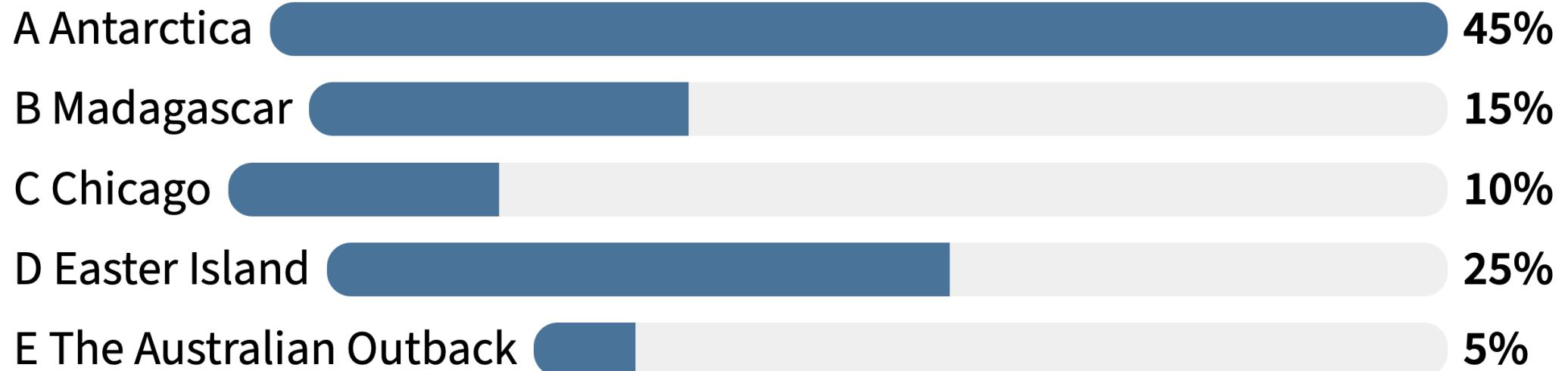




# Which location is the best place to avoid COVID-19?



# Fundamentals of Ecology

Week 7, Ecology Lecture 5

Cara Brook

February 20, 2025

**Office hours: On ZOOM**

**Friday, Feb 21, 2025**

**4-5pm**

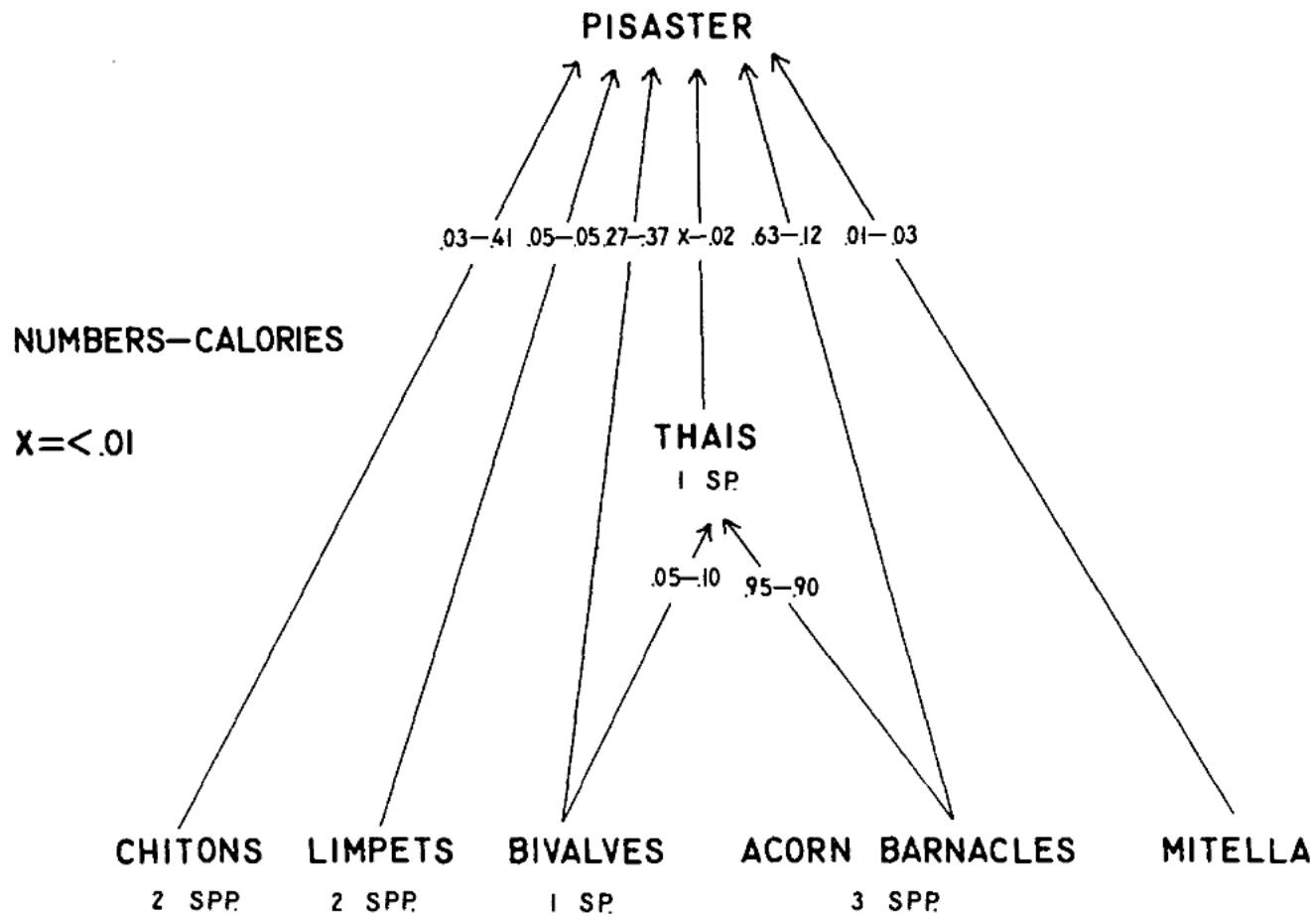
***I will email out a link!***

# Learning objectives from Lecture 4

*You should be able to:*

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

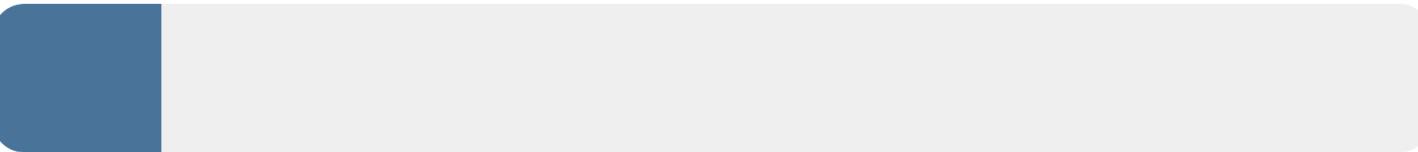
This work inspired empirical studies on **trophic cascades**:  
*Pisaster* removal on Tatoosh Island





