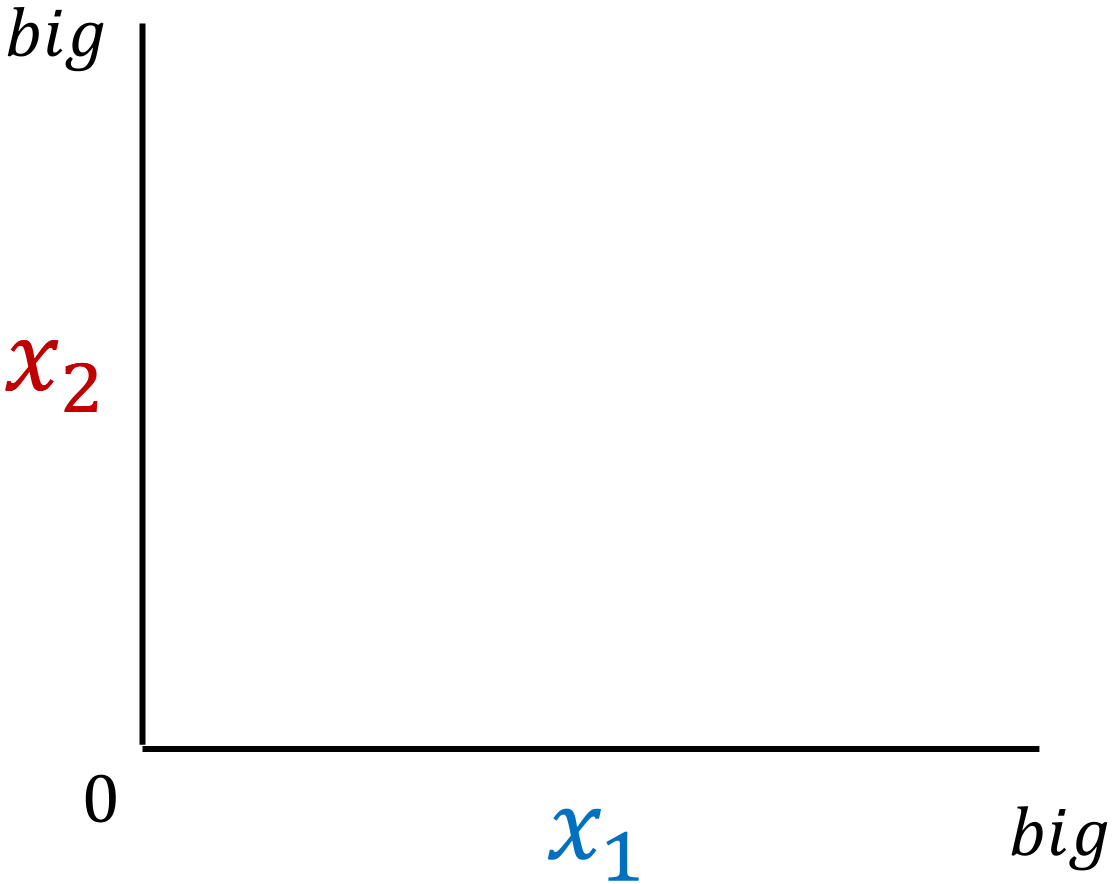
$$0 = r_1 x_1 \left(1 - \frac{x_1}{K_1} - \frac{x_2 \alpha_{12}}{K_1}\right)$$



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

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

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

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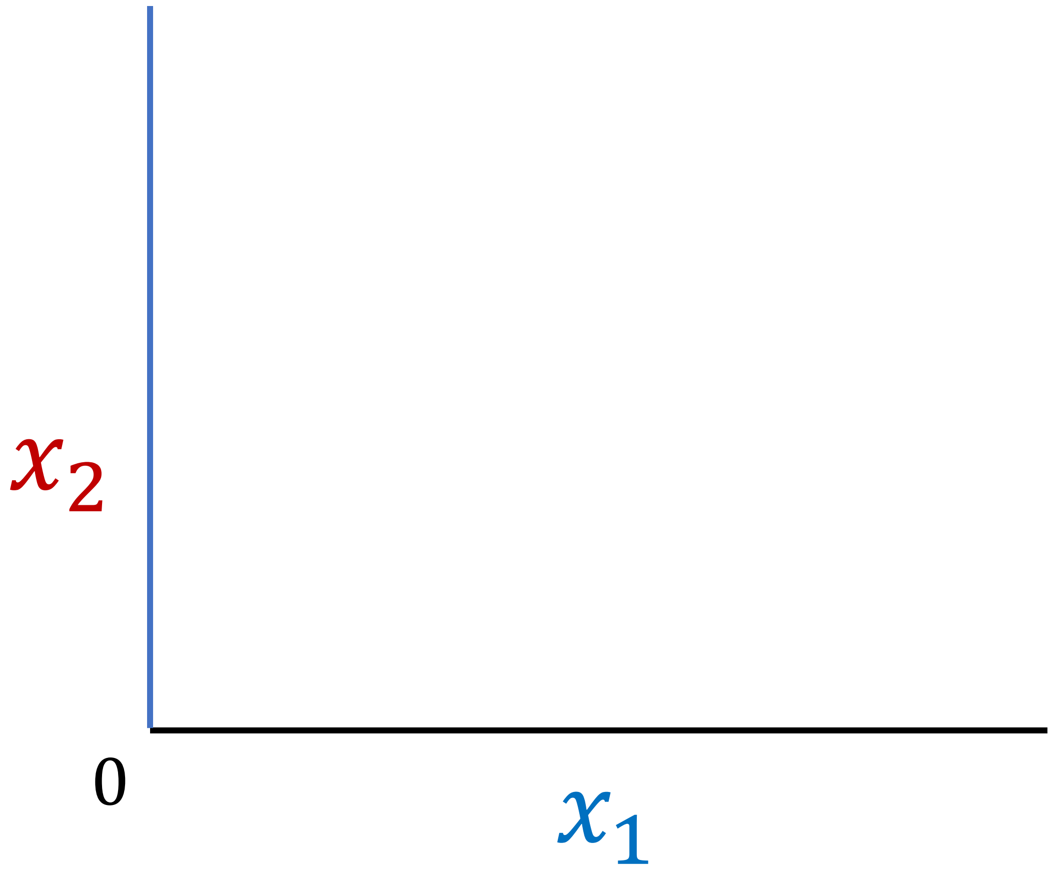
first nullcline at $x_1 = 0$



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

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

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

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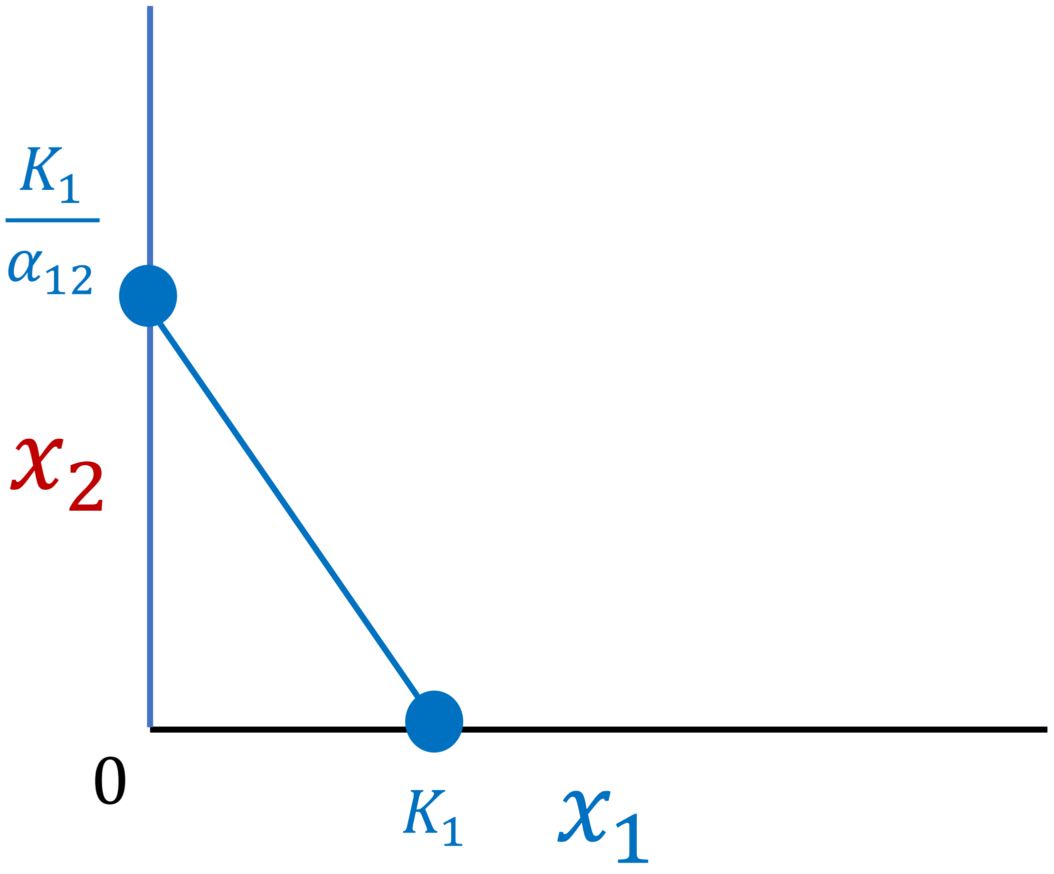
first nullcline at $x_1 = 0$

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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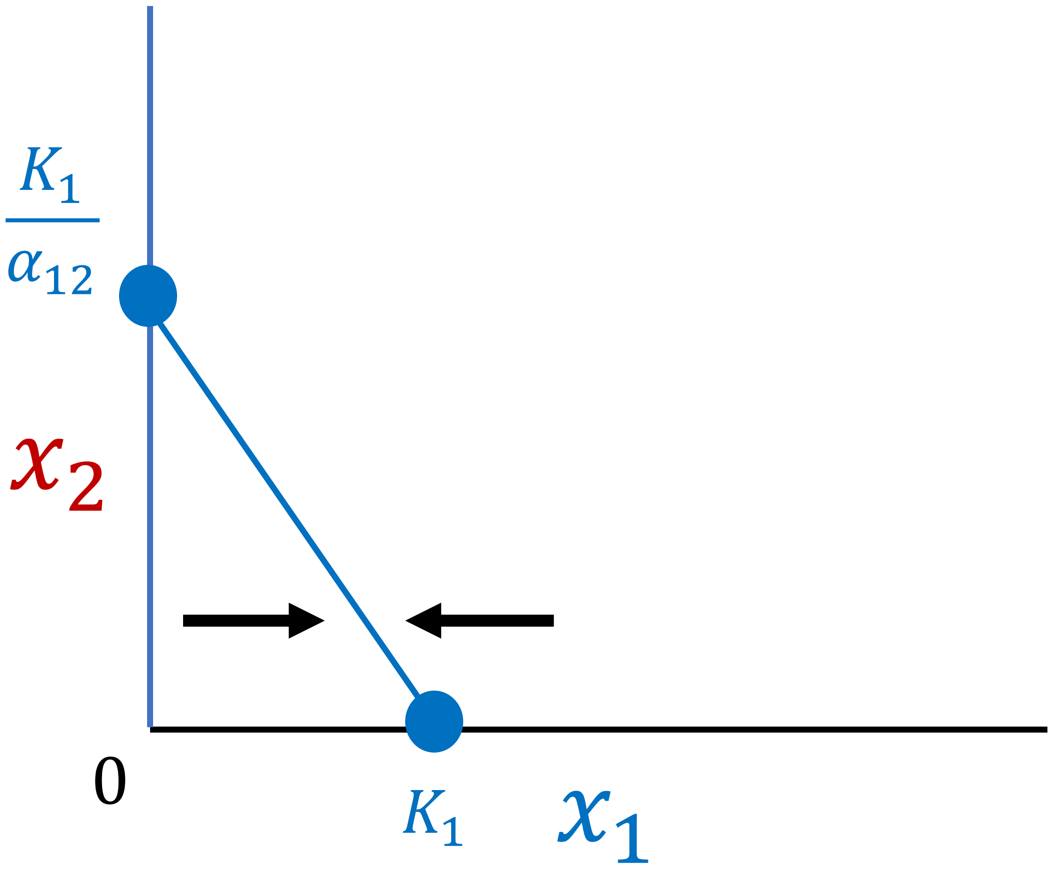


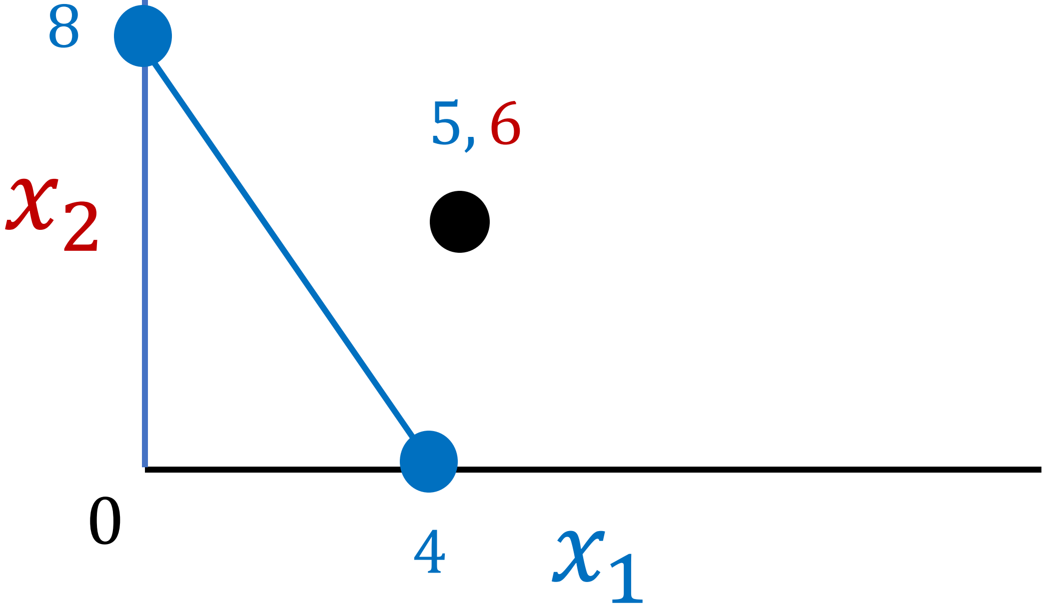
Nullclines (or **isoclines**) of the **Lotka-Volterra competition model**

- Following a perturbation, the population should return to equilibrium!
- For x_1, this will always mean moving along the x-axis to the nullcline, then along the nullcline to equilibrium.
- You can also test it by solving $\frac{dx_1}{dt}$ for different values!
- $K_1 = 4\,; \alpha_{12} = .5$

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

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

$$\frac{dx_1}{dt} = r_1 * 5(1 - 1.25 - .75)$$



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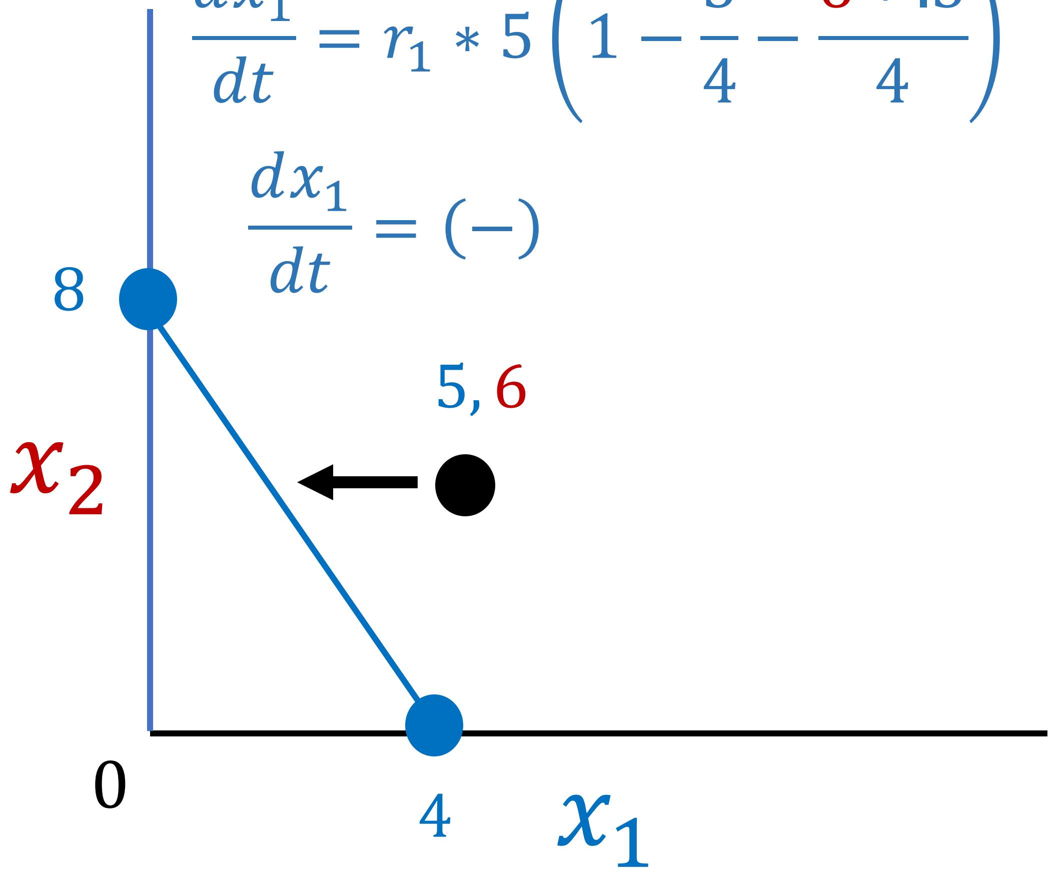
$$\frac{dx_1}{dt} = (-)$$



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

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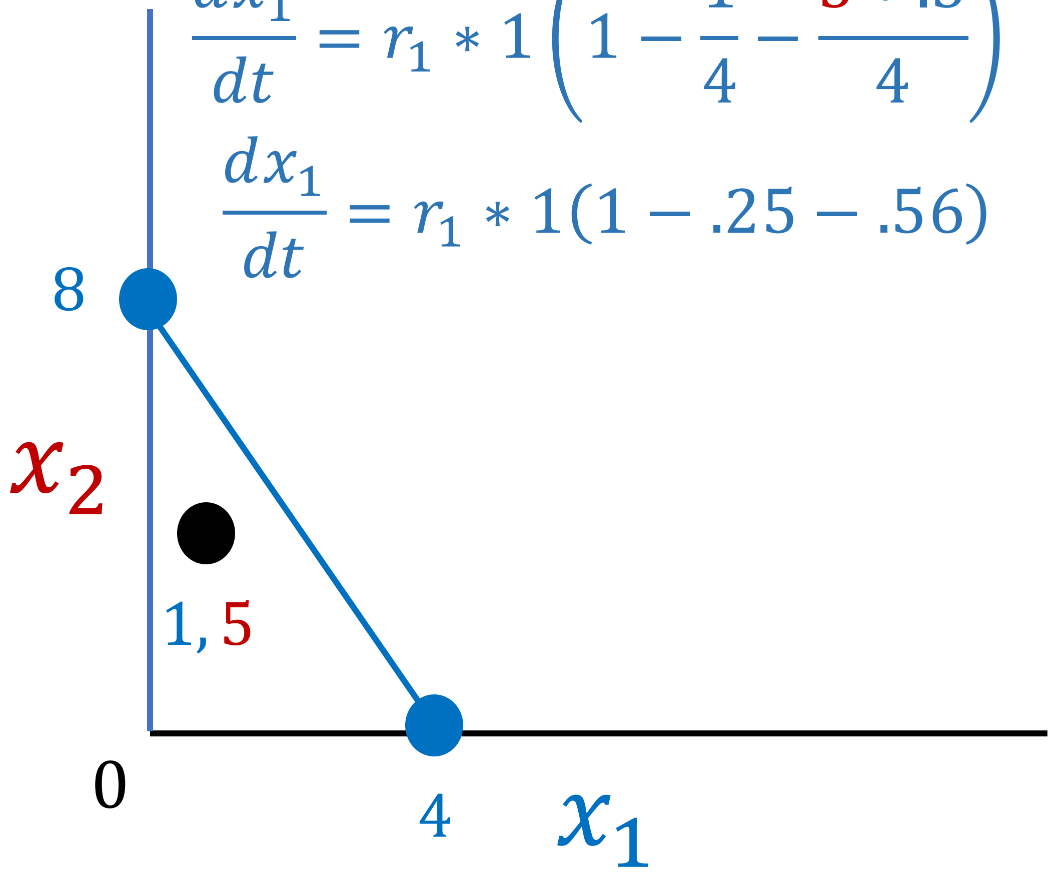
$$\frac{dx_1}{dt} = r_1 x_1\left(1 - \frac{x_1}{K_1} - \frac{x_2\alpha_{12}}{K_1}\right)$$