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

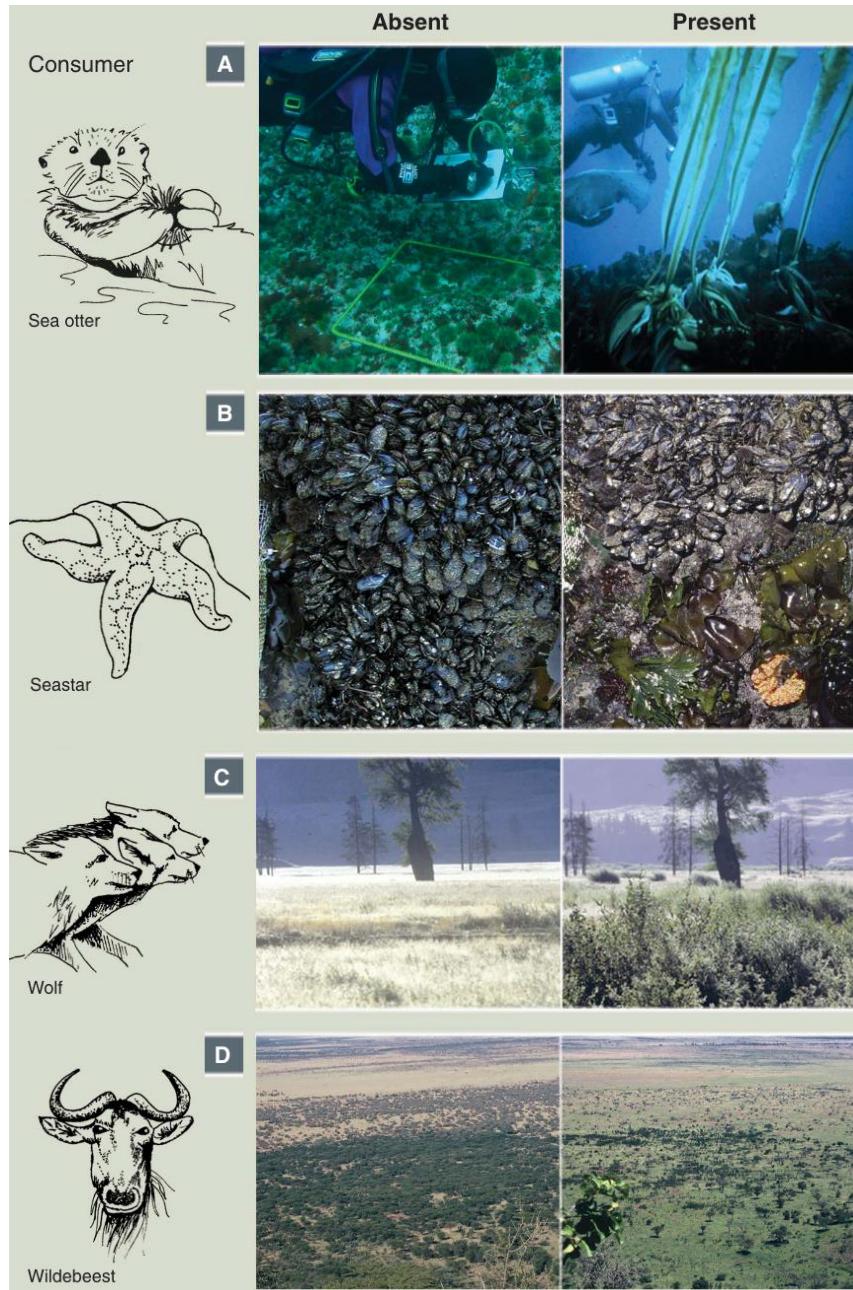
- A. Lion and zebra populations cyclically track one another in population booms and busts in the...



10%

# Other famous **trophic cascades**:

Estes et al. 2011. *Science*.

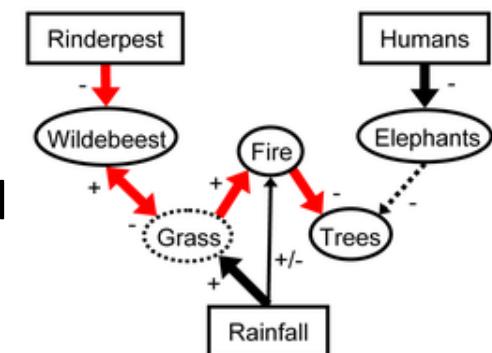


CA sea otters maintain kelp forest diversity by consuming herbivorous sea urchins. (Estes & Duggins 1995. *Ecological Monographs*)

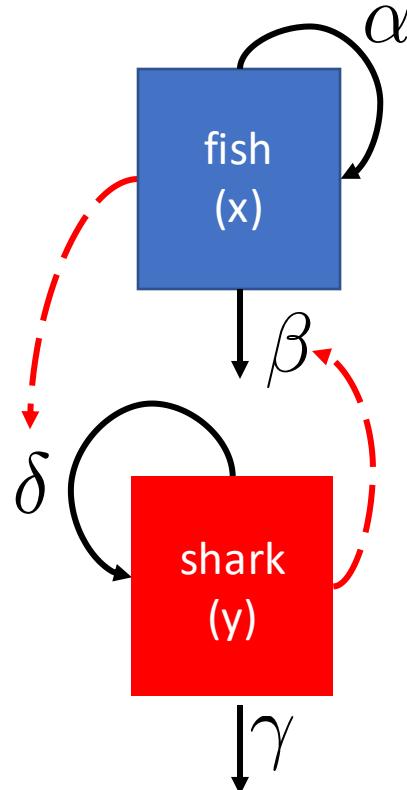
Starfish maintain diversity in Pacific intertidal by consuming space-dominating mussels. (Paine 1966 *The American Naturalist*)

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

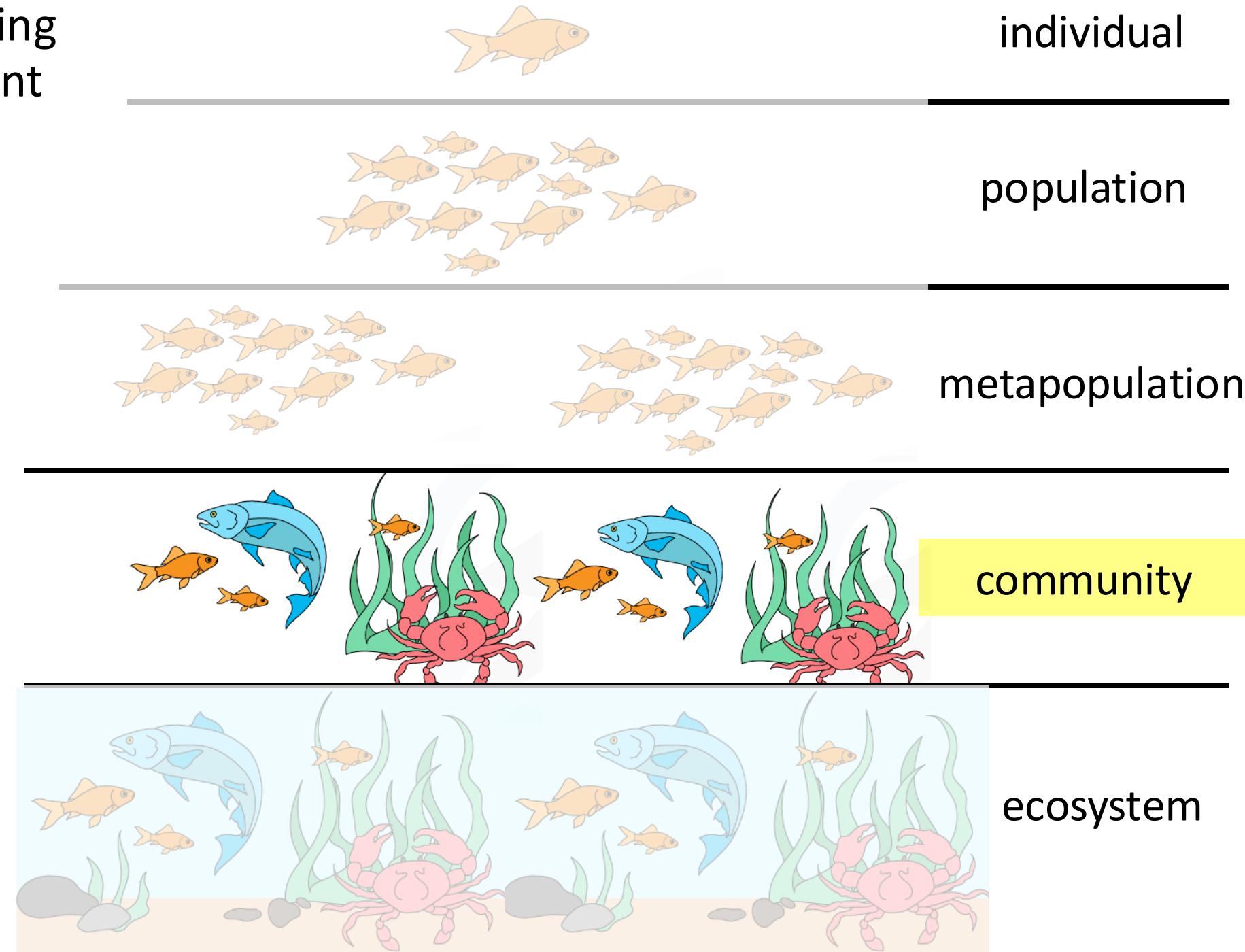
Rinderpest eradication releases wildebeest populations that control savanna, limit fire, and promote tree regrowth (Holdo et al. 2009. *PLoS Biology*)



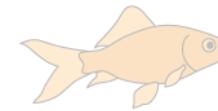
**Community** = interacting populations of different species



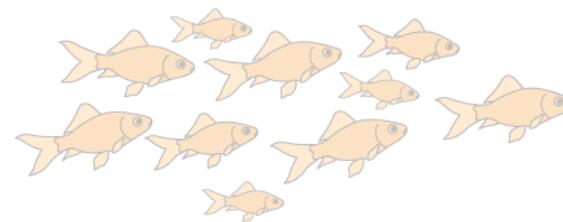
How does fish abundance **vary** with changes in shark abundance?