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

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



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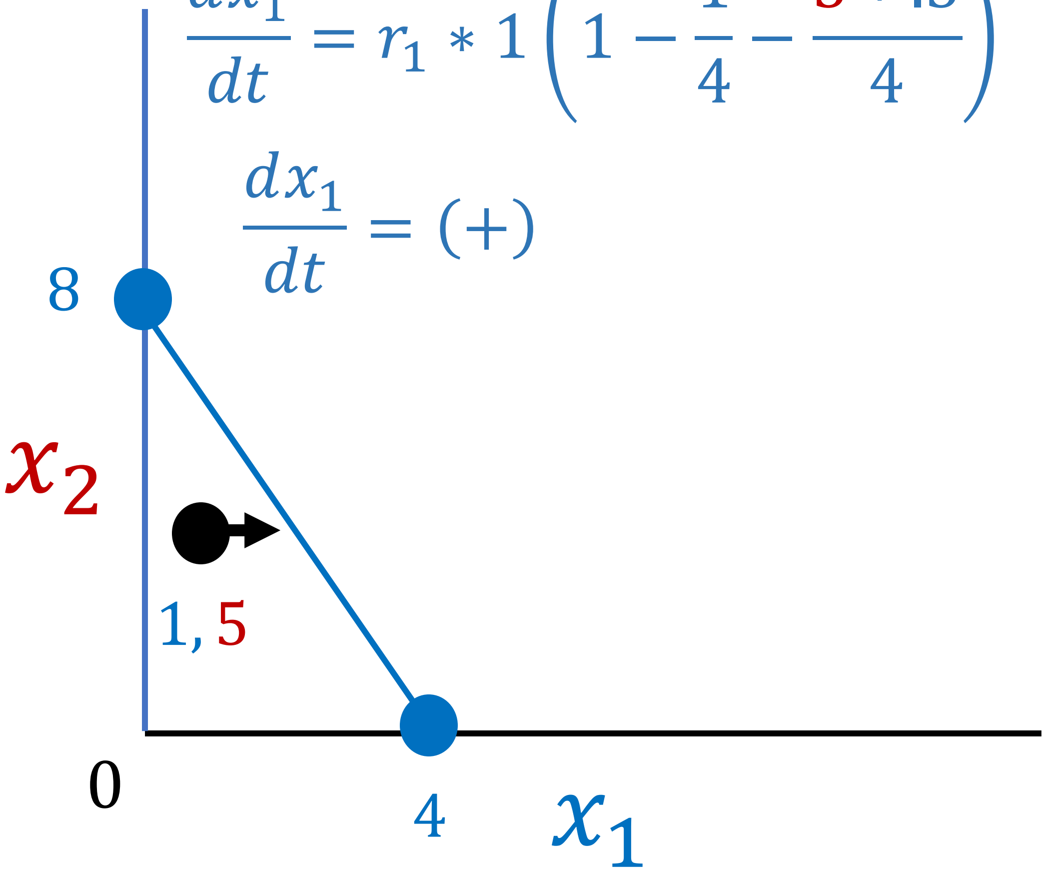
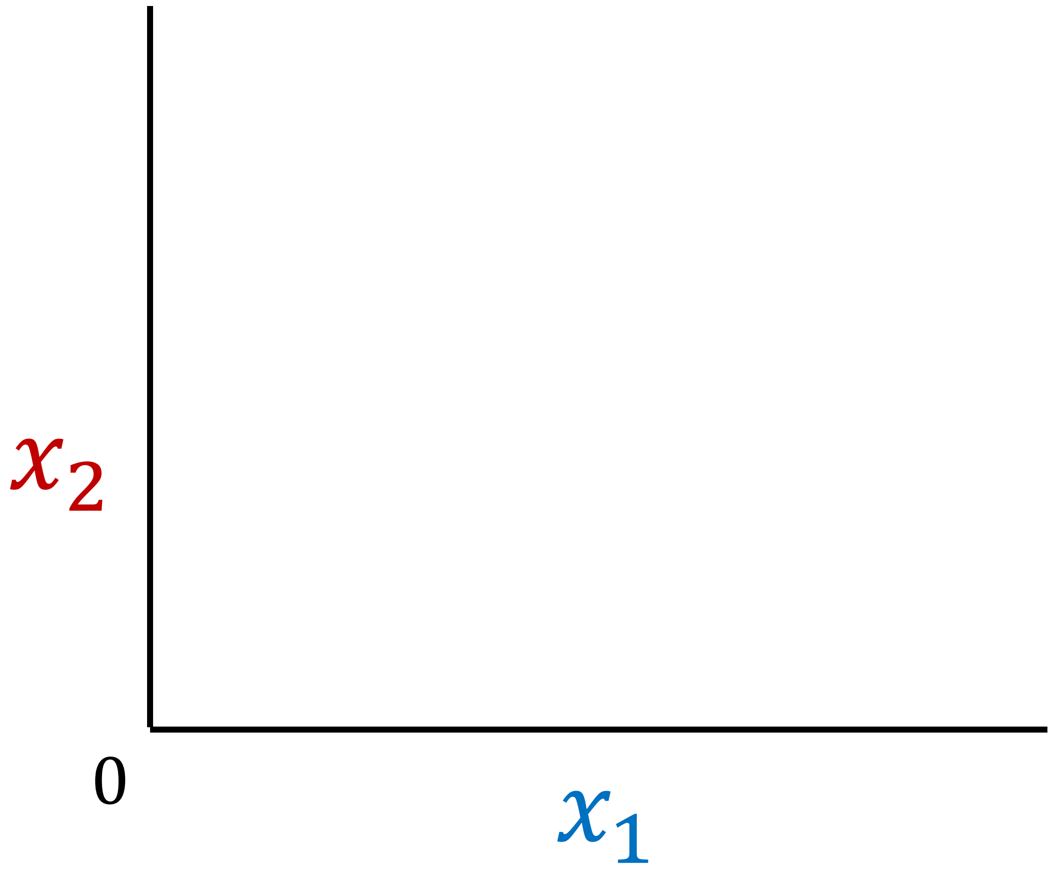


Nullclines (or **isoclines**) of the **Lotka-Volterra competition model**

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

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



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

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

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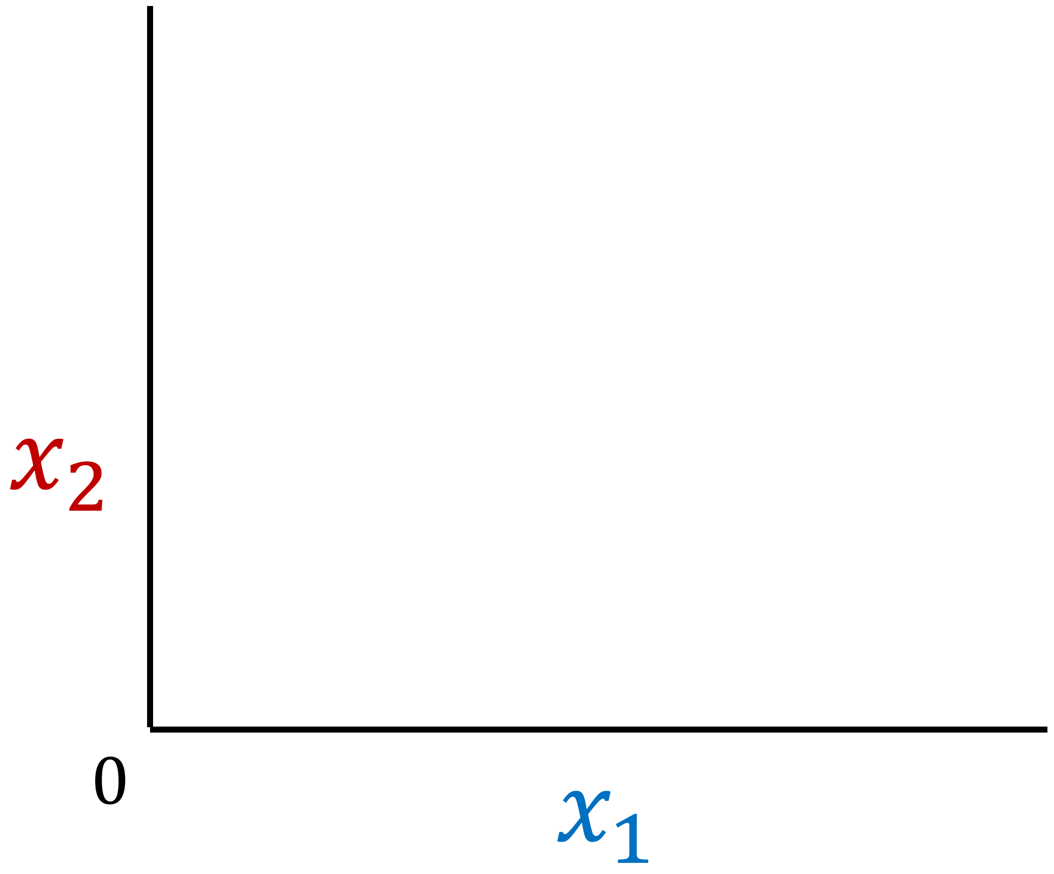

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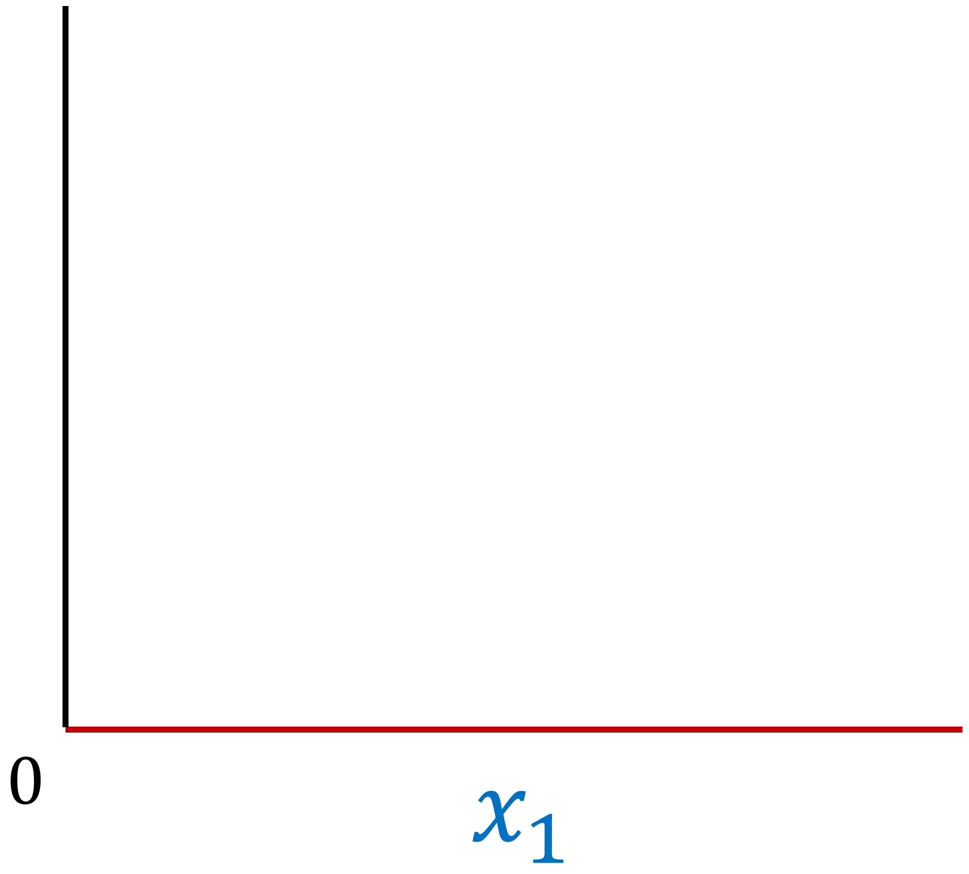
first nullcline at $x_2 = 0$



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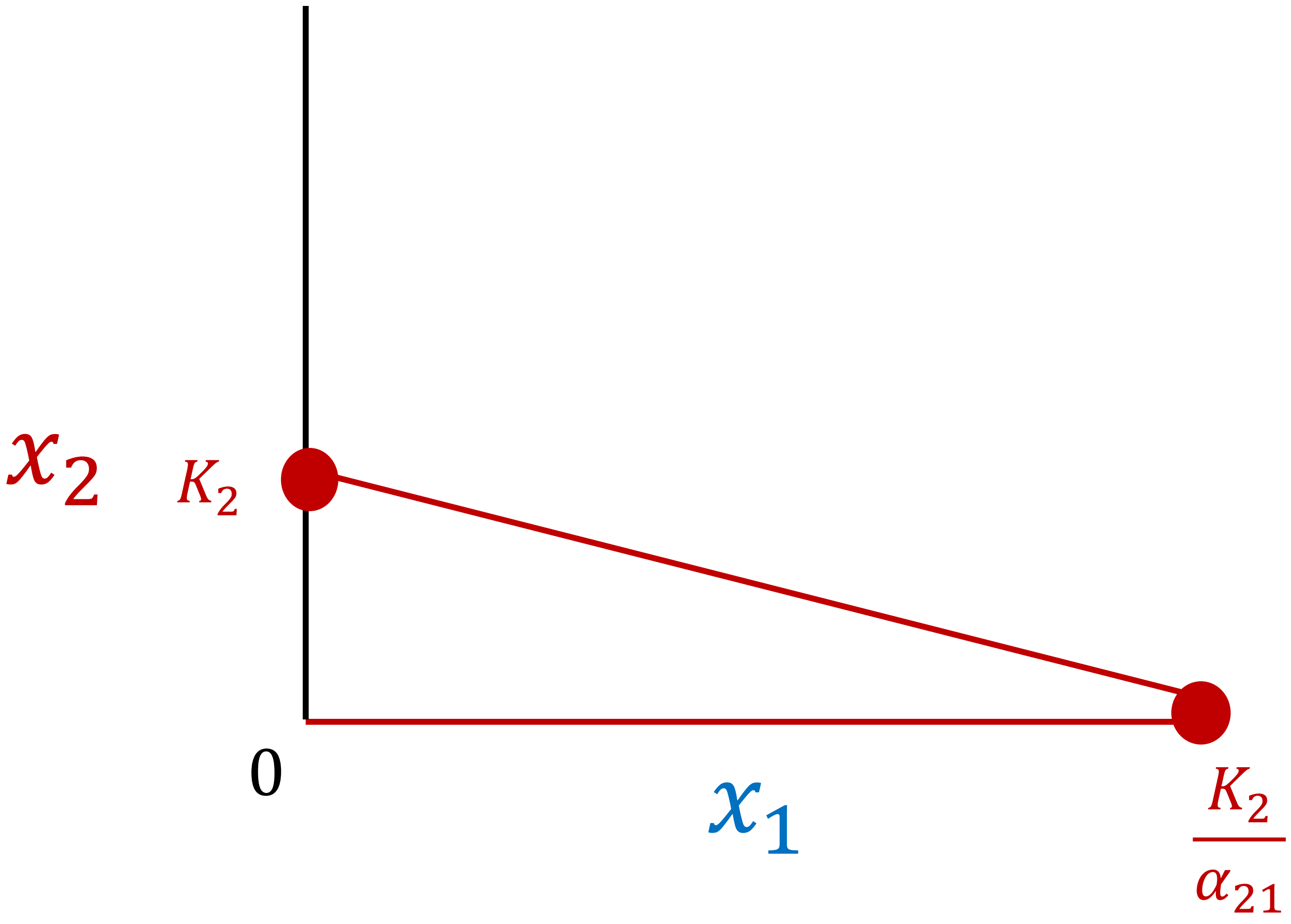
second nullcline at $x_2 = -\alpha_{21}x_1 + K_2$



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

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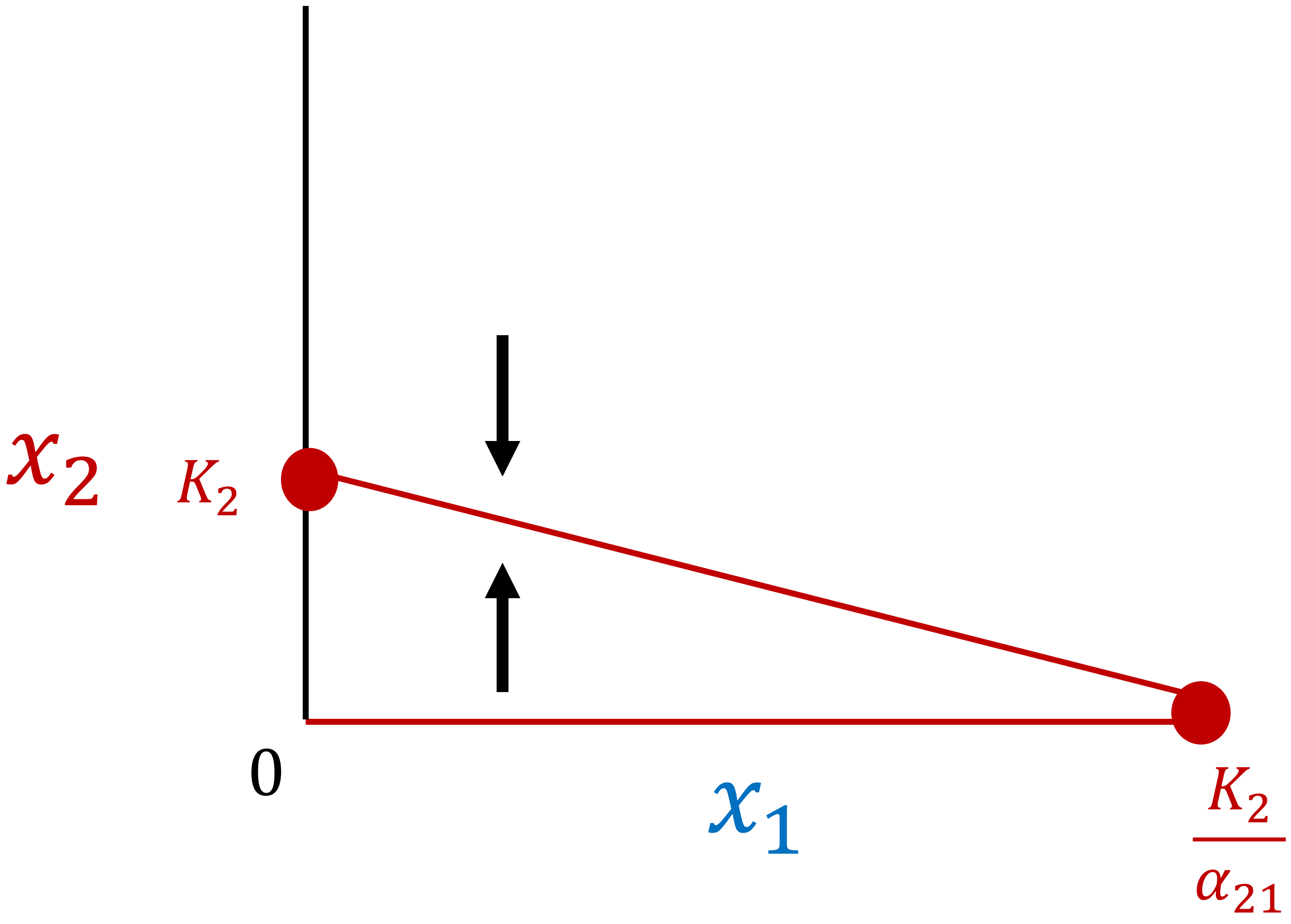

Nullclines (or isoclines) of the Lotka-Volterra competition model

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

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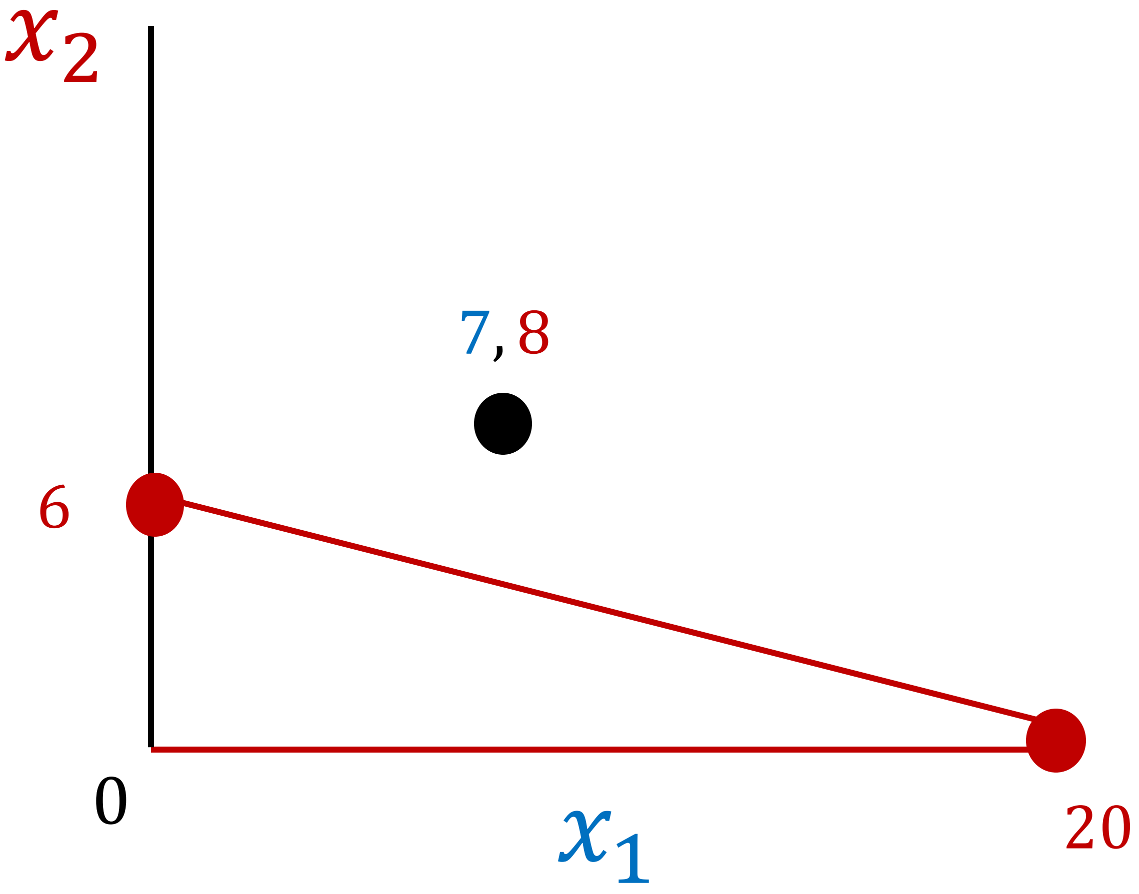

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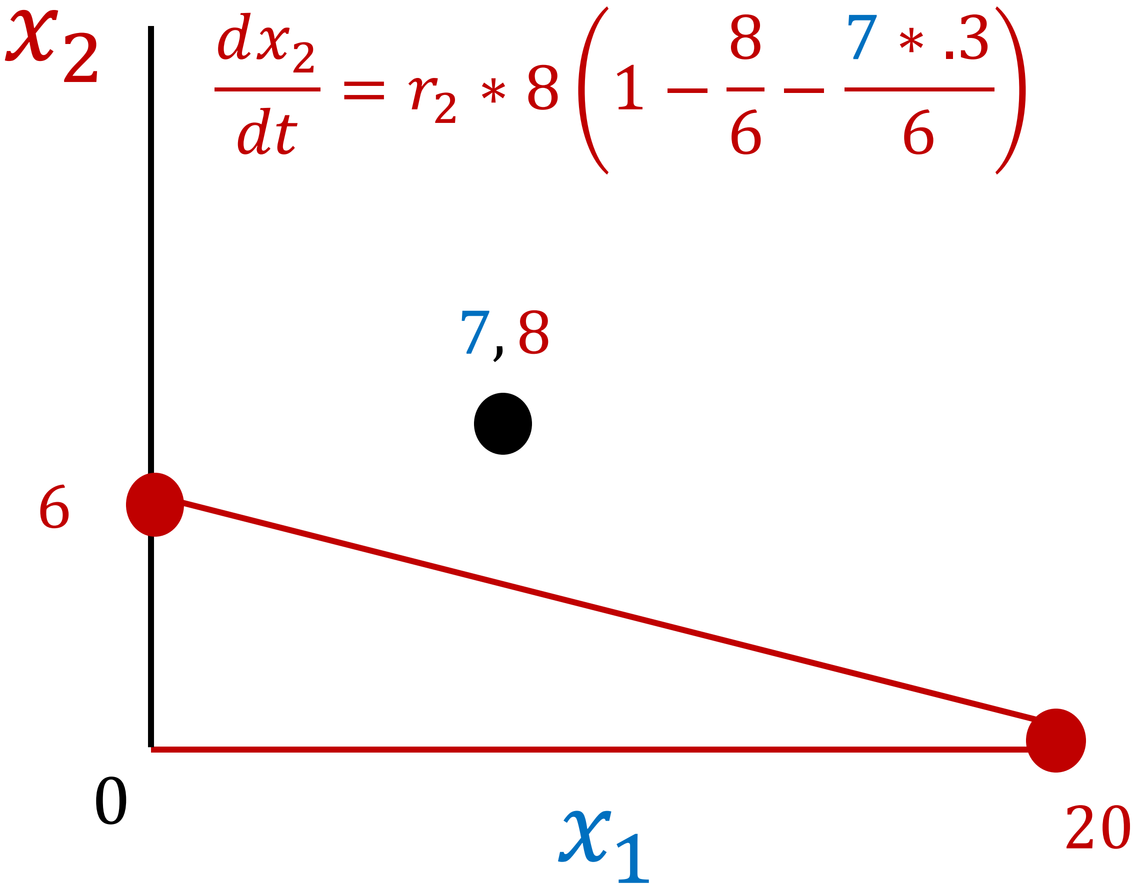

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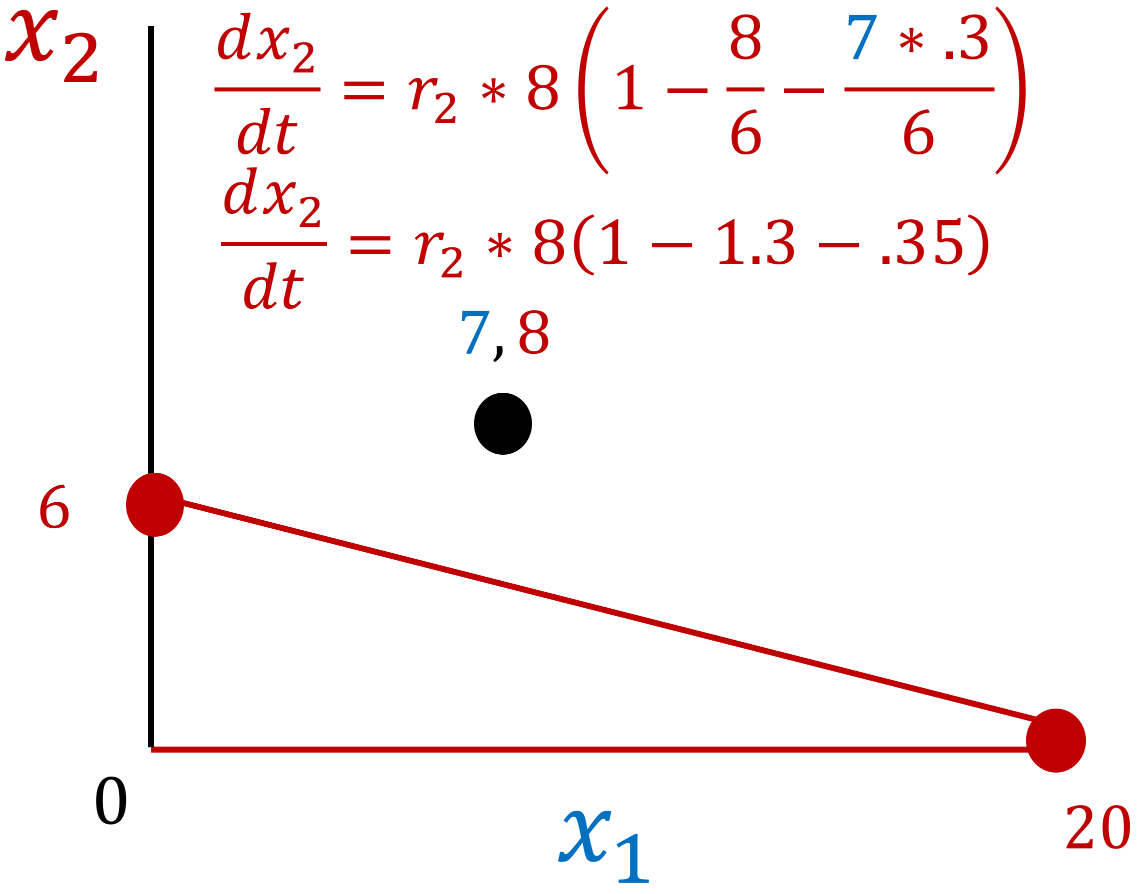
$$\frac{dx_2}{dt} = r_2 * 8(1 - 1.3 - .35)$$



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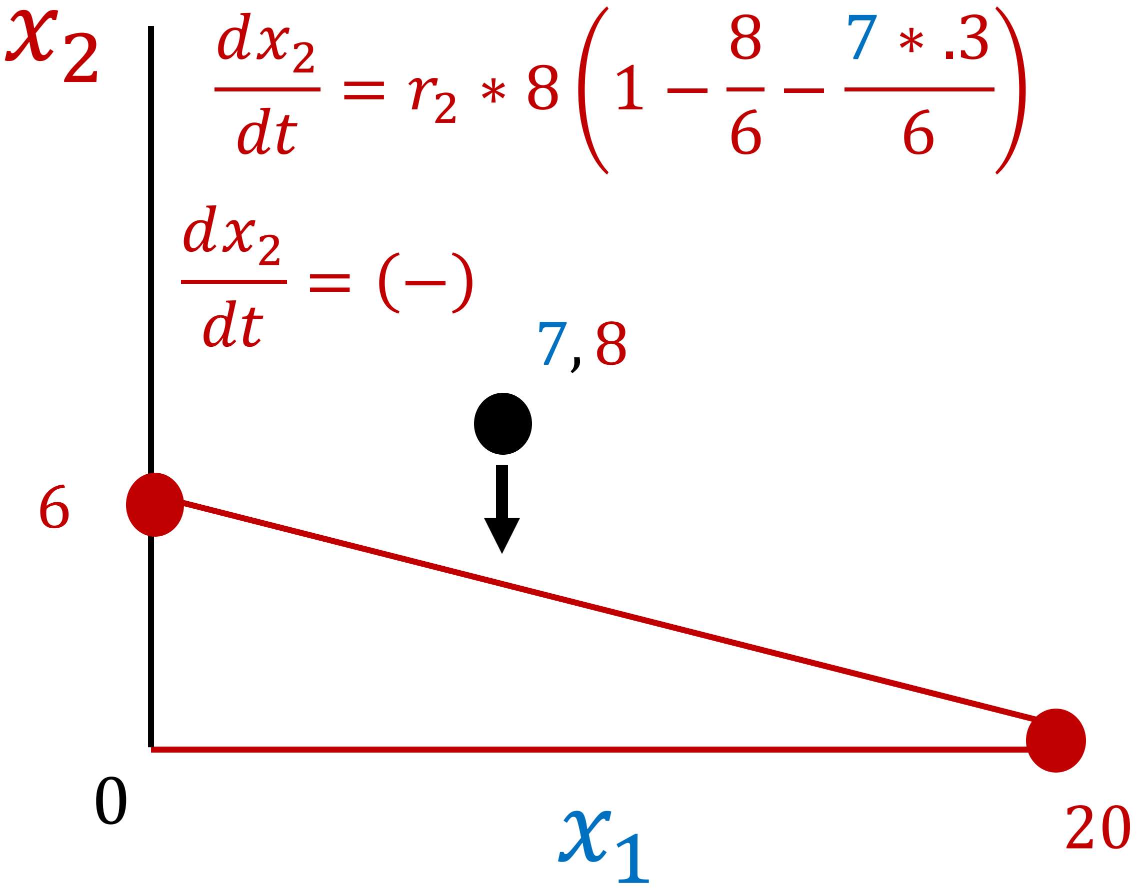

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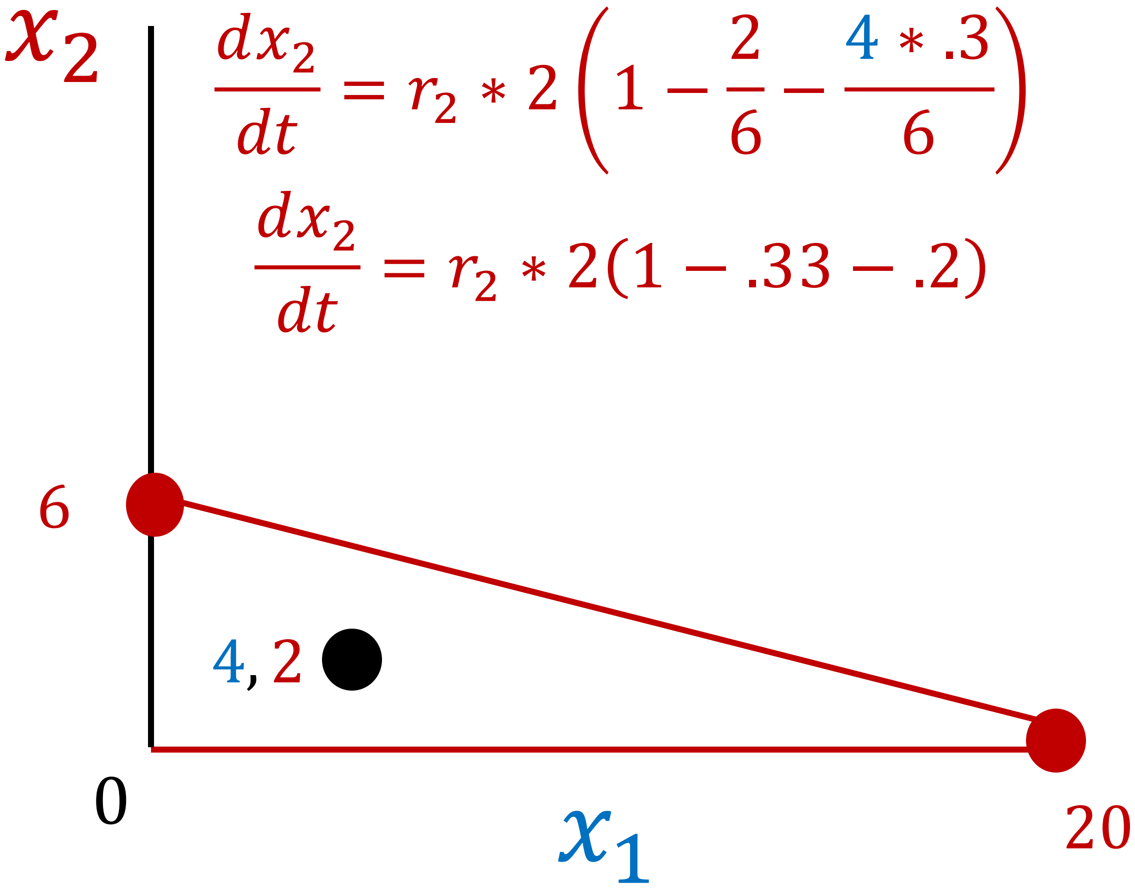
$$\frac{dx_2}{dt} = r_2 * 2 \left(1 - \frac{2}{6} - \frac{4 * .3}{6}\right)$$

$$\frac{dx_2}{dt} = r_2 * 2(1 - .33 - .2)$$



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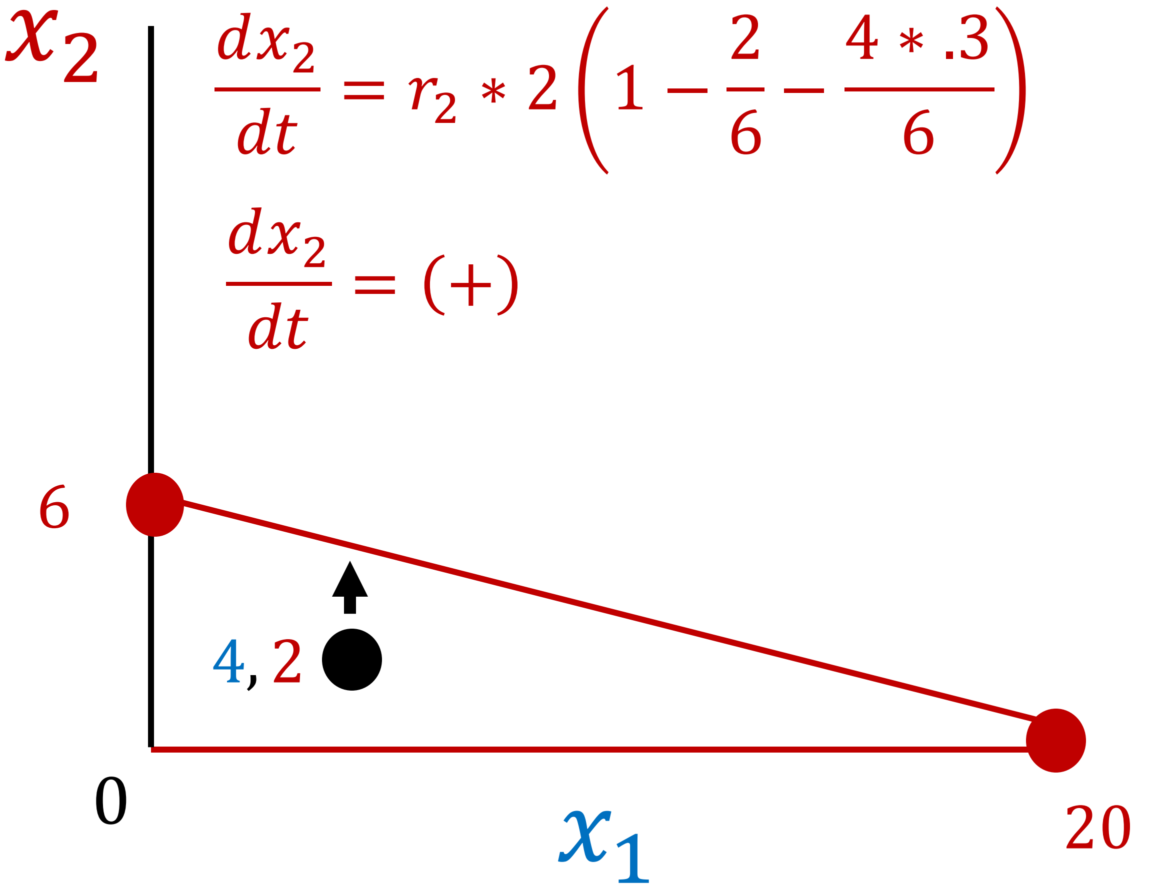
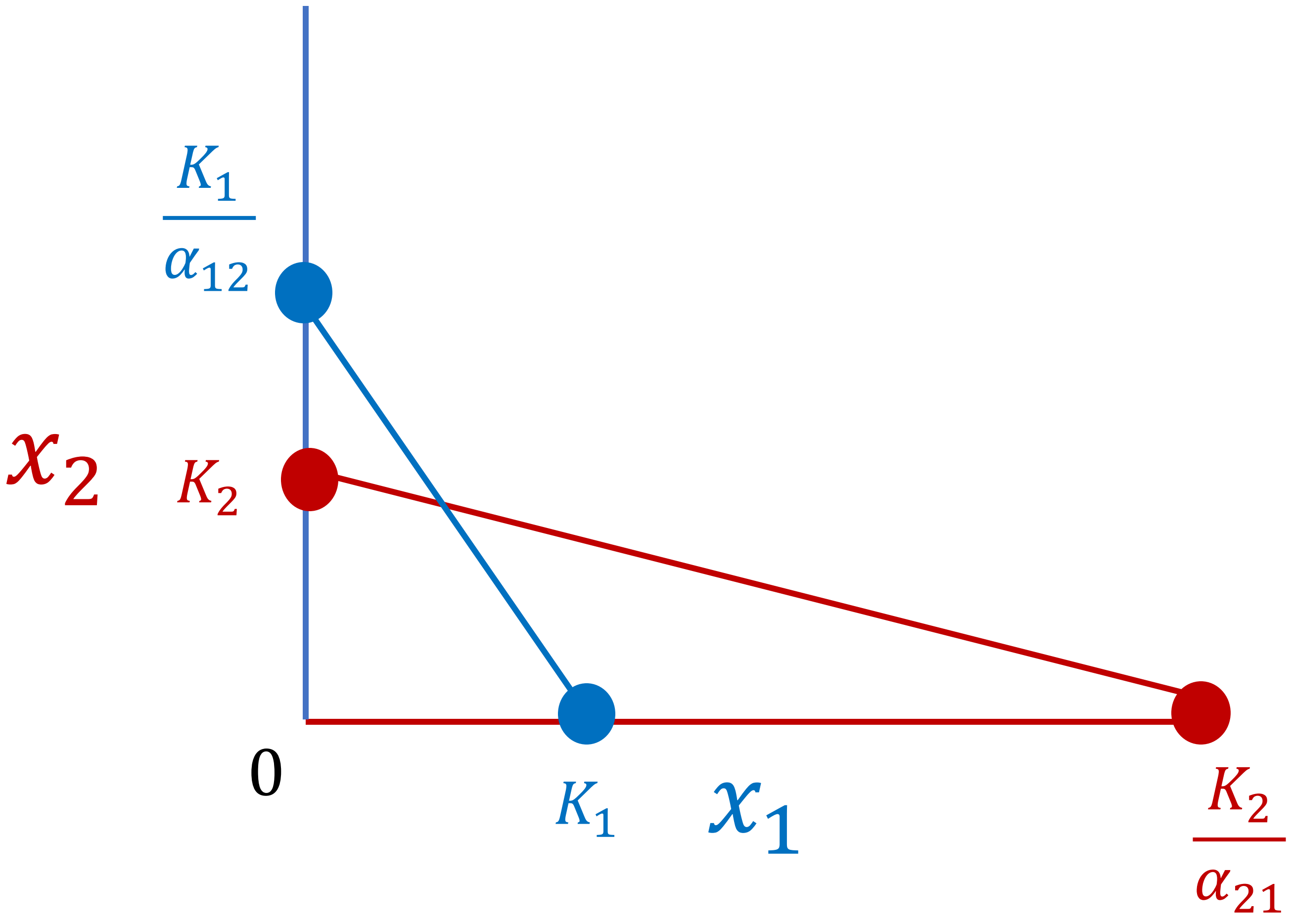
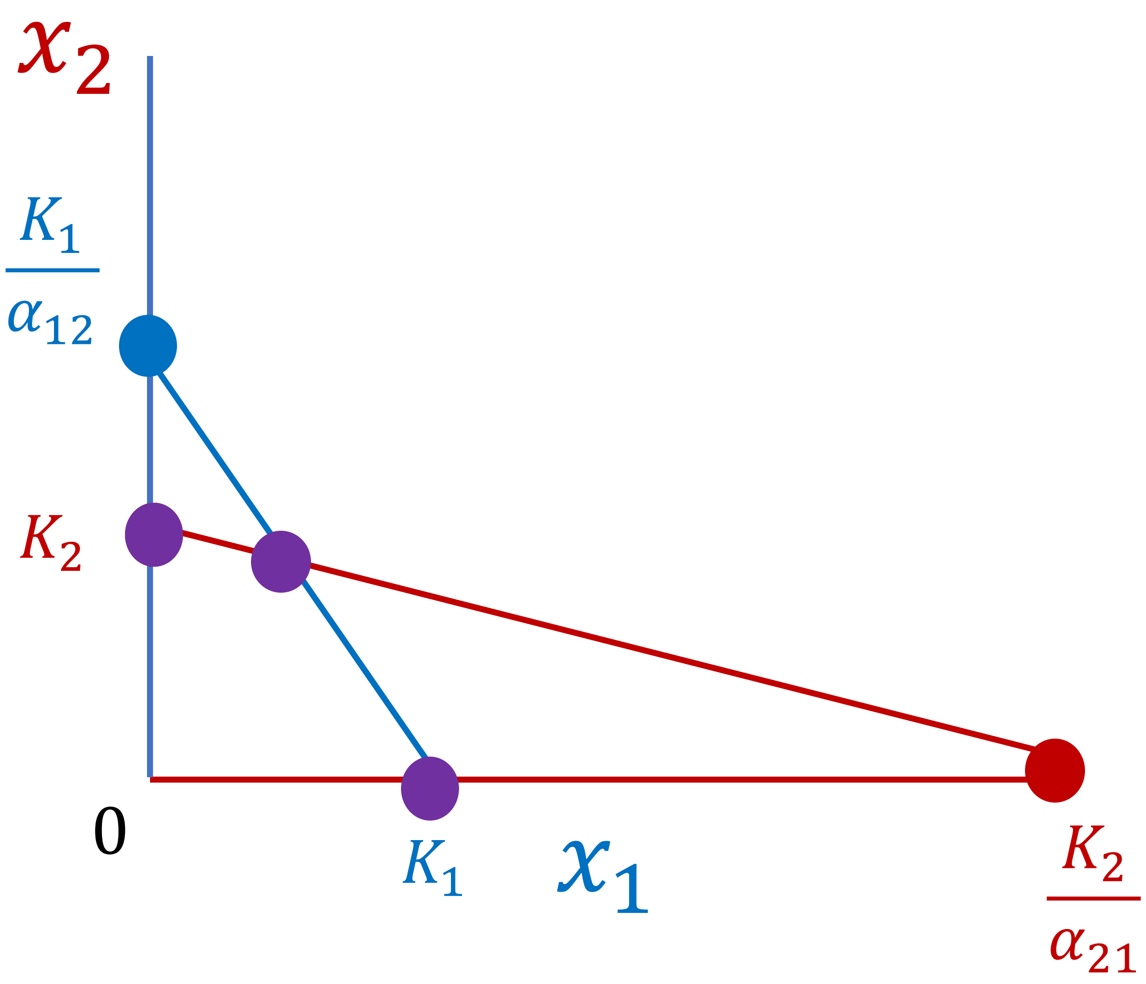


Given different combinations of x_1 and x_2 what is the outcome of competition?