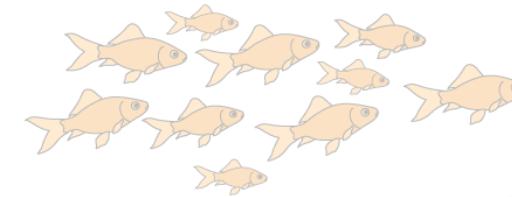
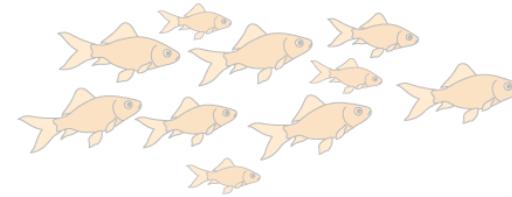
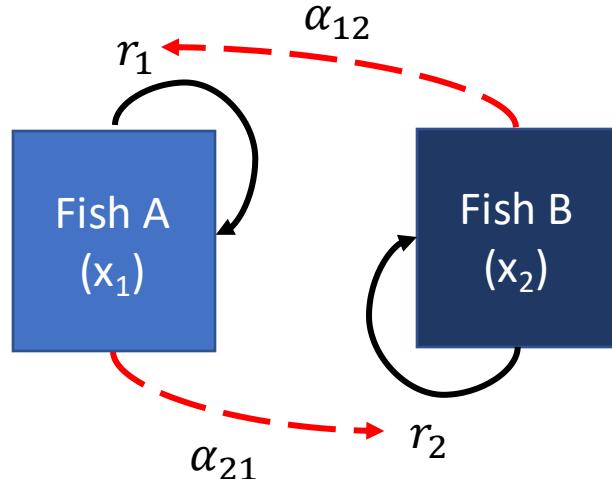
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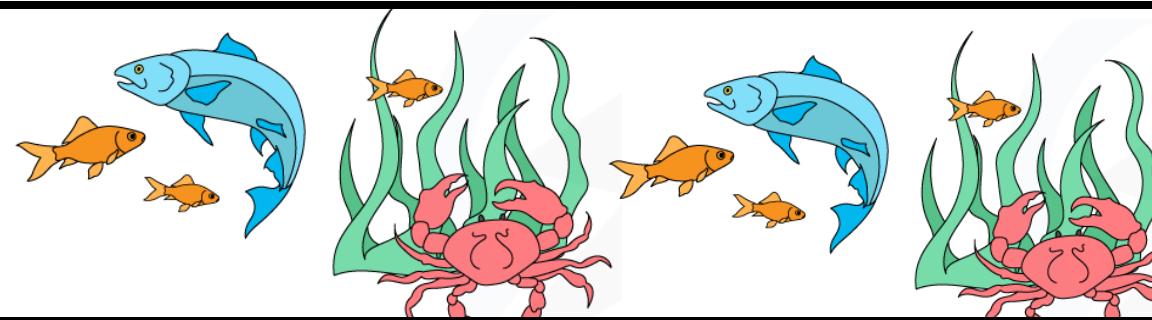
individual



population

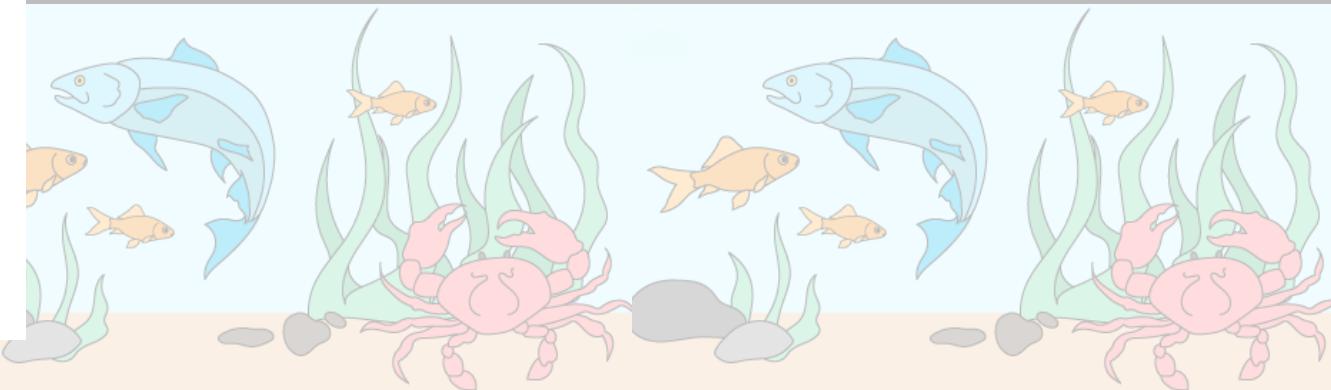


metapopulation



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**.

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

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

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

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intraspecies competition  
of species 1 (akin to  
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intraspecies competition  
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Each species is **self-regulated** by logistic growth and its own carrying capacity (**K**) and growth rate (**r**).

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

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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).

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

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

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

Remember: equilibrium occurs when  
neither population is changing!

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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:

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

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

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

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

Coexistence.



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

01:00

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

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

A) Species 1 on its o...

6%

B) Species 2 on its o...

0%

C) Species 1 on the growth...

4%

D) Species 2 on the growth...

91%



Instructions

Responses

Correctness

More



Clear responses

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

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

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

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

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

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*big*

*x*<sub>2</sub>

0

*x*<sub>1</sub>

*big*

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big

$x_2$

0

$x_1$

big

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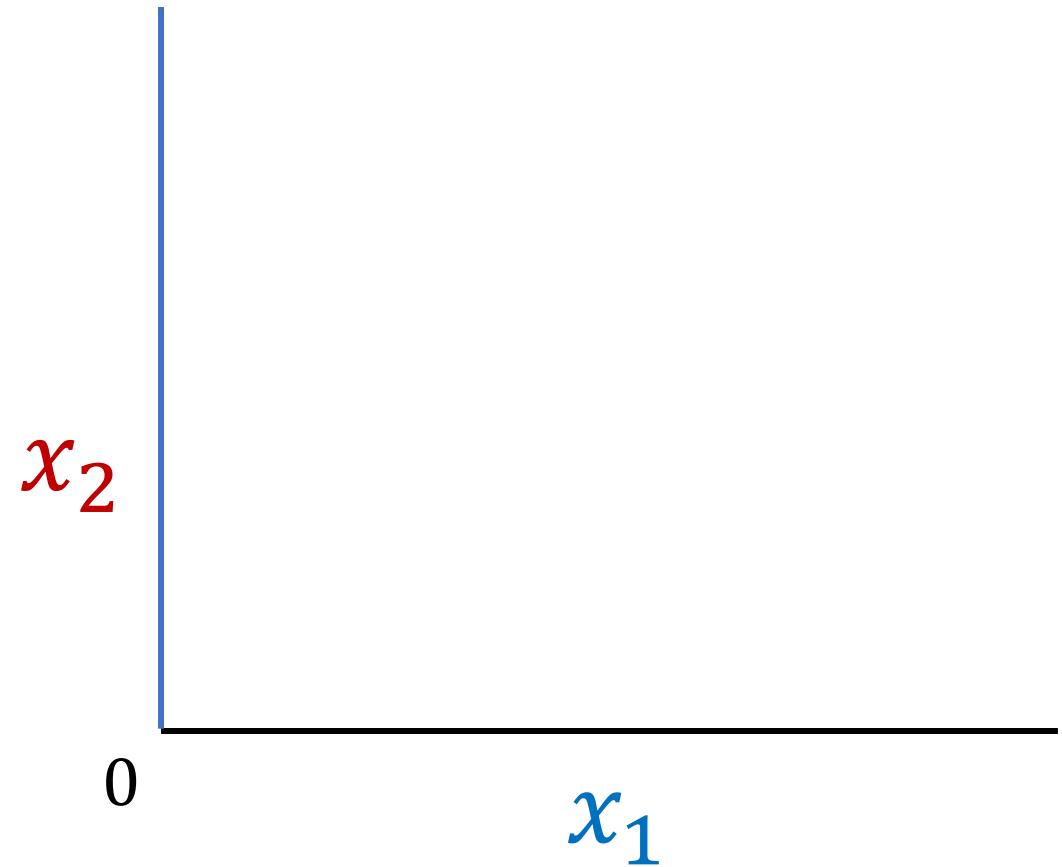
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first nullcline at  $x_1 = 0$