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

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



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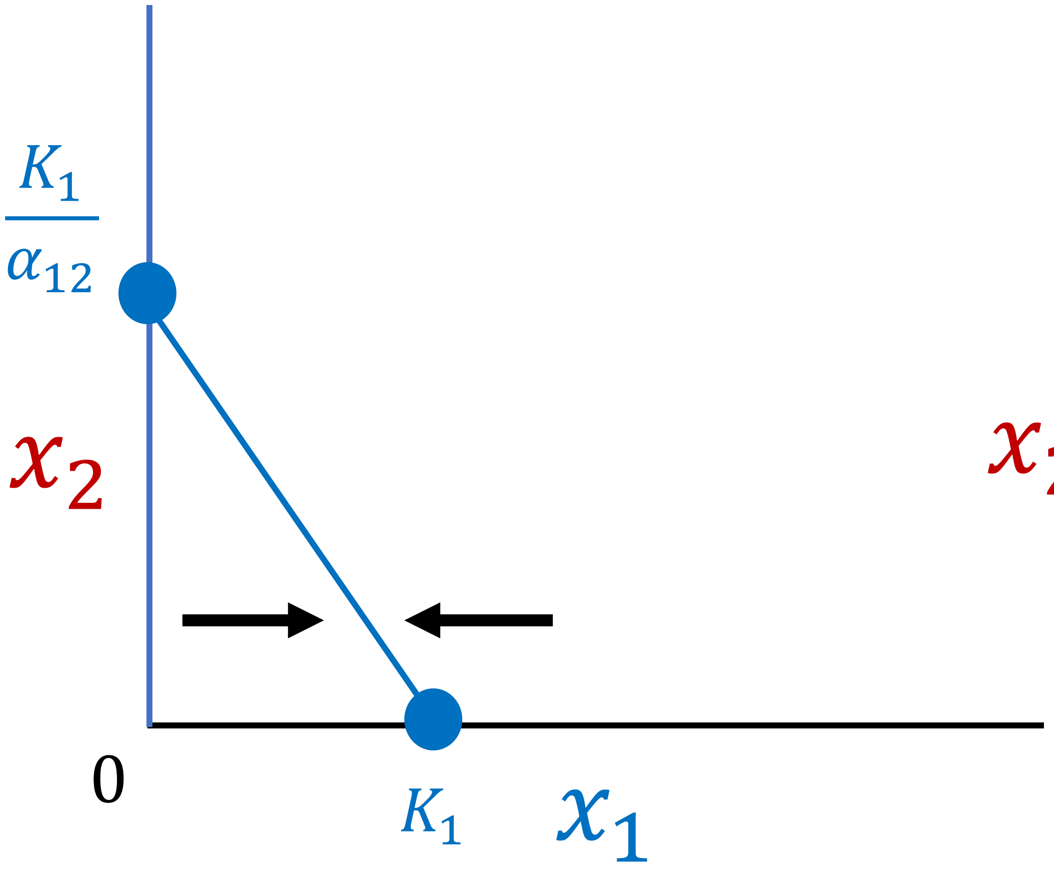
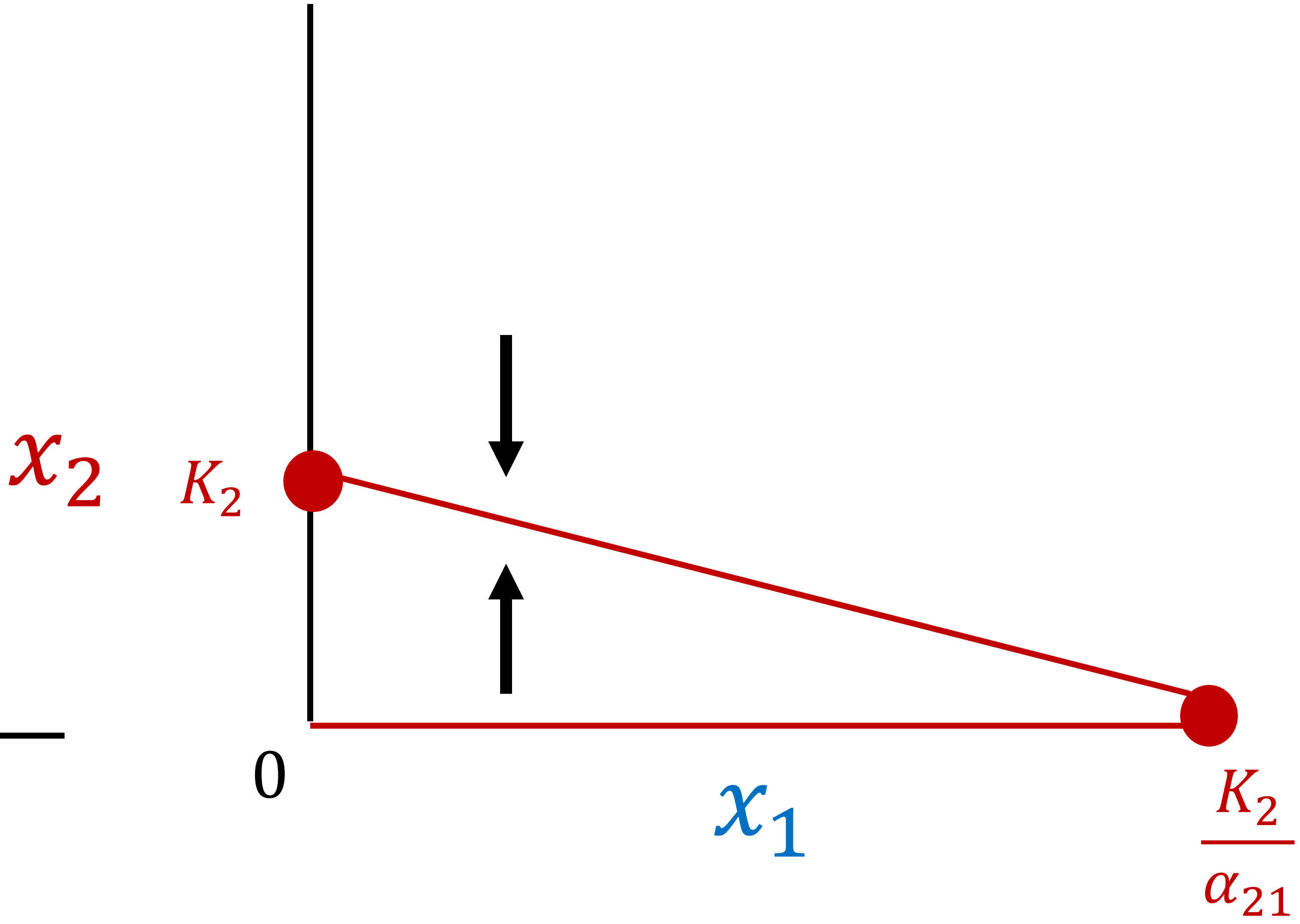


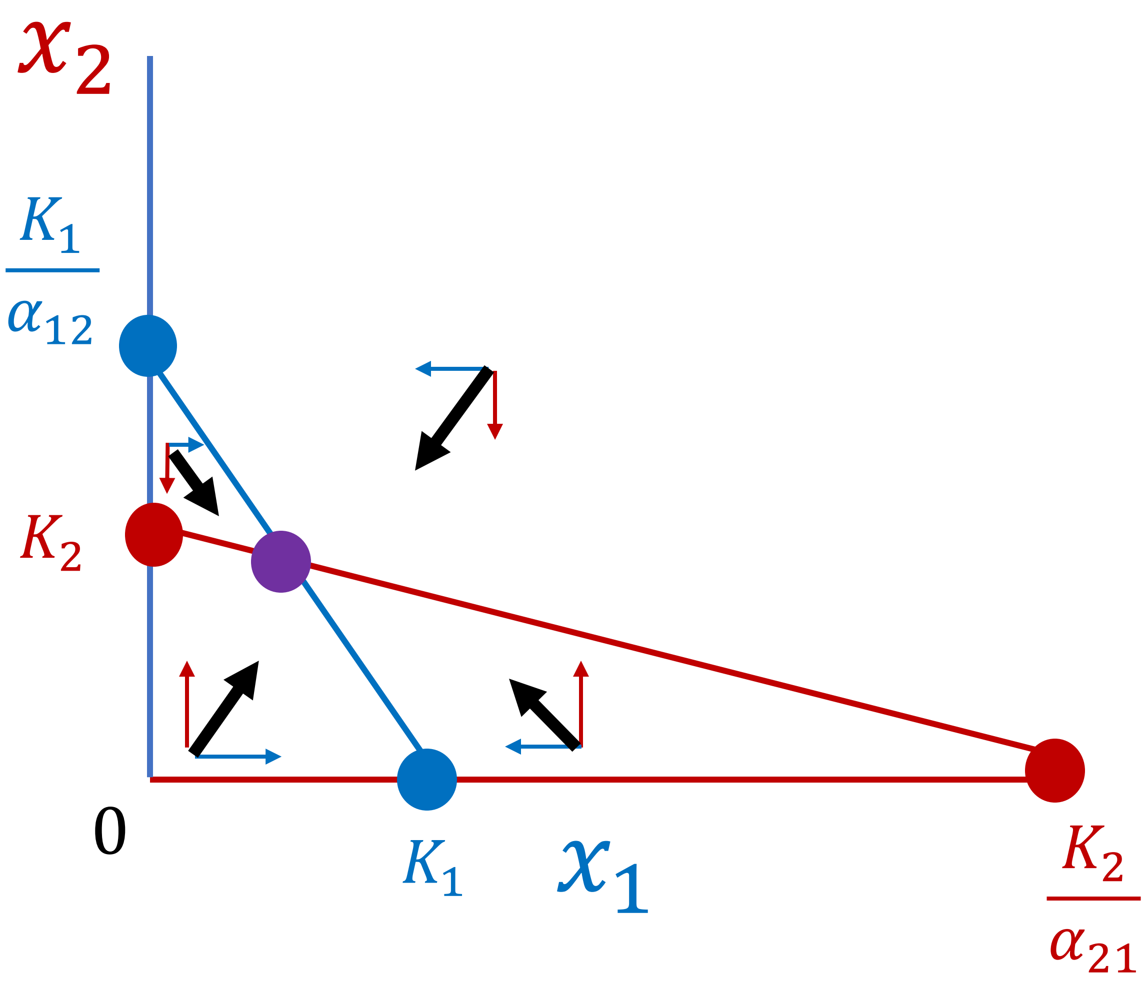


We can use vector addition from the individual nullclines to determine the outcome of competition.

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

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

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



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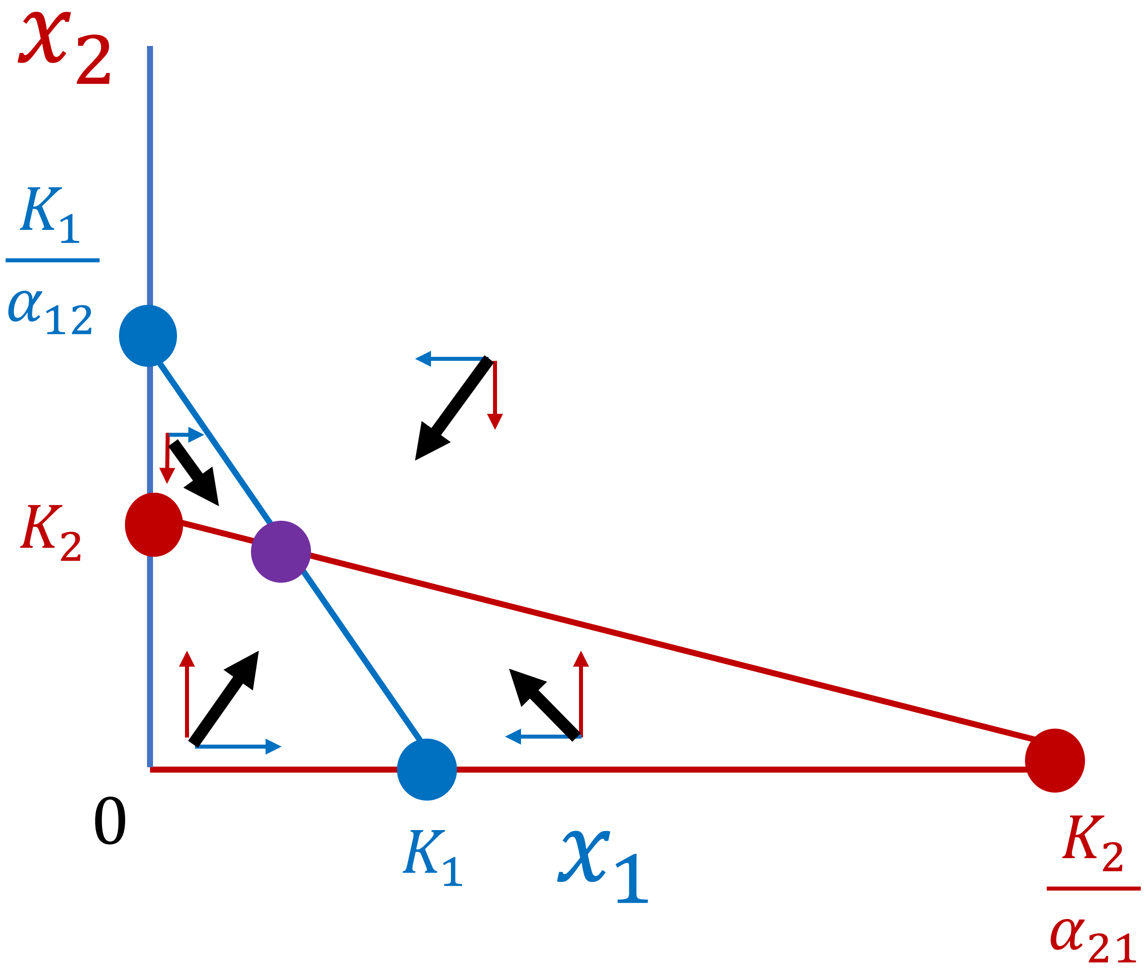
System will converge to one of its equilibria, depending on the values of the competition and carrying capacity parameters.

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

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

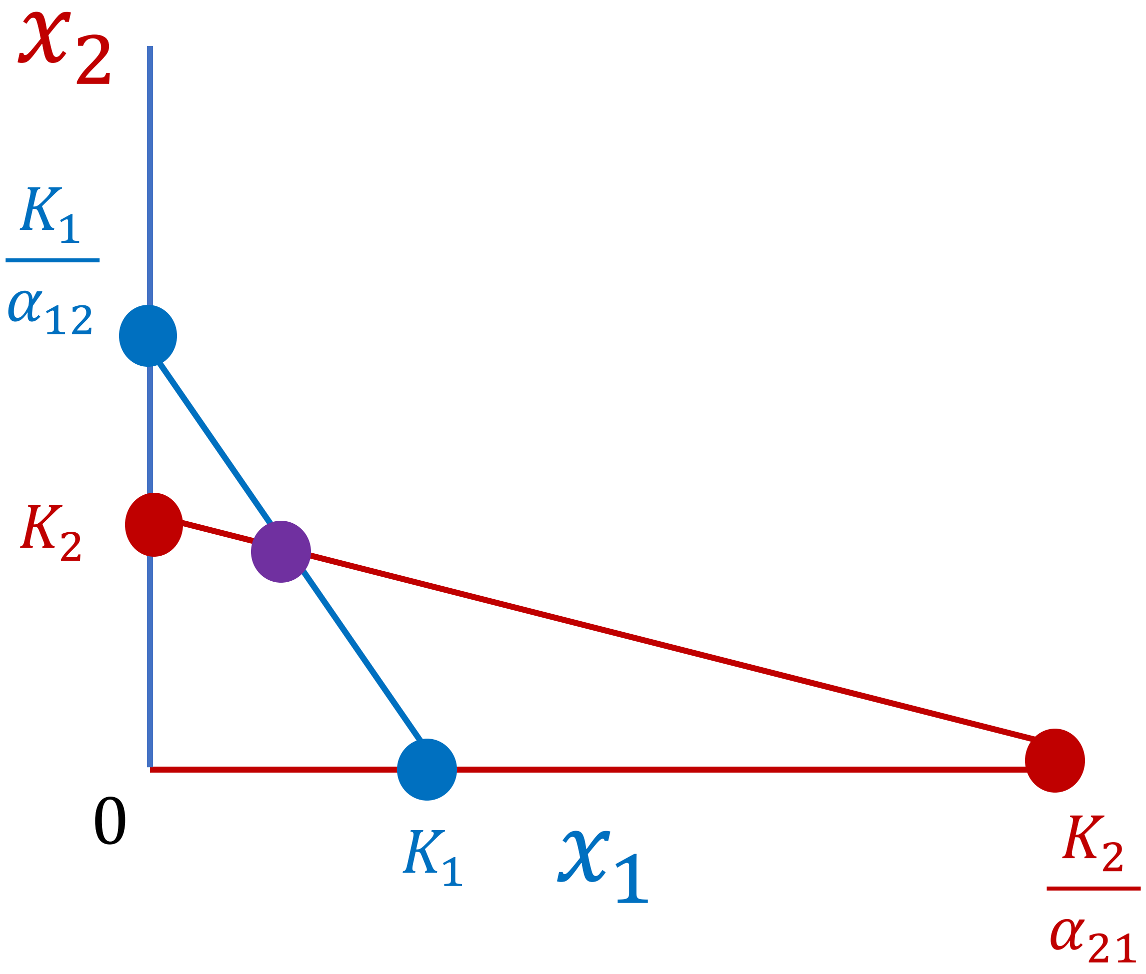
$$x_1^* = \frac{K_1 - K_2\alpha_{12}}{1 - \alpha_{21}\alpha_{12}} \quad x_2^* = \frac{K_2 - K_1\alpha_{21}}{1 - \alpha_{12}\alpha_{21}}$$



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

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

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



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

Let's try it!

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

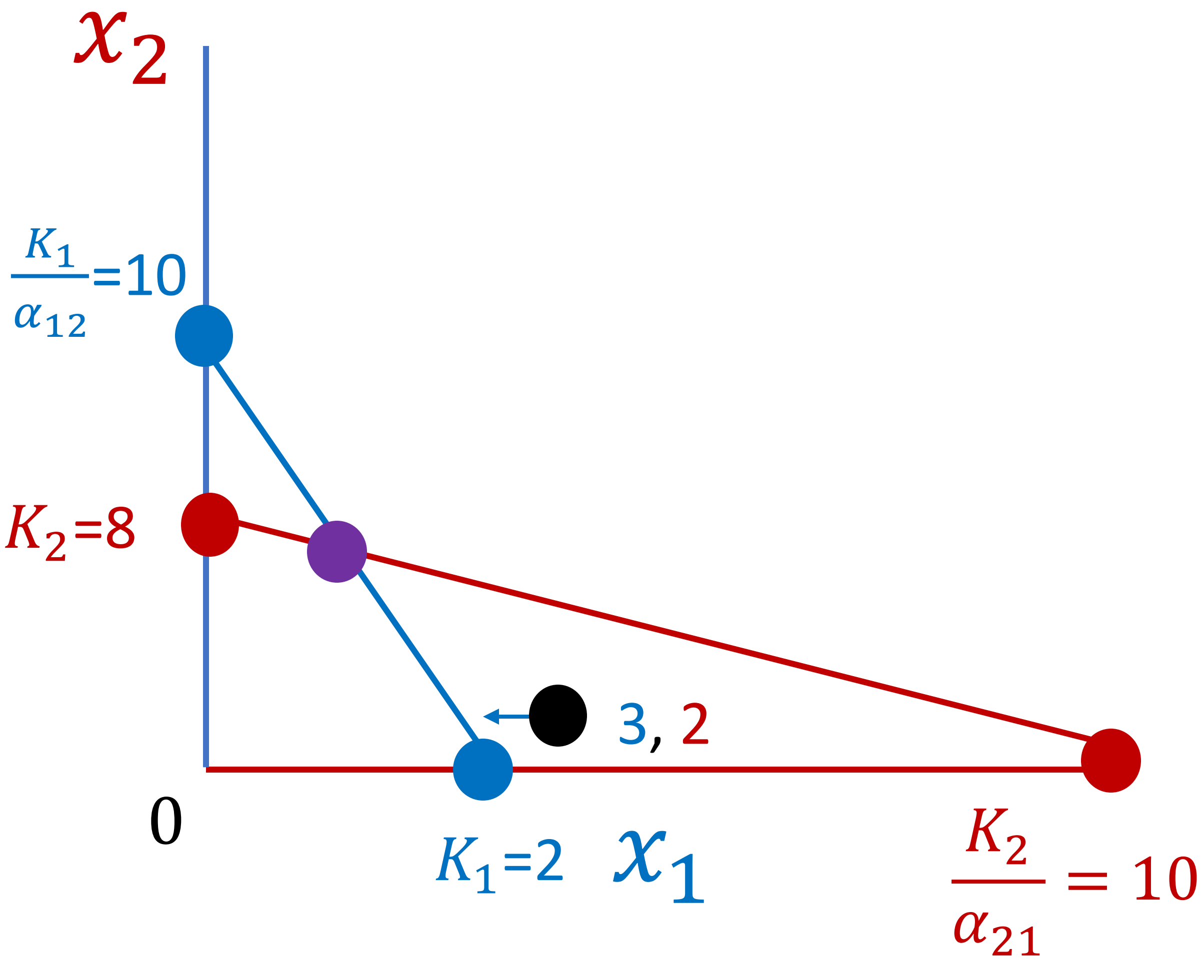
$K_2 = 8\,;\alpha_{21} = .8$

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

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

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

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



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

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

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

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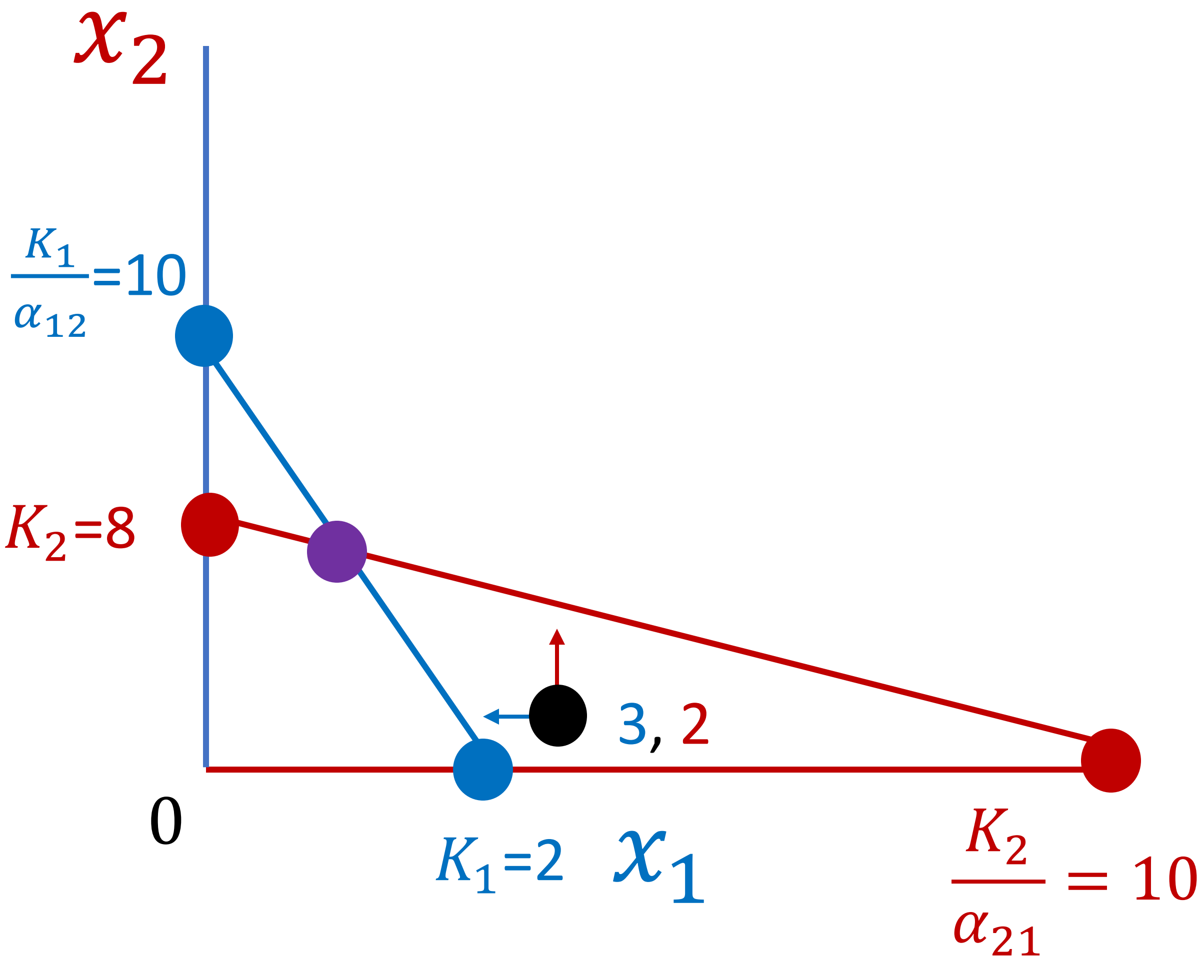