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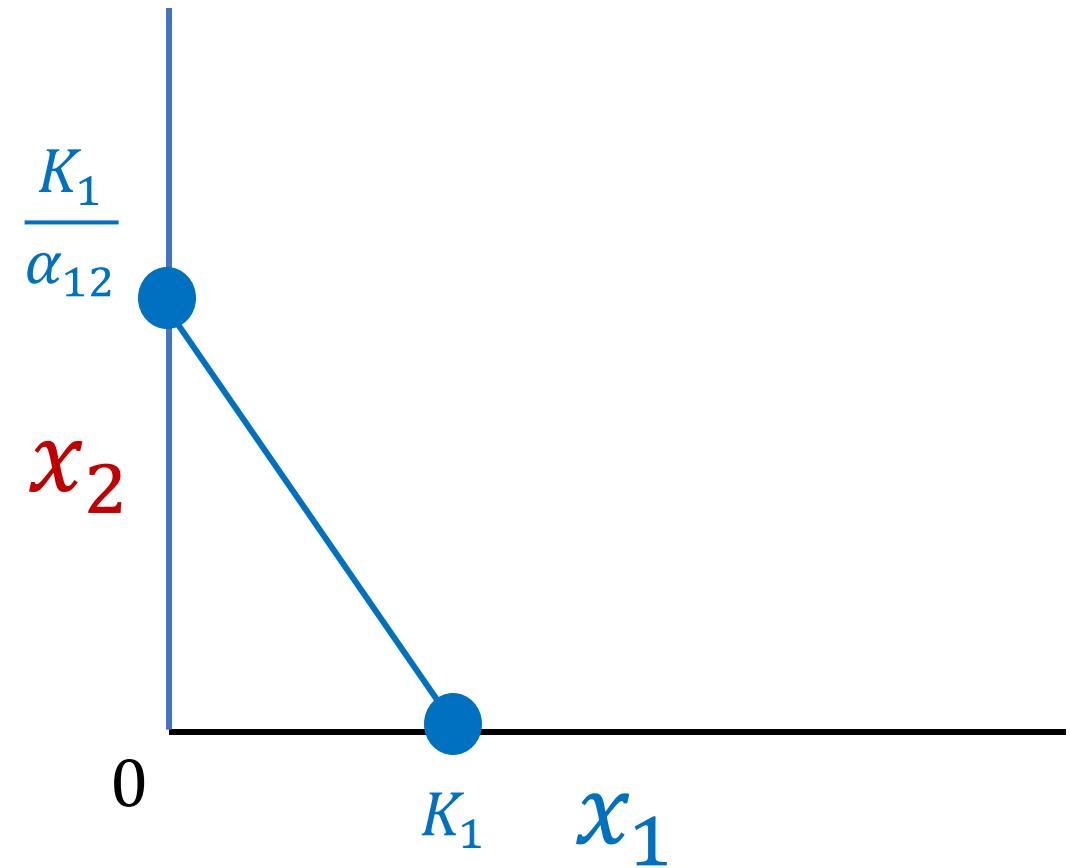
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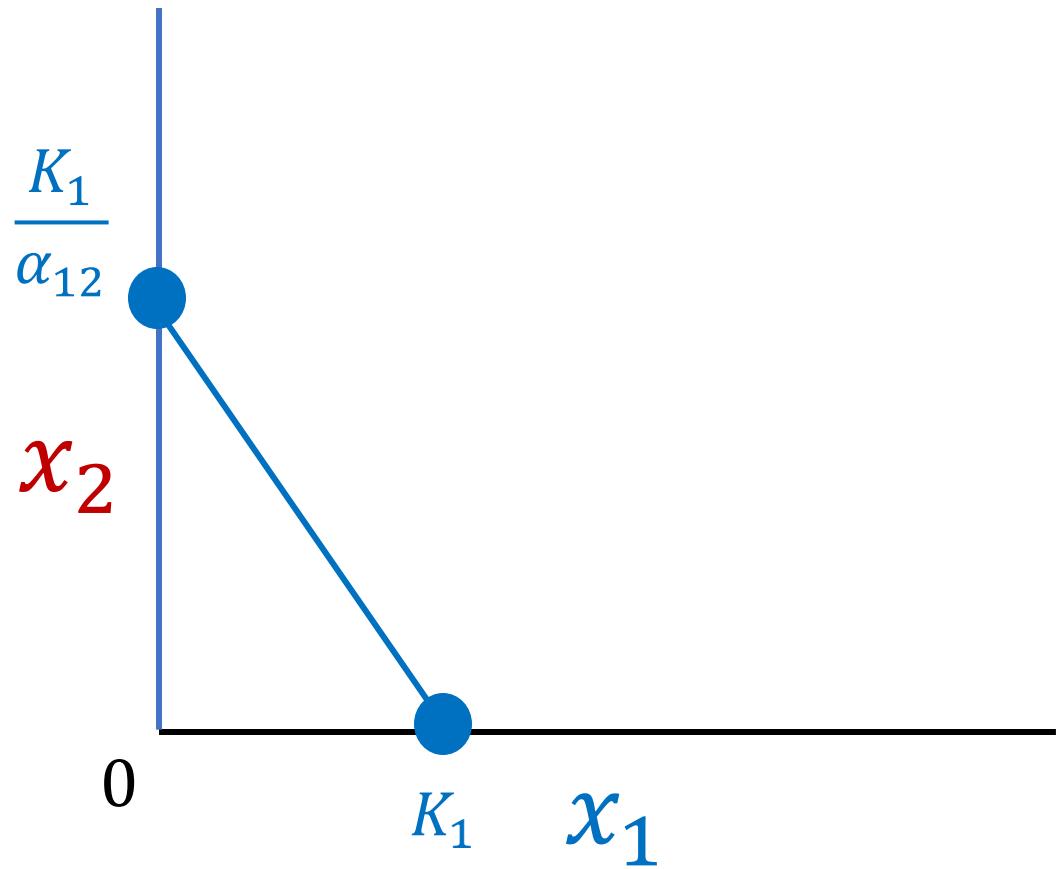
first nullcline at  $x_1 = 0$