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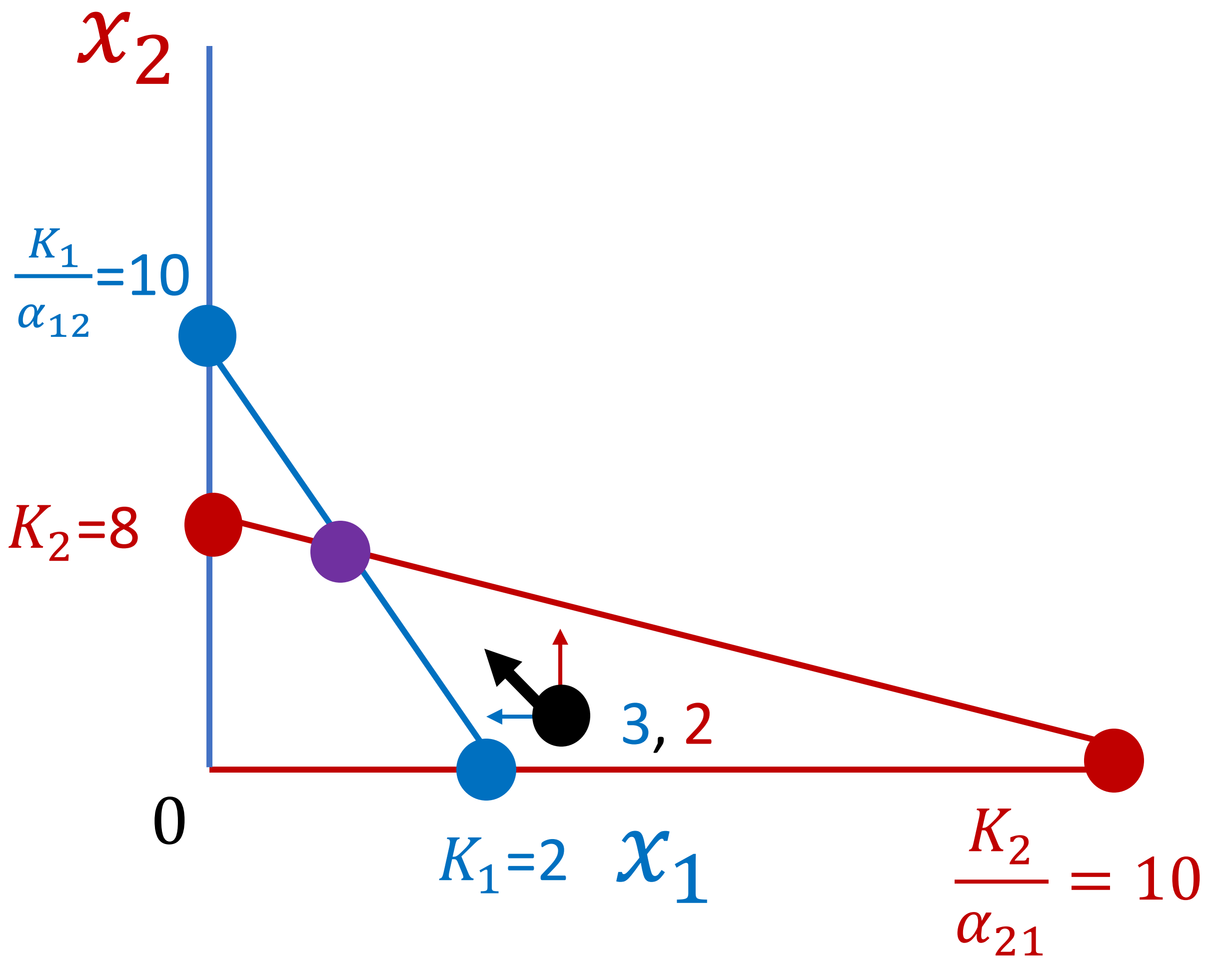
Let's try it!

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

Results replicate graphical approach!



Four possible outcomes for competition

Case 1:

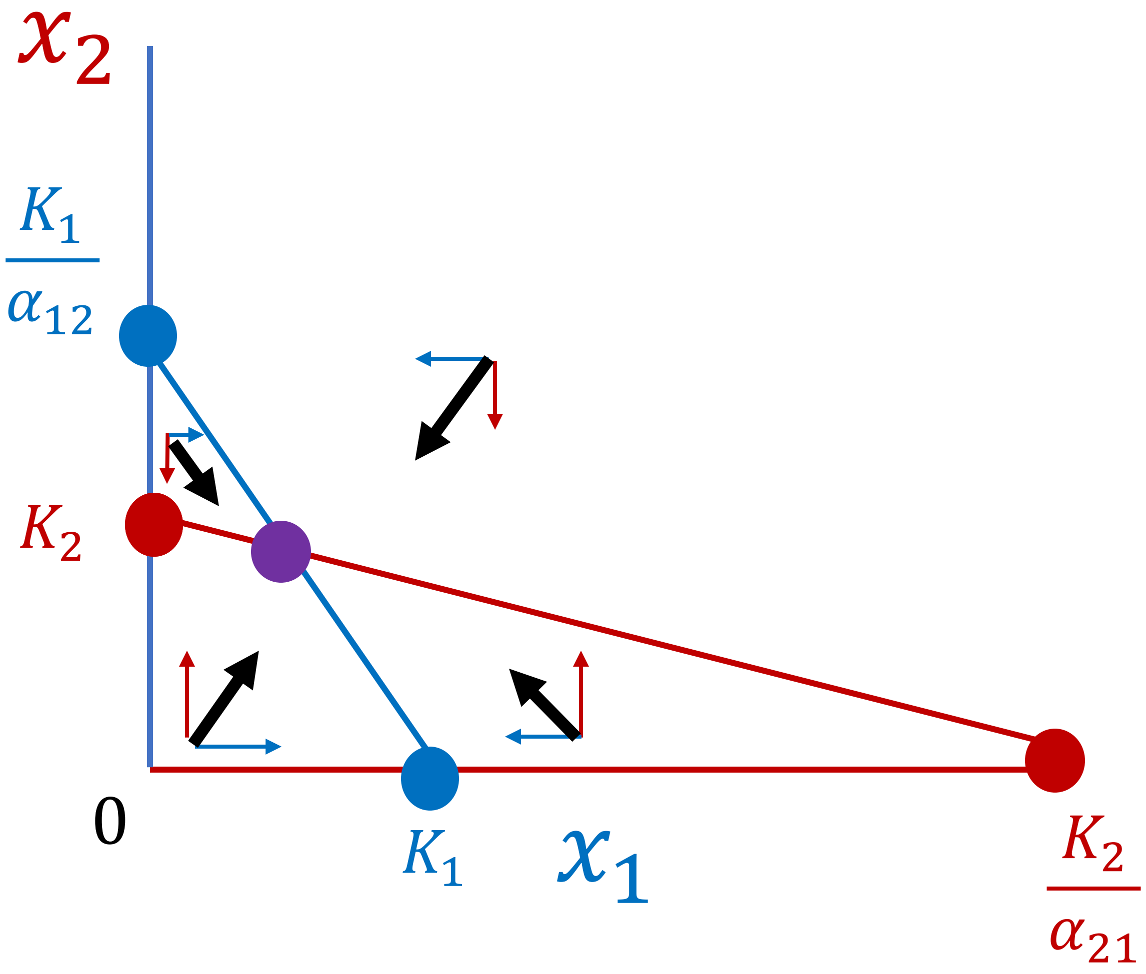
Stable equilibrium, with **coexistence** at:

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

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

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

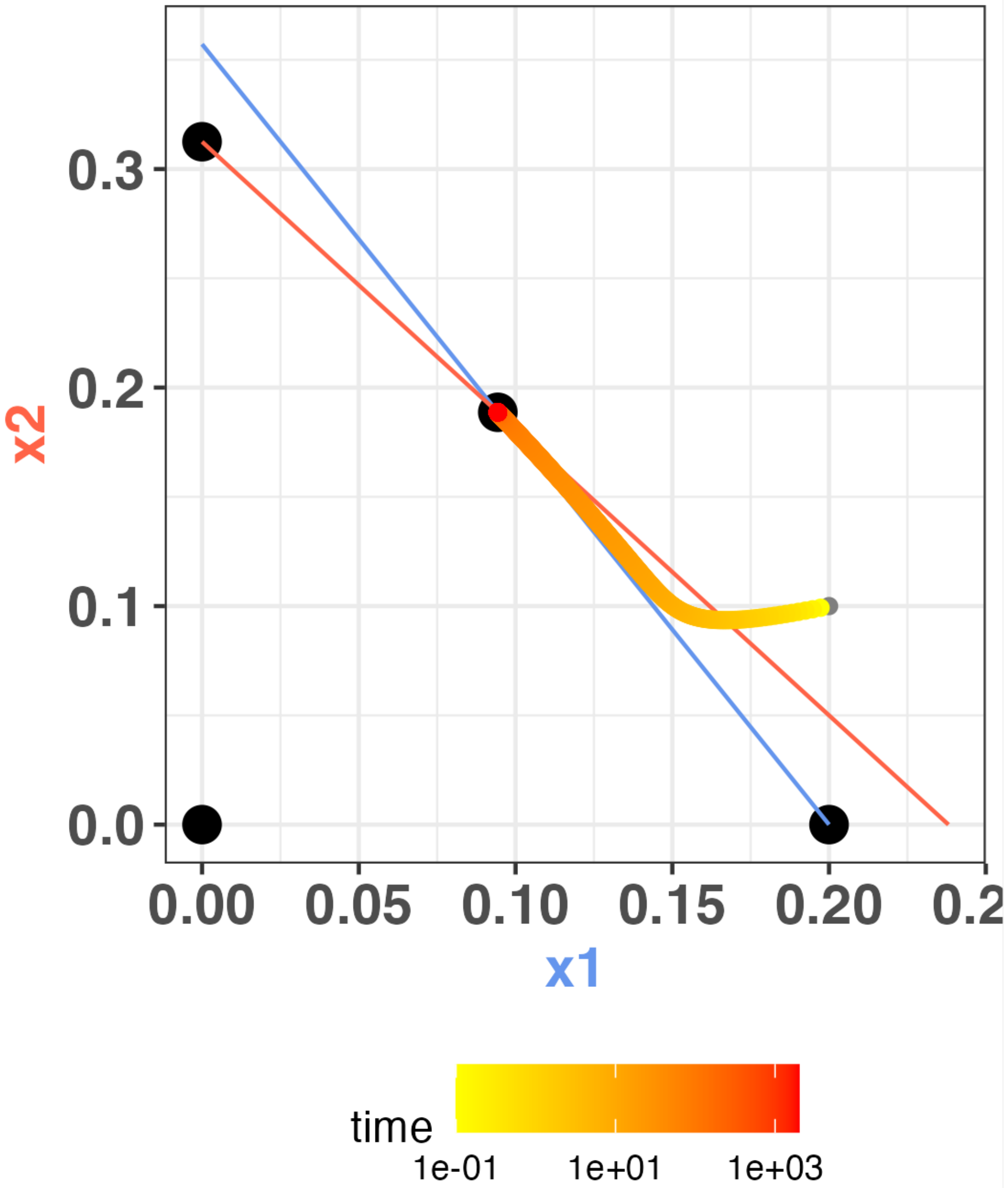
- Species coexist stably but **below carrying capacity** for each individual population.
- **Intraspecific** competition is stronger than **interspecific** competition.

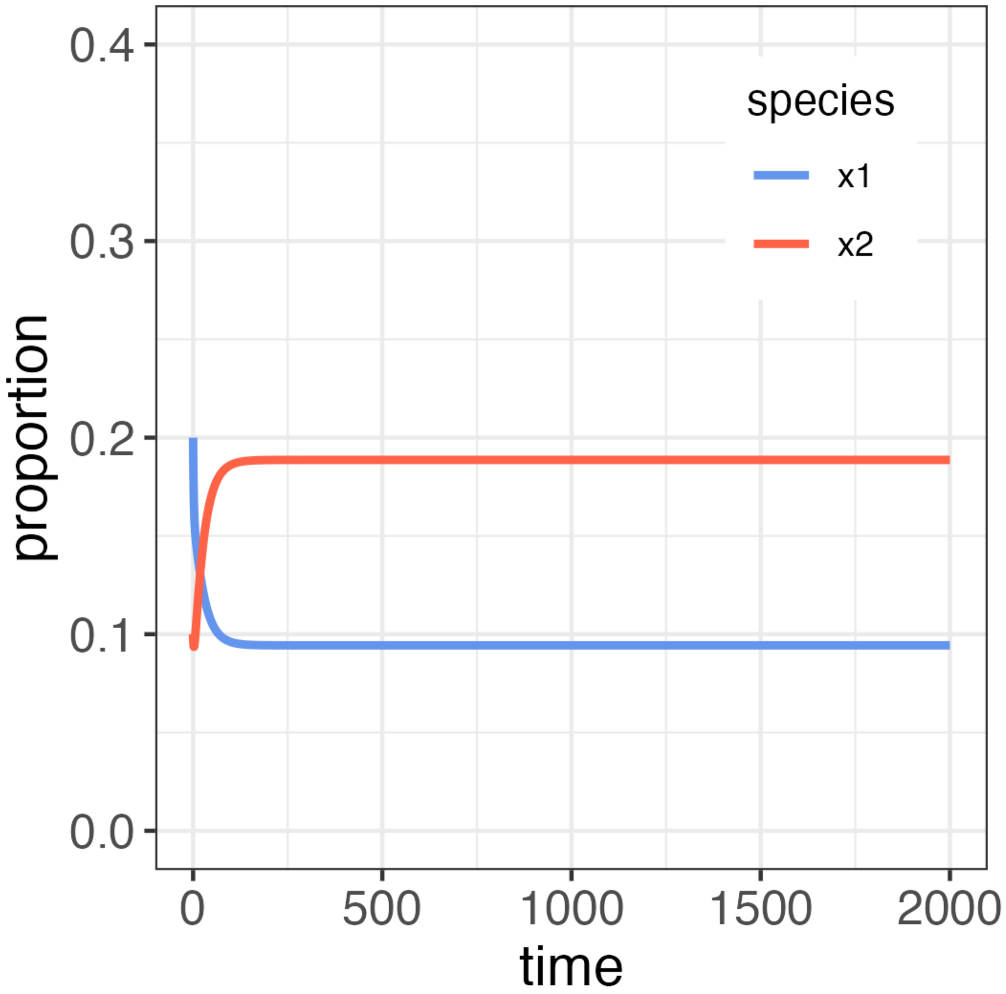


Case 1:

Stable equilibrium, with **coexistence**:

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





Four possible outcomes for competition

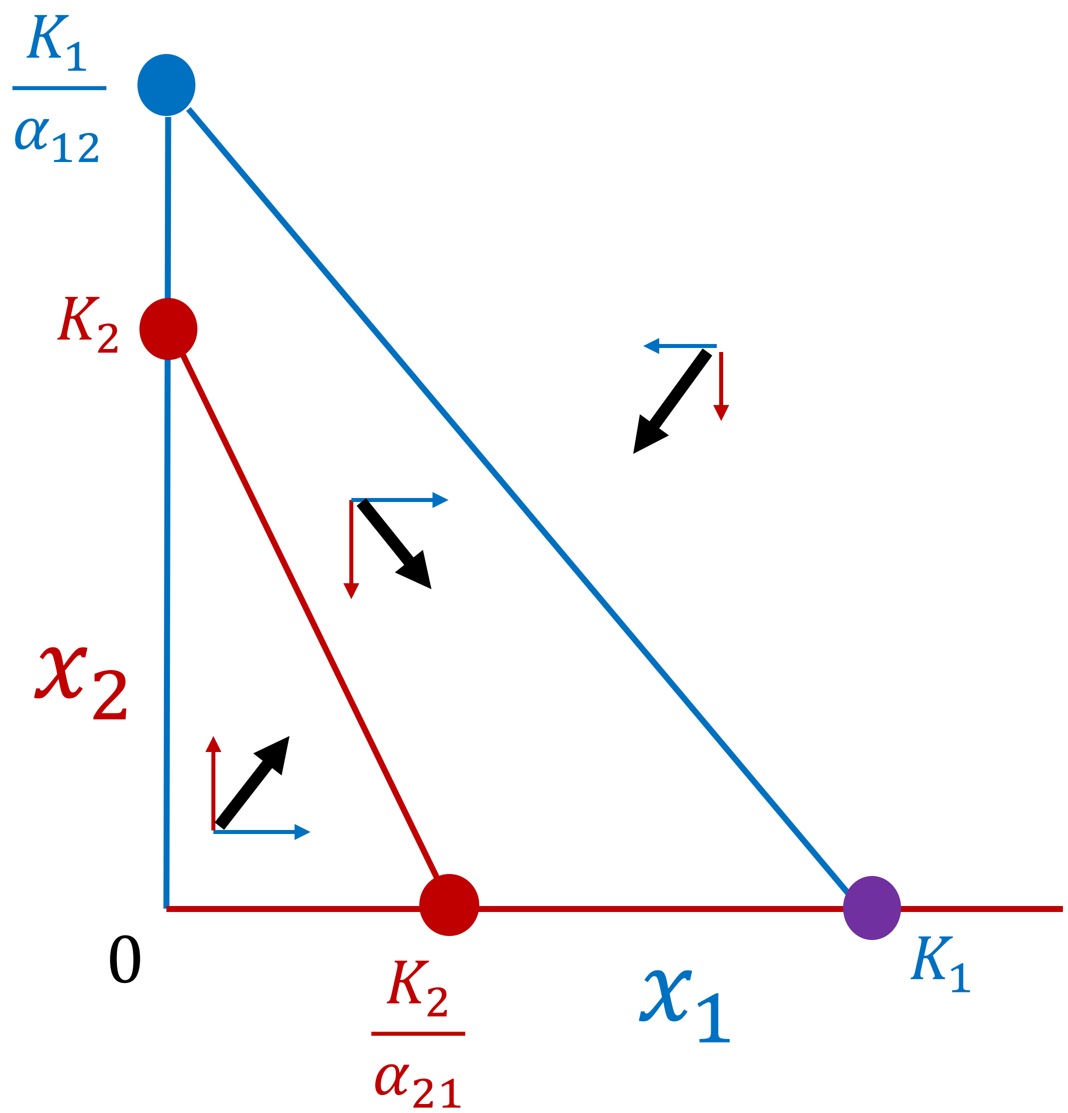
Case 2:

Species 1 outcompetes species 2

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

System collapses to equilibrium:

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



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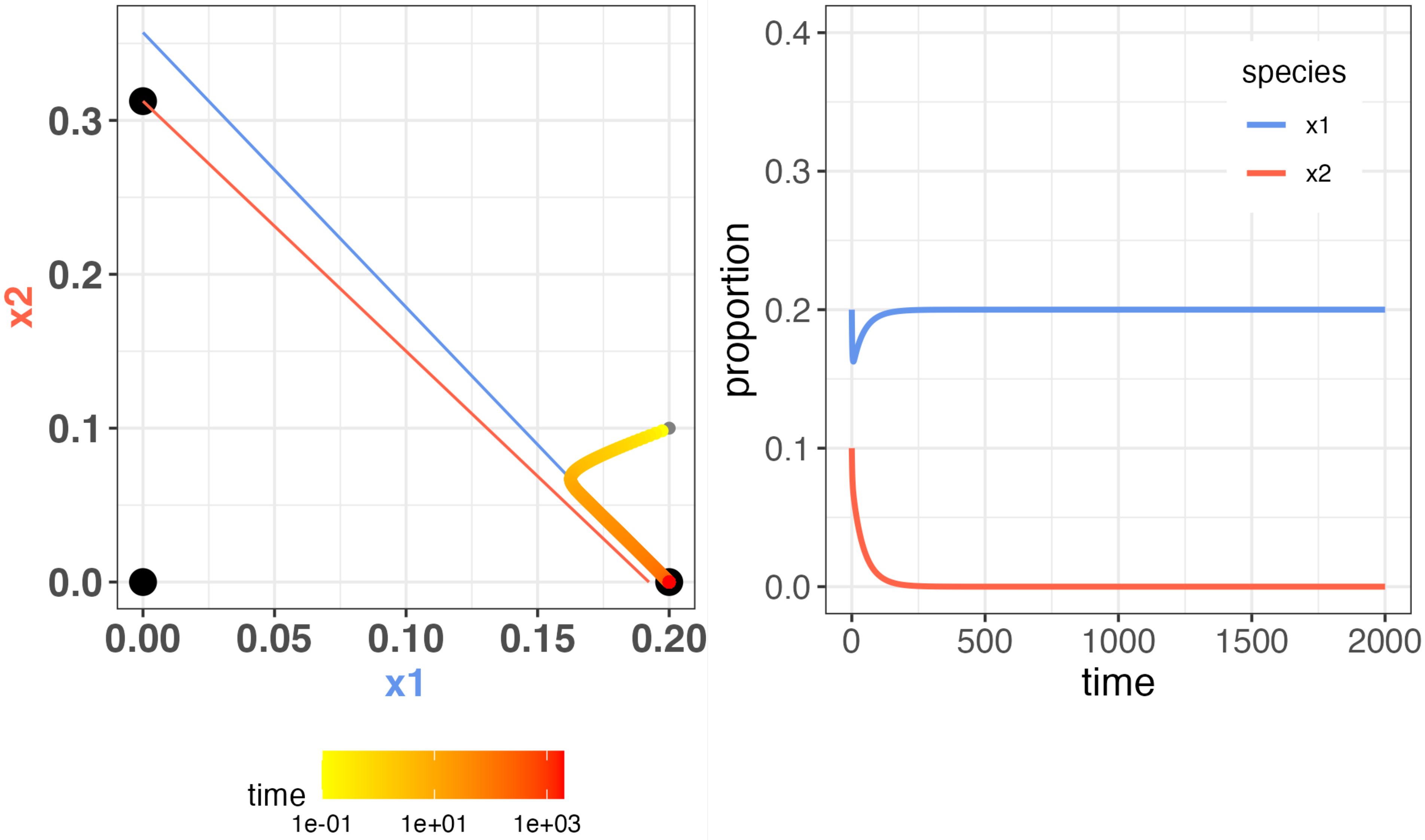
Species 1 outcompetes species 2

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



Four possible outcomes for competition

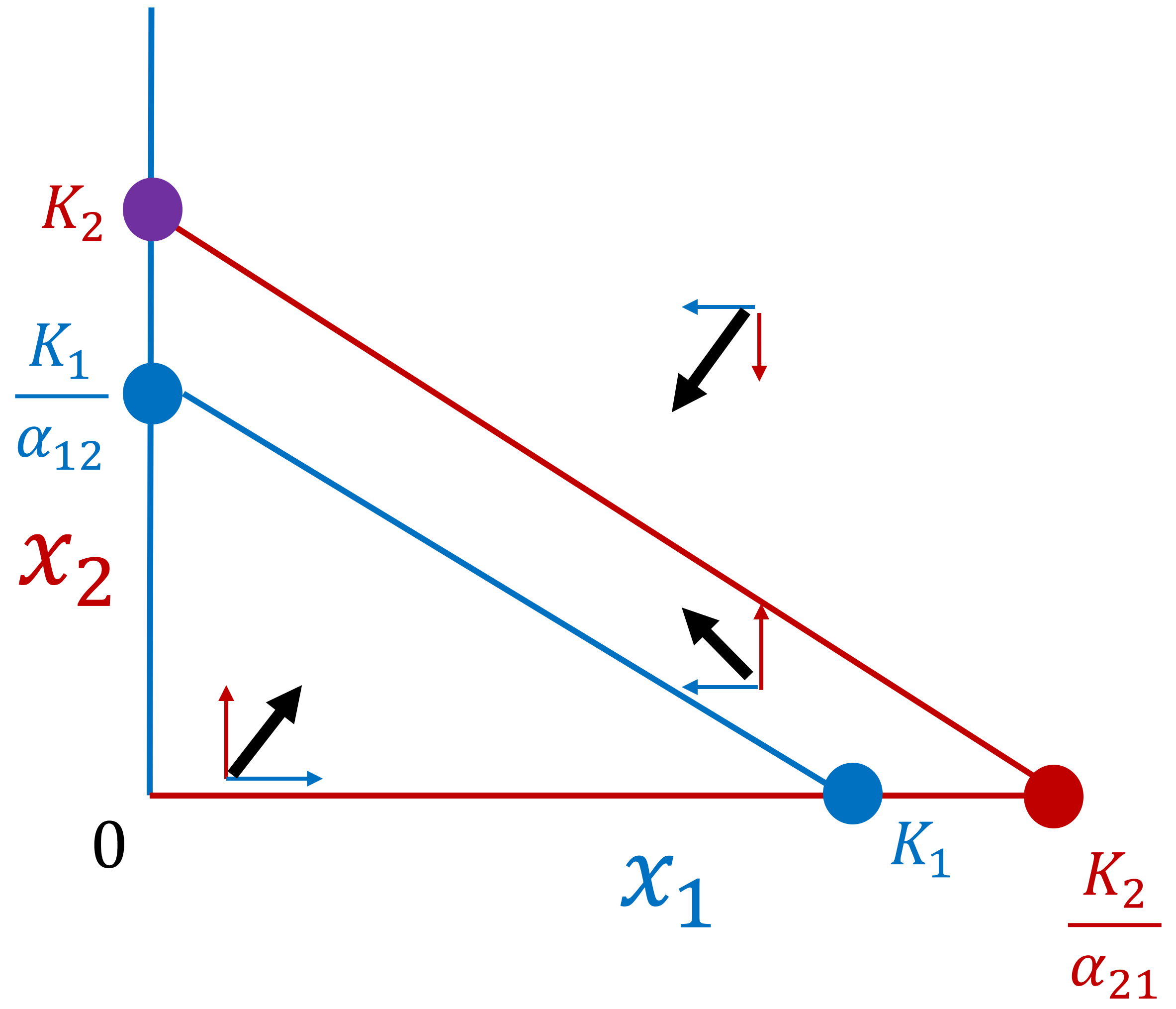
Case 3:

Species 2 outcompetes species 1

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

System collapses to equilibrium:

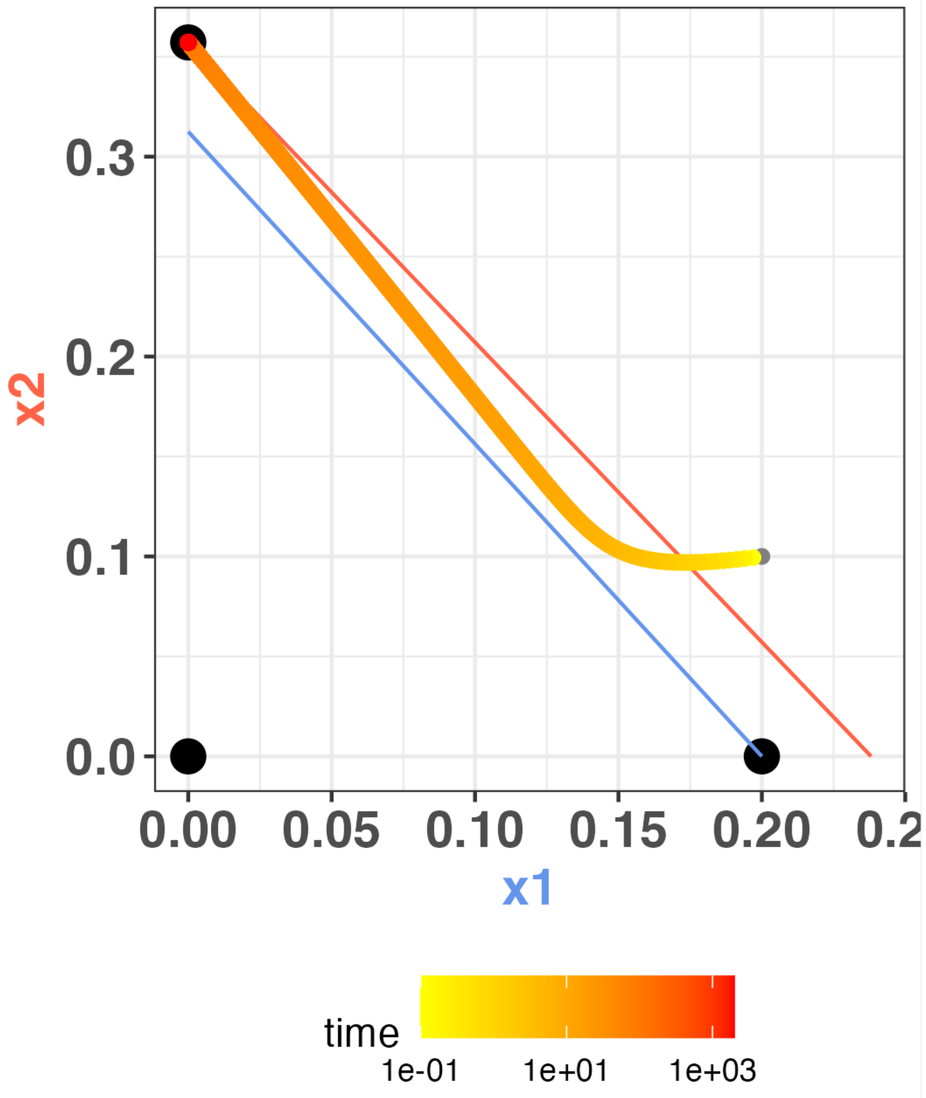
$$x_1^* = 0;\; x_2^* = K_2$$

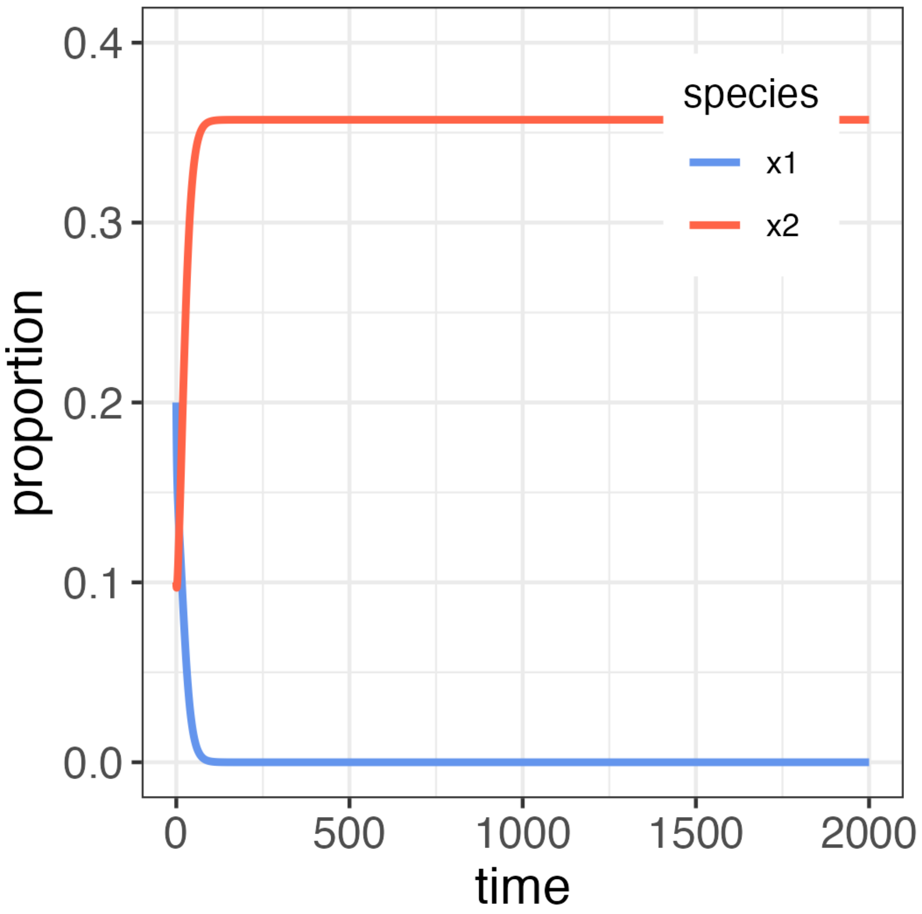


Case 3:

Species 2 outcompetes species 1

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





Four possible outcomes for competition

Case 4: Precedence

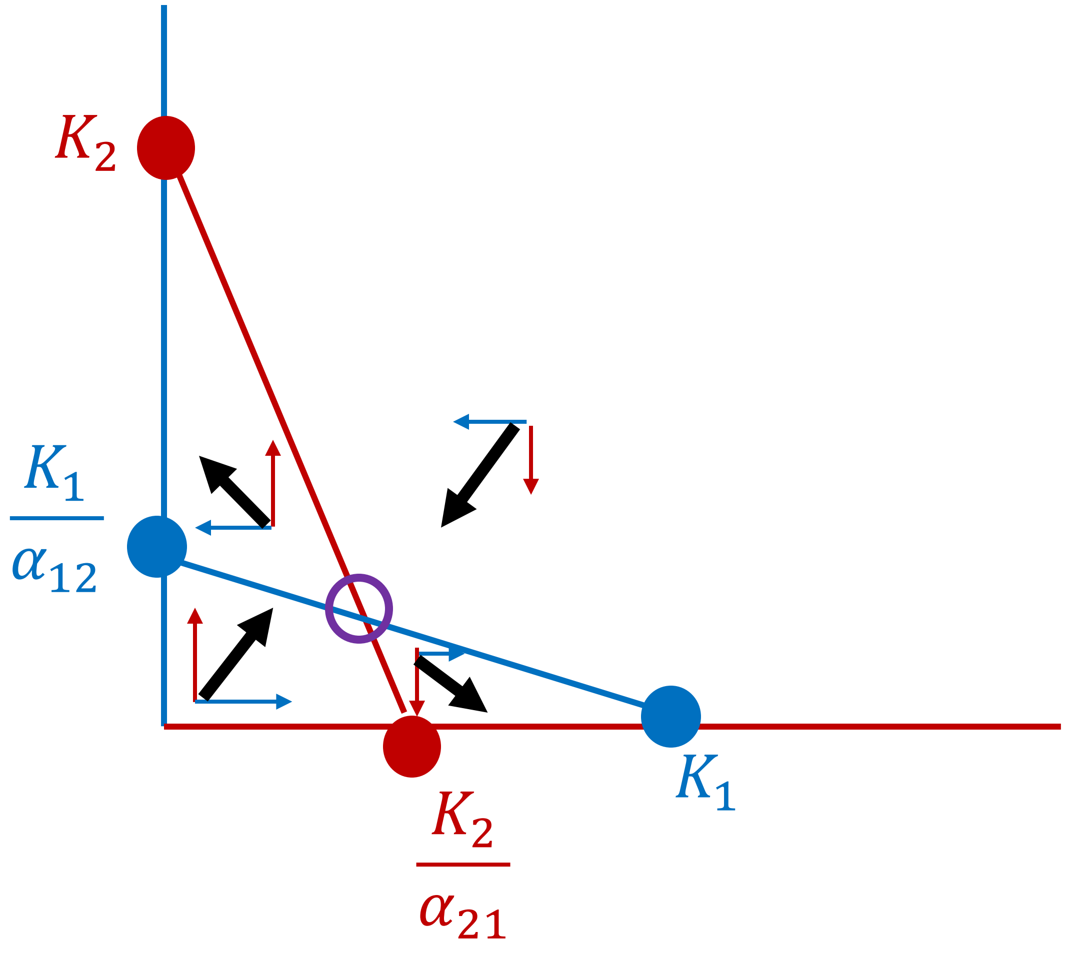
Aggressive interspecific competition.

Outcome depends on starting conditions.

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

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

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

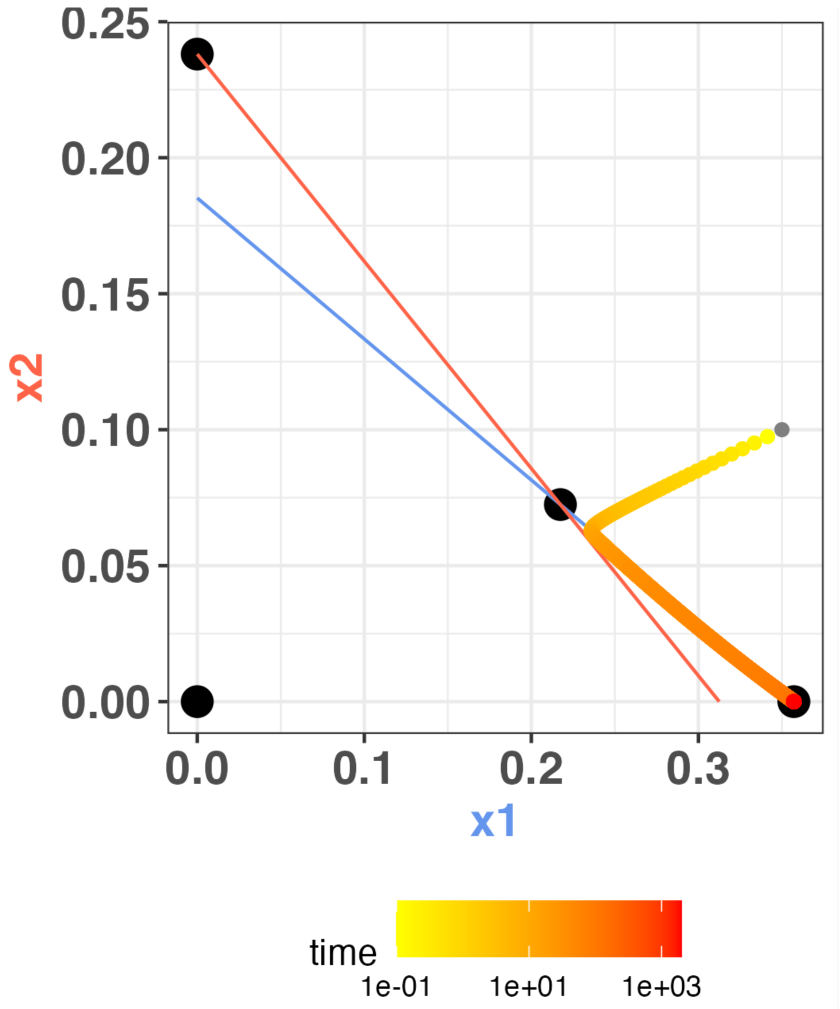


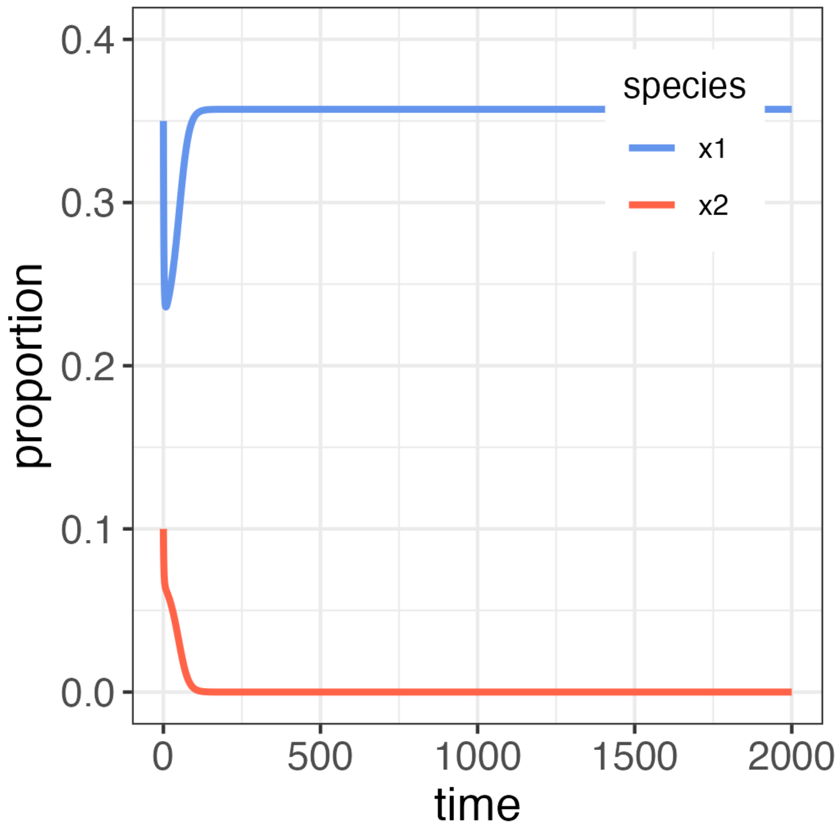
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

Here, **x1 outcompetes x2**



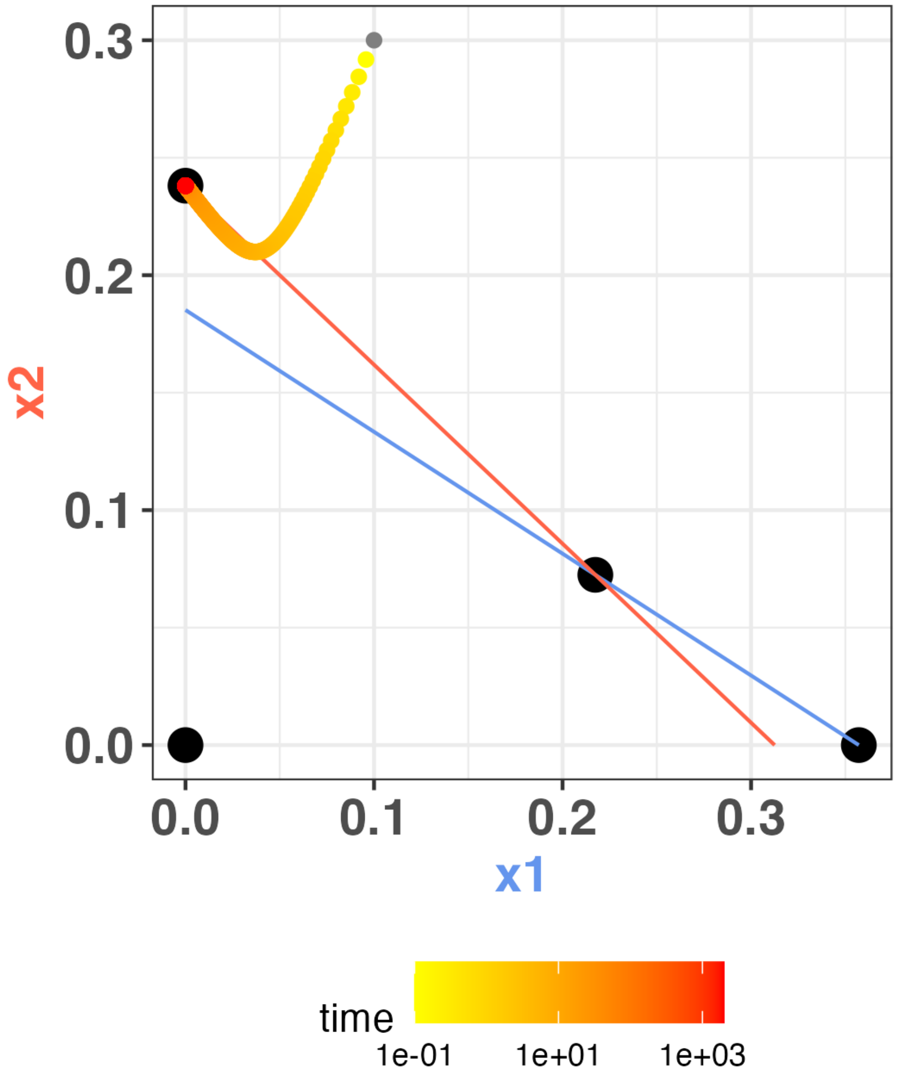


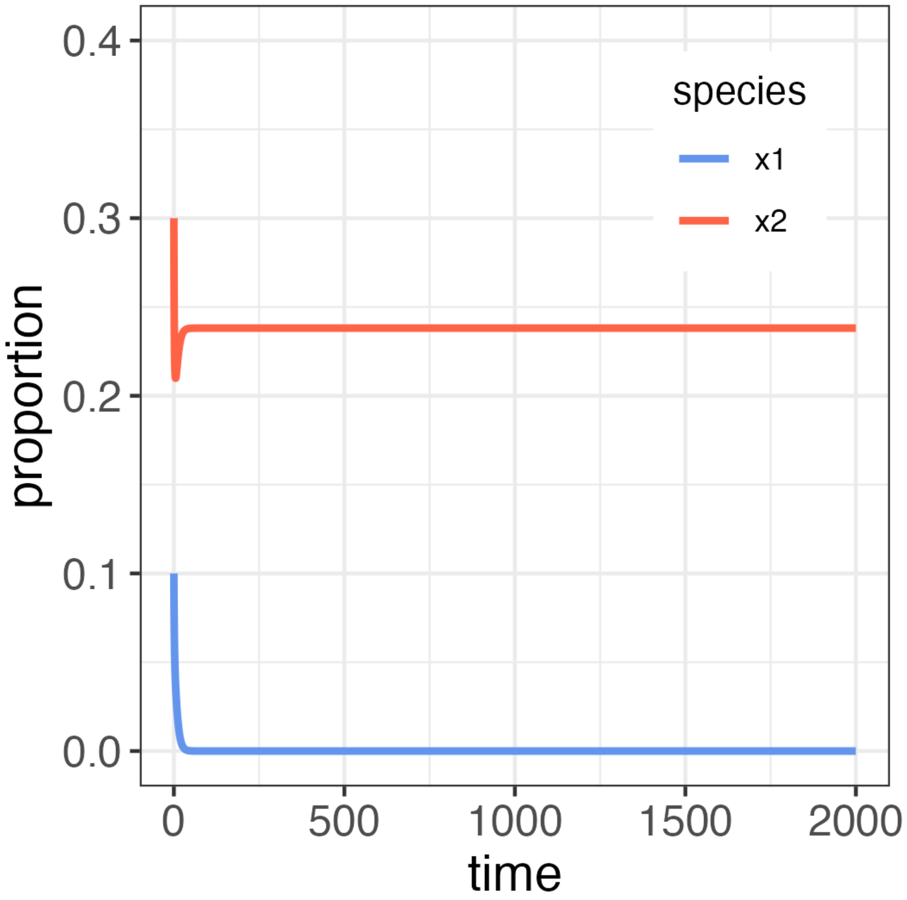
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

Here, x2 outcompetes x1



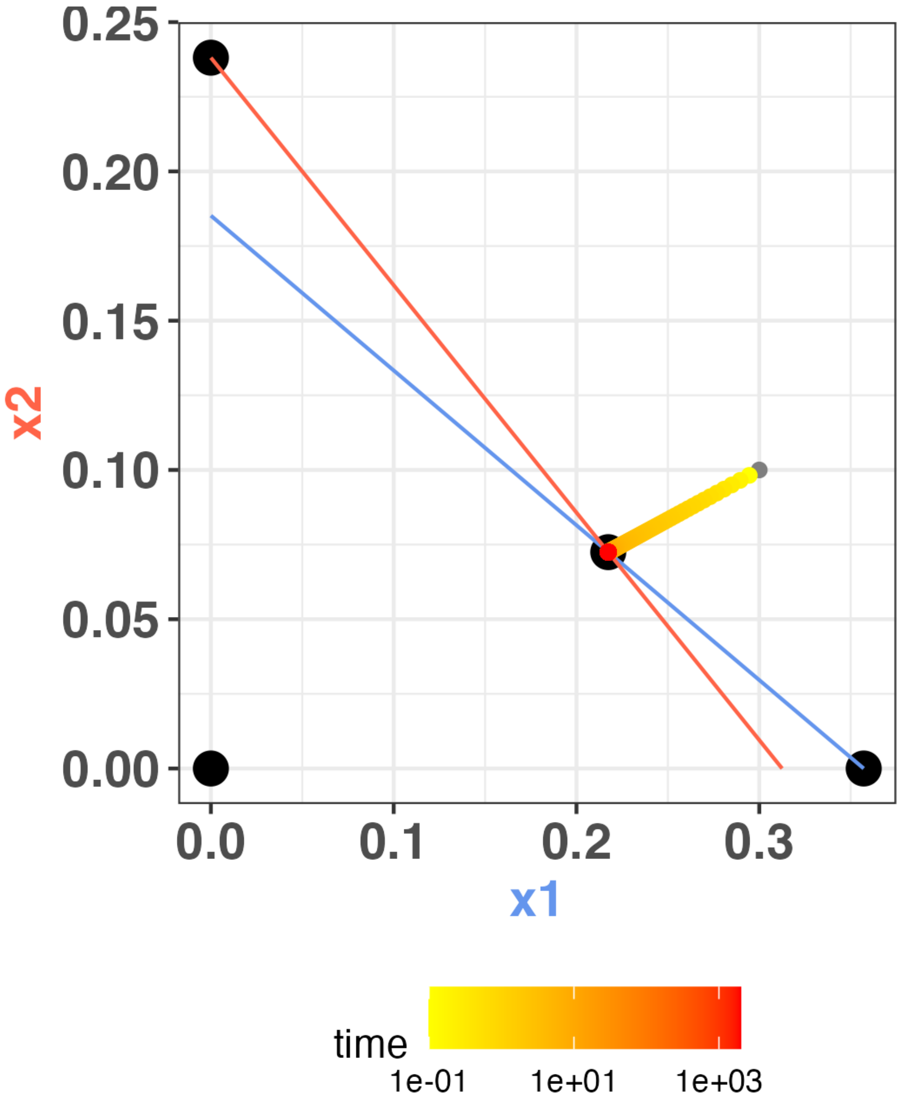


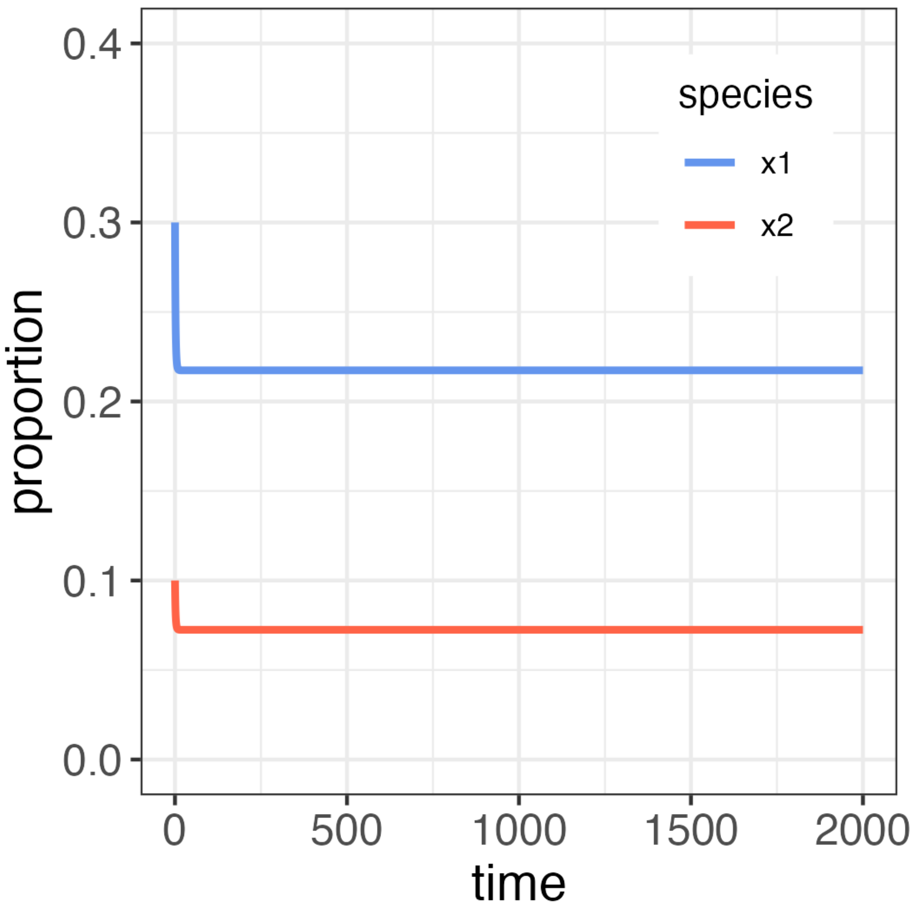
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

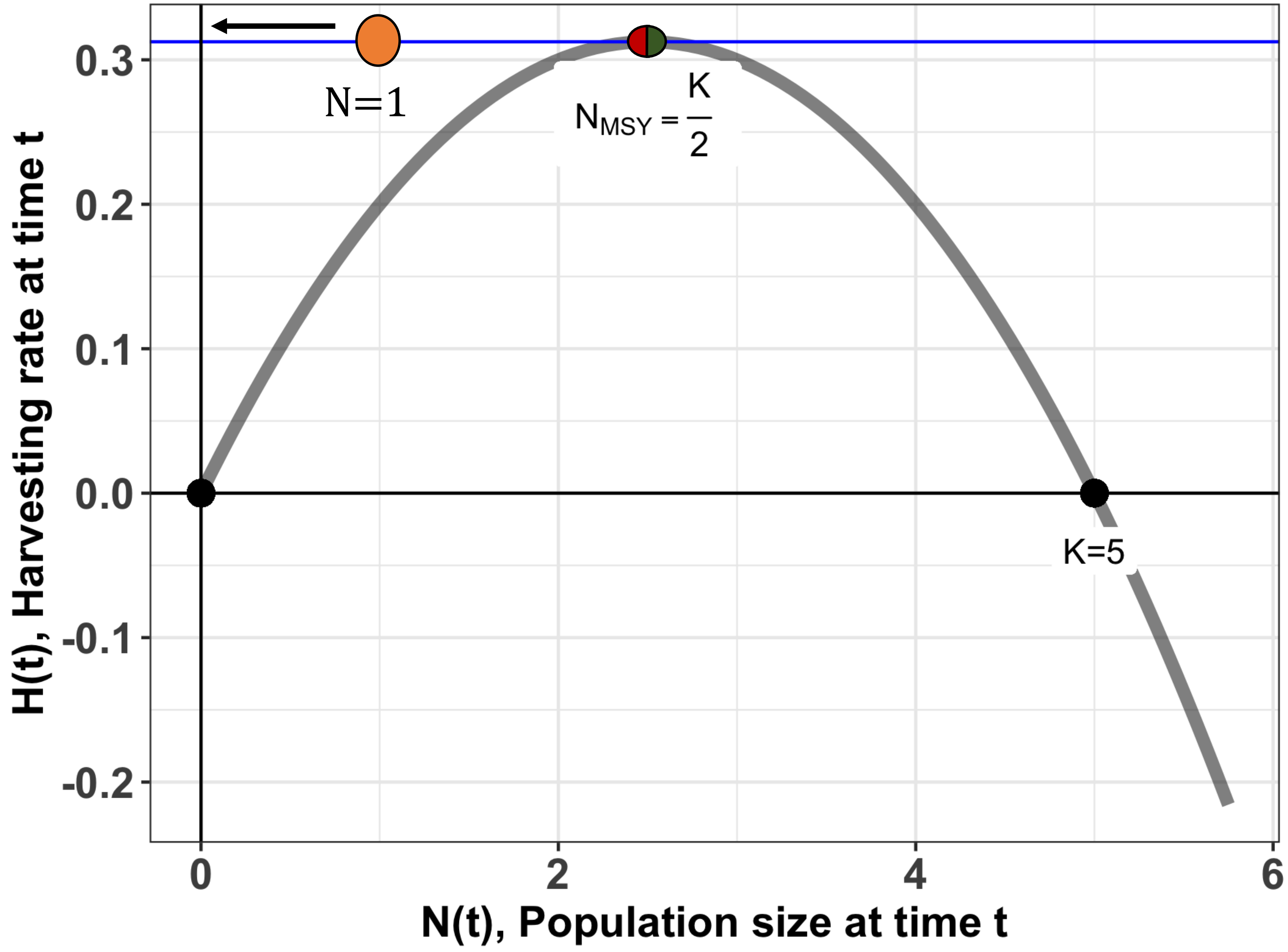
Here, **coexistence**





Remember MSY, the semi-stable equilibrium:

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



K=5
r=0.25
H=.3125

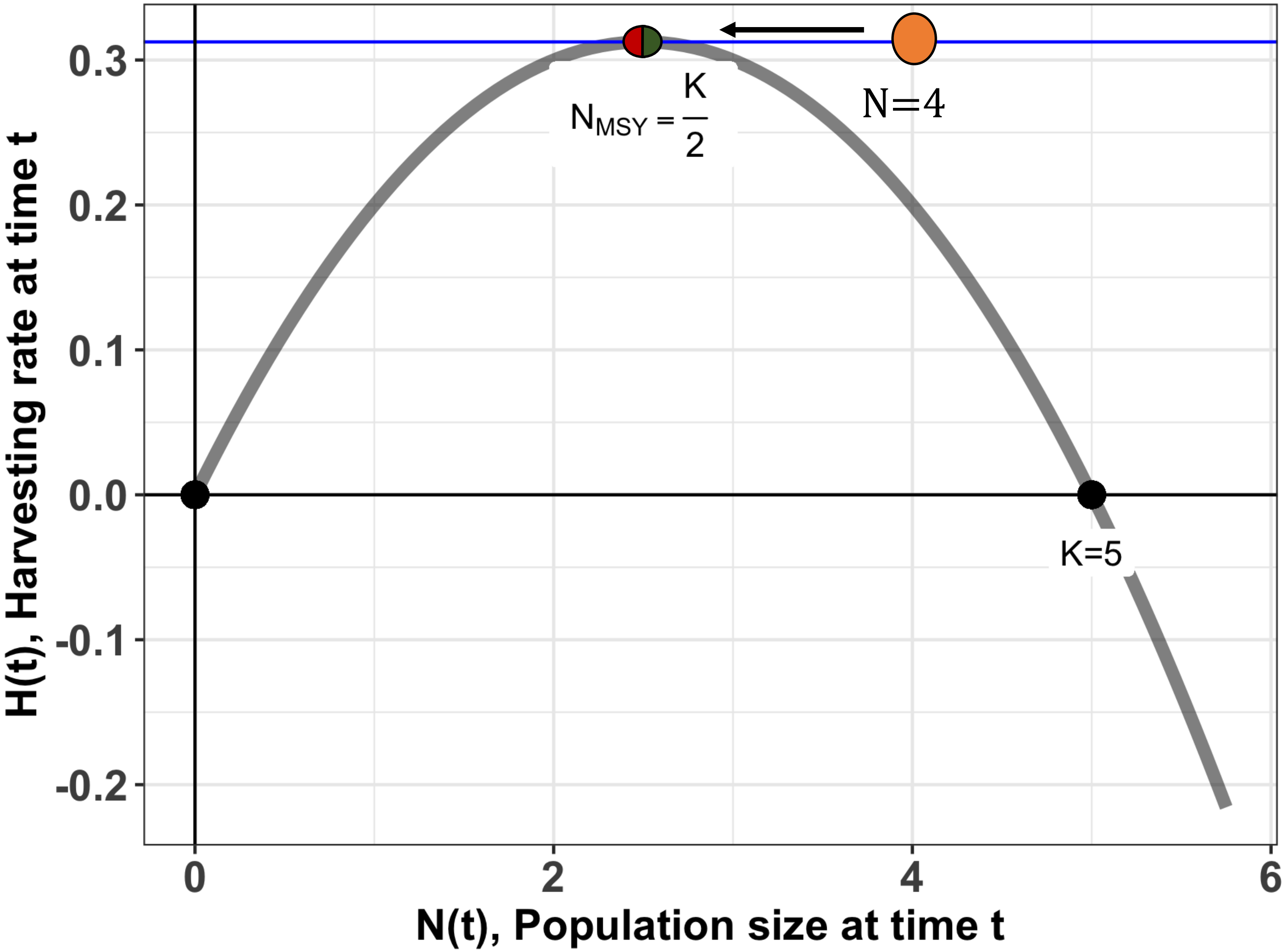
$$\frac{dN}{dt} = 0.25 * 1\left(1 - \frac{1}{5}\right) - .3125$$

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

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

Remember MSY, the semi-stable equilibrium:

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



K=5

r=0.25

H=.3125

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

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

Four possible outcomes for competition

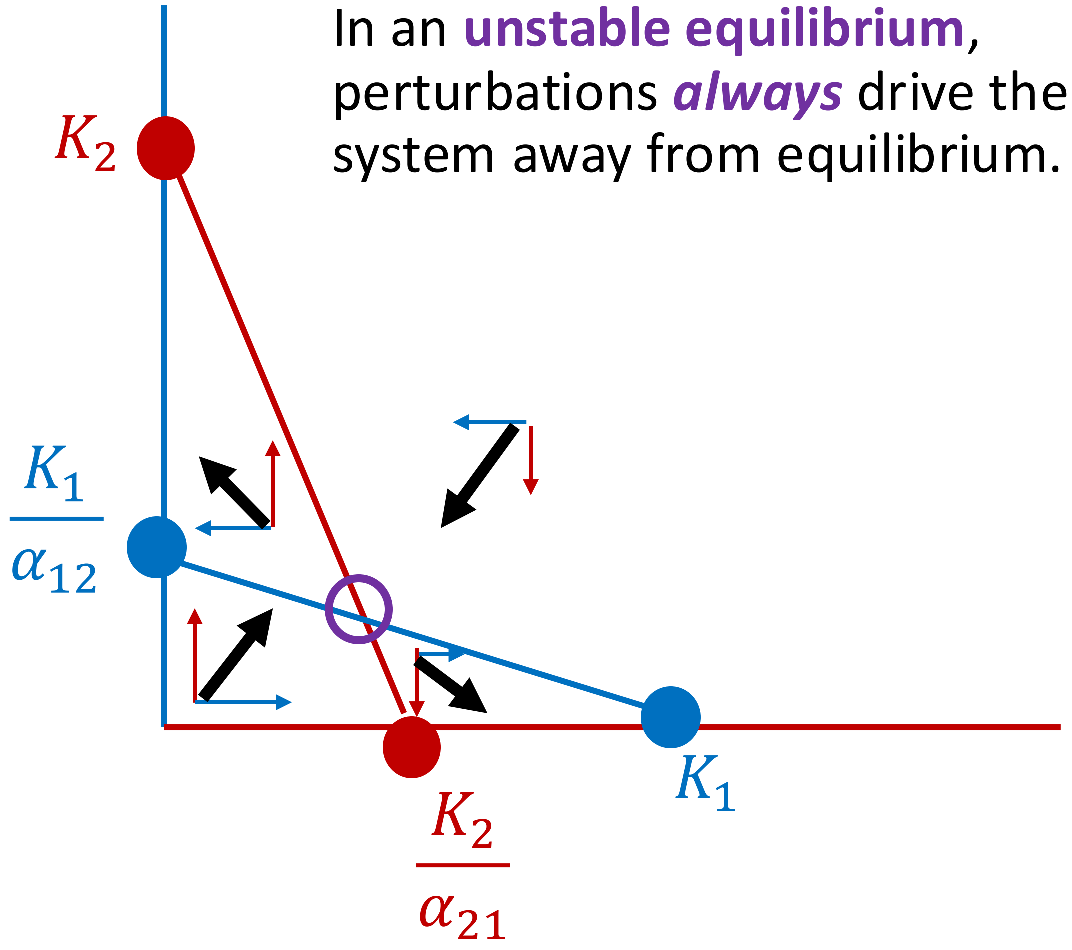
Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

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

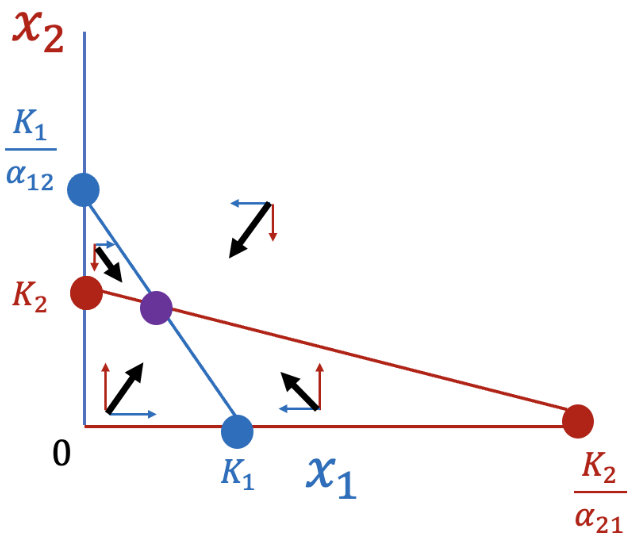
$$(\alpha_{12} * \alpha_{21} > 1)$$



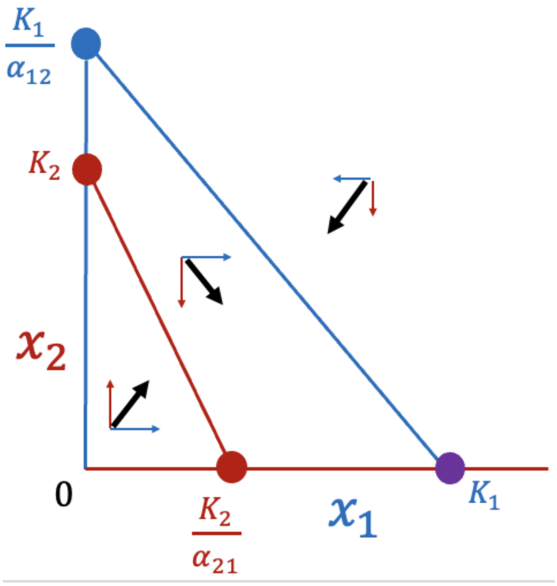
In an **unstable equilibrium**, perturbations ***always*** drive the system away from equilibrium.

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

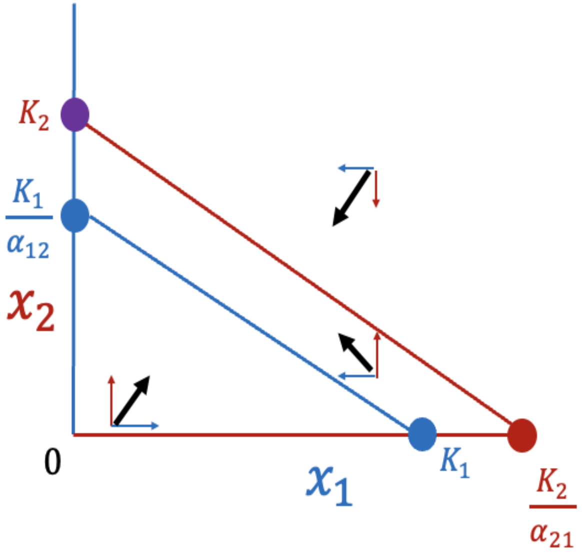
Case 1: Stable coexistence



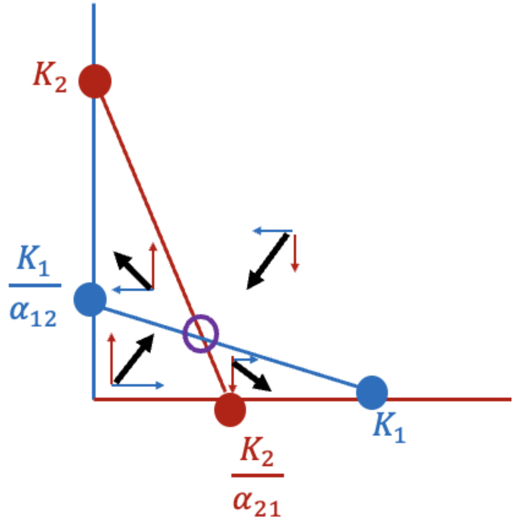
Case 2: Spp. 1 wins



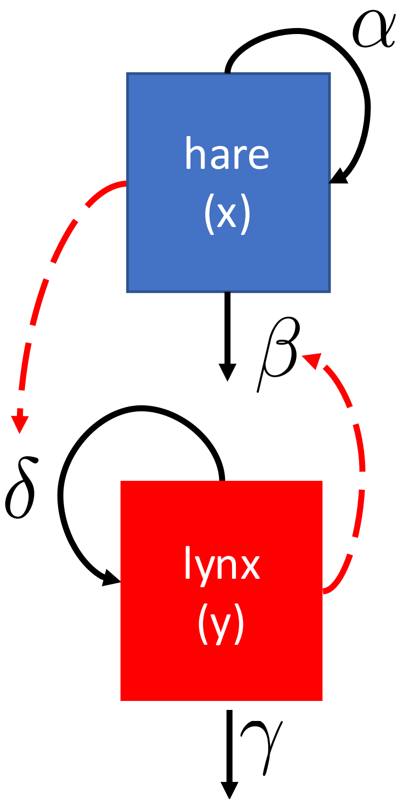
Case 3: Spp. 2 wins



Case 4: Precedence



Note the difference with a predator-prey model!

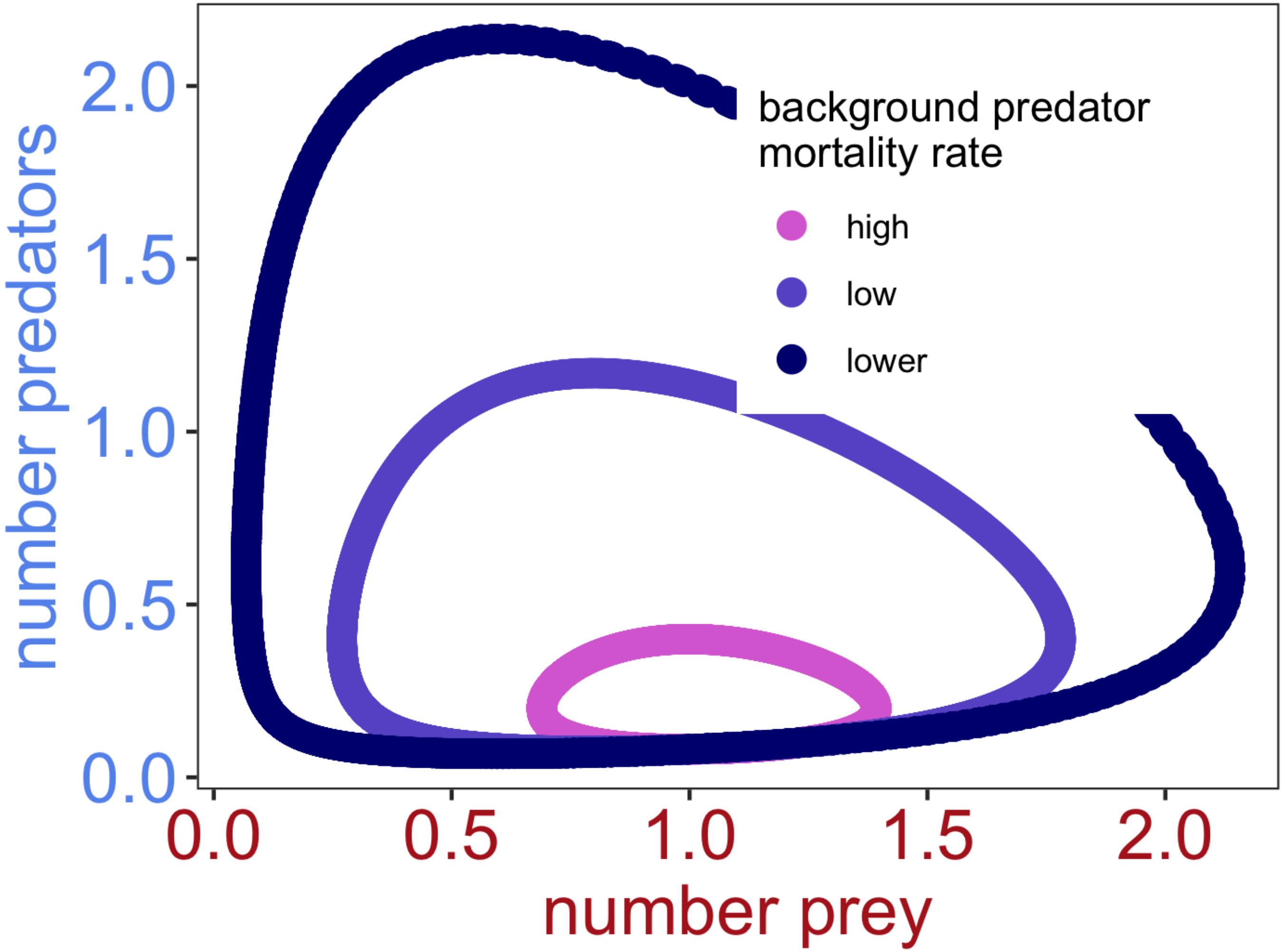


$$\frac{dx}{dt} = \alpha x \; - \beta x y$$

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

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

Predator-prey cycles can be visualized as oscillations.



Phase plane analysis: Why do we care?

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

Principle of **competitive exclusion**

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

- Joseph Grinnell, 1904:

Museum of Vertebrate Zoology

University of California at Berkeley

"Neither can live while the other survives."

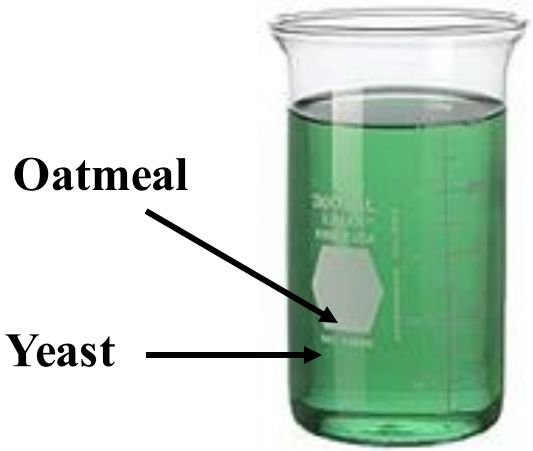
- J.K. Rowling, 2003

Principle of **competitive exclusion**

Paramecium aurelia

Paramecium caudatum

Paramecium bursaria



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

Gause first grew each species in isolation

Paramecium aurelia

Paramecium caudatum

Paramecium bursaria

Gause 1934. *J Experimental Biology.*

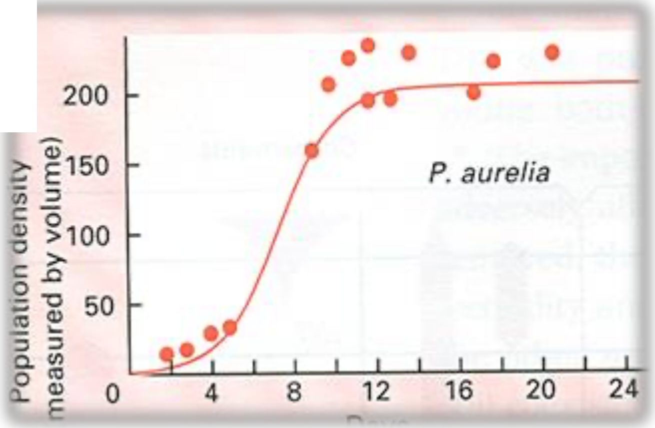
Gause 1935. *Science.*

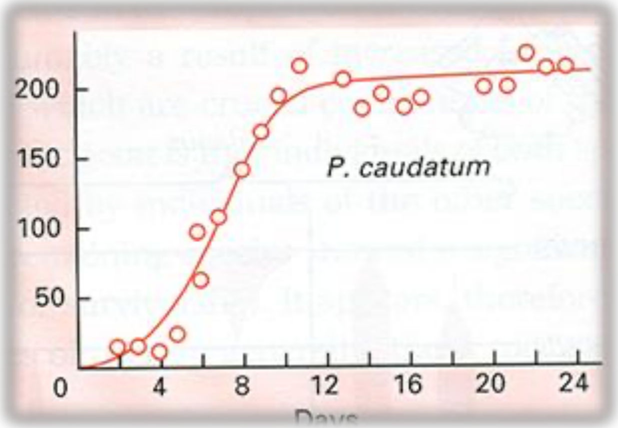
In isolation, each species grew logistically.

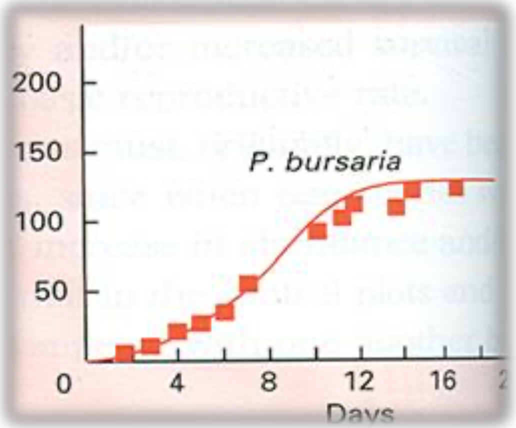
Paramecium aurelia

Paramecium caudatum

Paramecium bursaria







Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

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

Paramecium aurelia

Paramecium caudatum

Paramecium caudatum

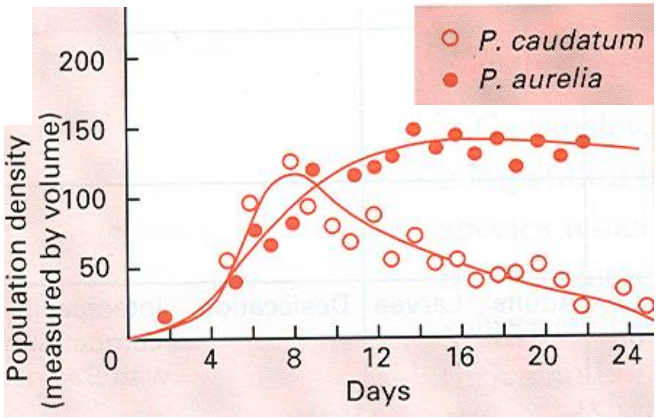
Paramecium bursaria

Gause 1934. *J Experimental Biology.*

Gause 1935. *Science*.

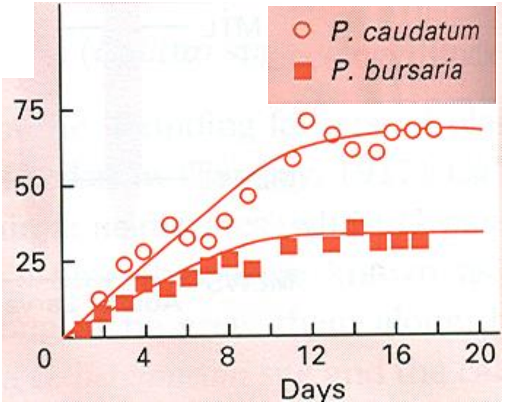
Competitive exclusion was observed:

Paramecium aurelia ***Paramecium caudatum***



Coexistence was observed:

Paramecium caudatum ***Paramecium bursaria***

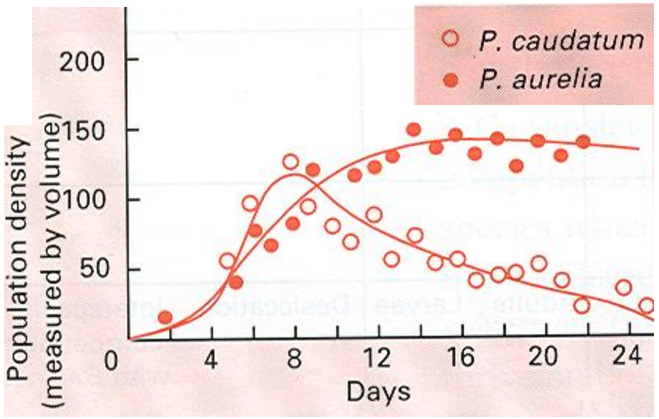


Gause 1934. *J Experimental Biology.*
Gause 1935. *Science.*

Competitive exclusion was observed:

Paramecium aurelia

Paramecium caudatum

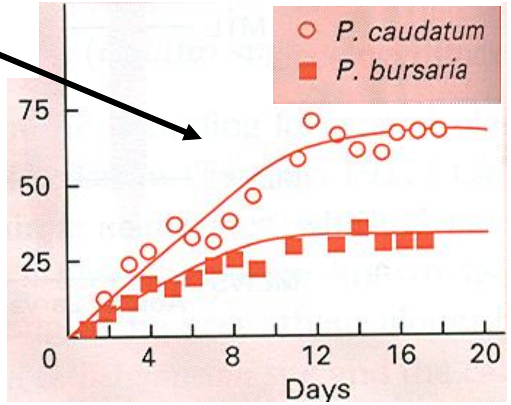


Coexistence was observed:

Paramecium caudatum

Paramecium bursaria

Species coexisted below each species' respective individual carrying capacity.



Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

Competitive exclusion was observed:

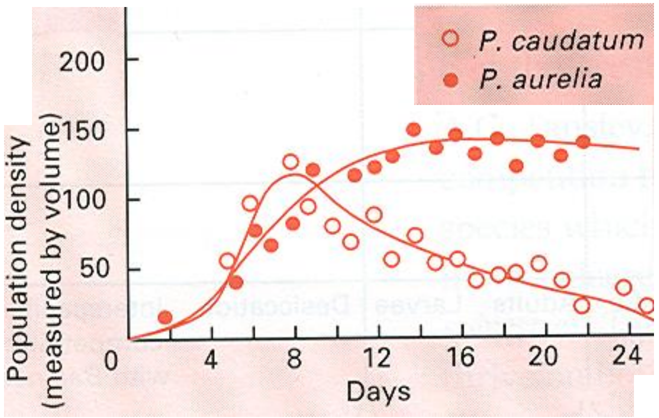
Coexistence was observed:

Paramecium aurelia

Paramecium caudatum

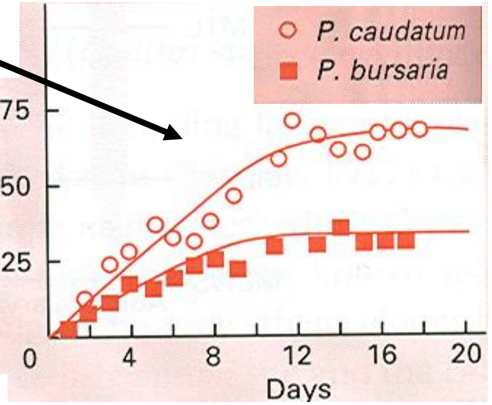
Paramecium caudatum

Paramecium bursaria



Species coexisted below each species' respective individual carrying capacity.

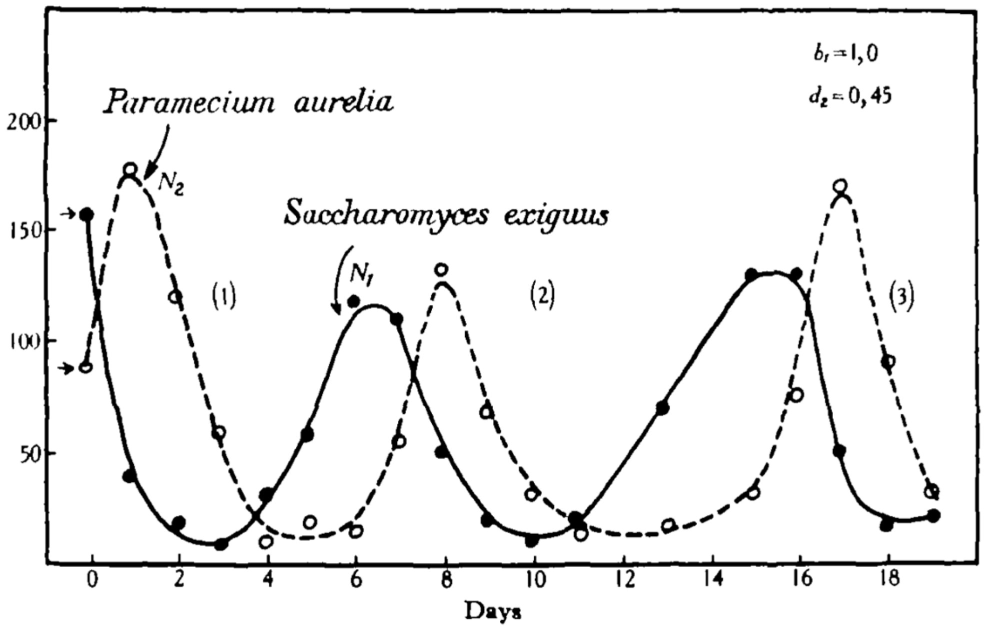
The two coexisting species were largely partitioned in space. *P. bursaria* ate yeast at the bottom and *P. caudatum* consumed bacteria suspended in the medium.

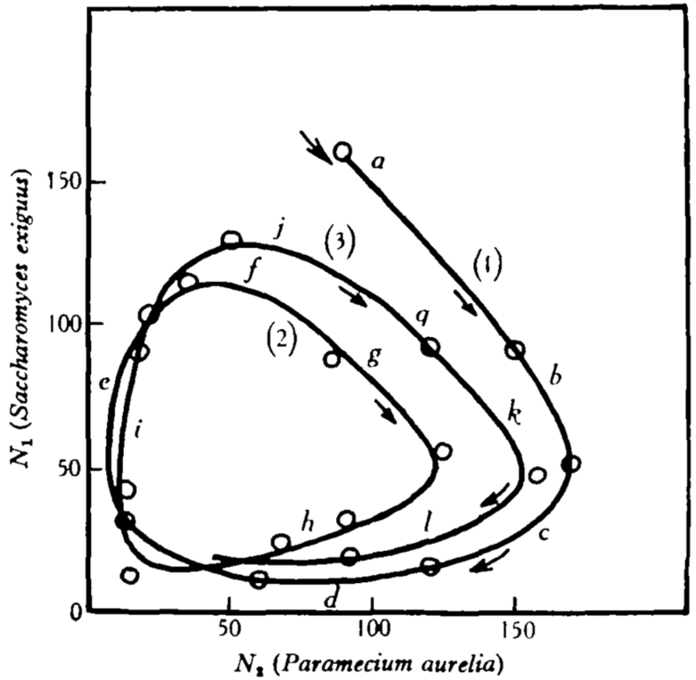


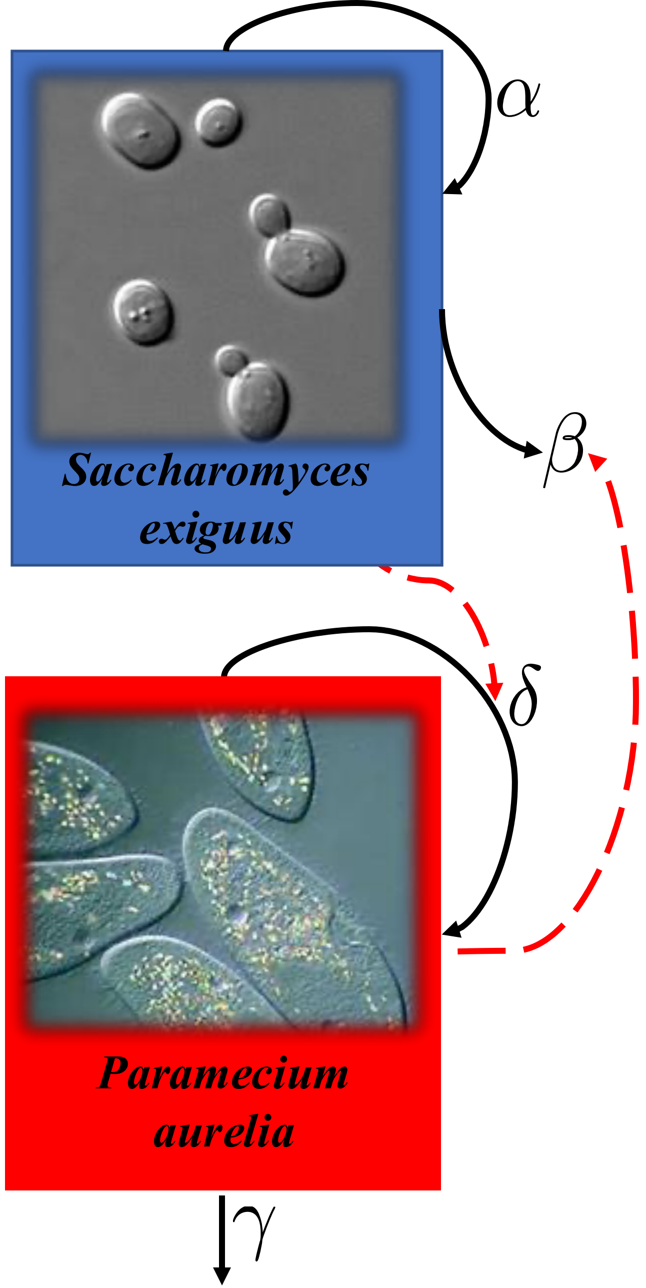
Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

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







Gause 1935. *Science*.