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



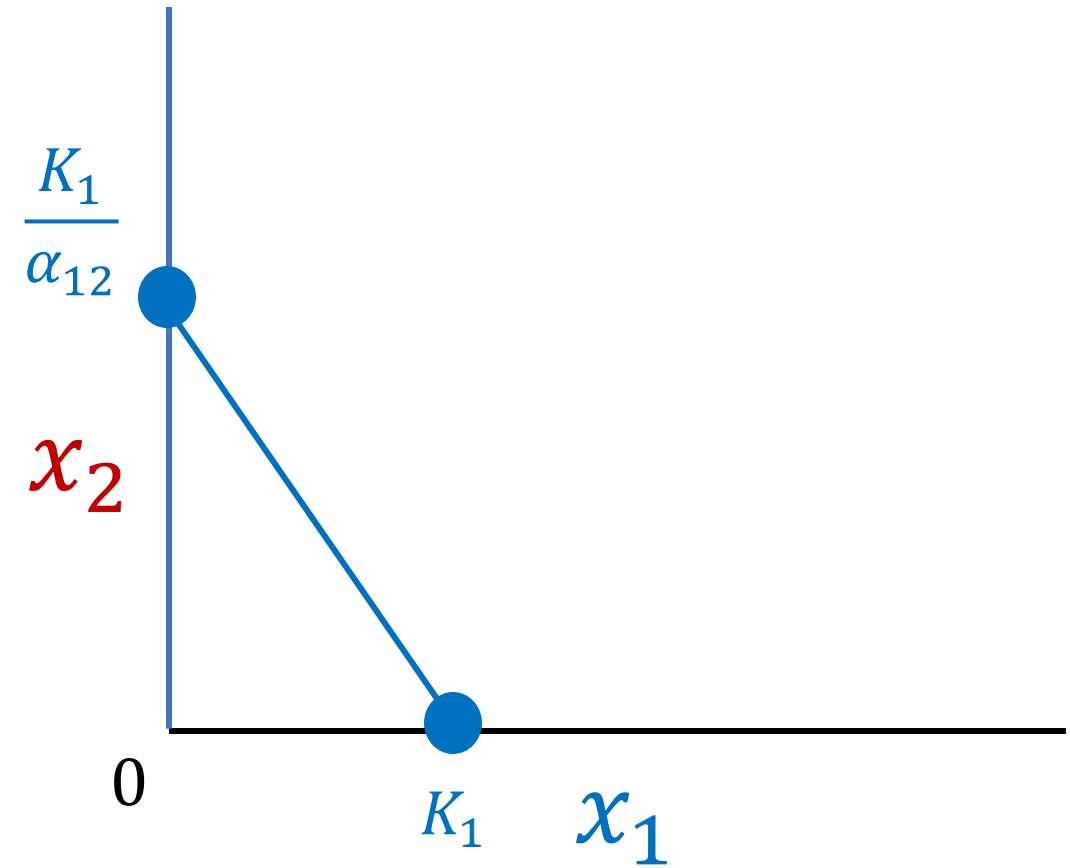
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- Following a perturbation, the population should return to equilibrium!



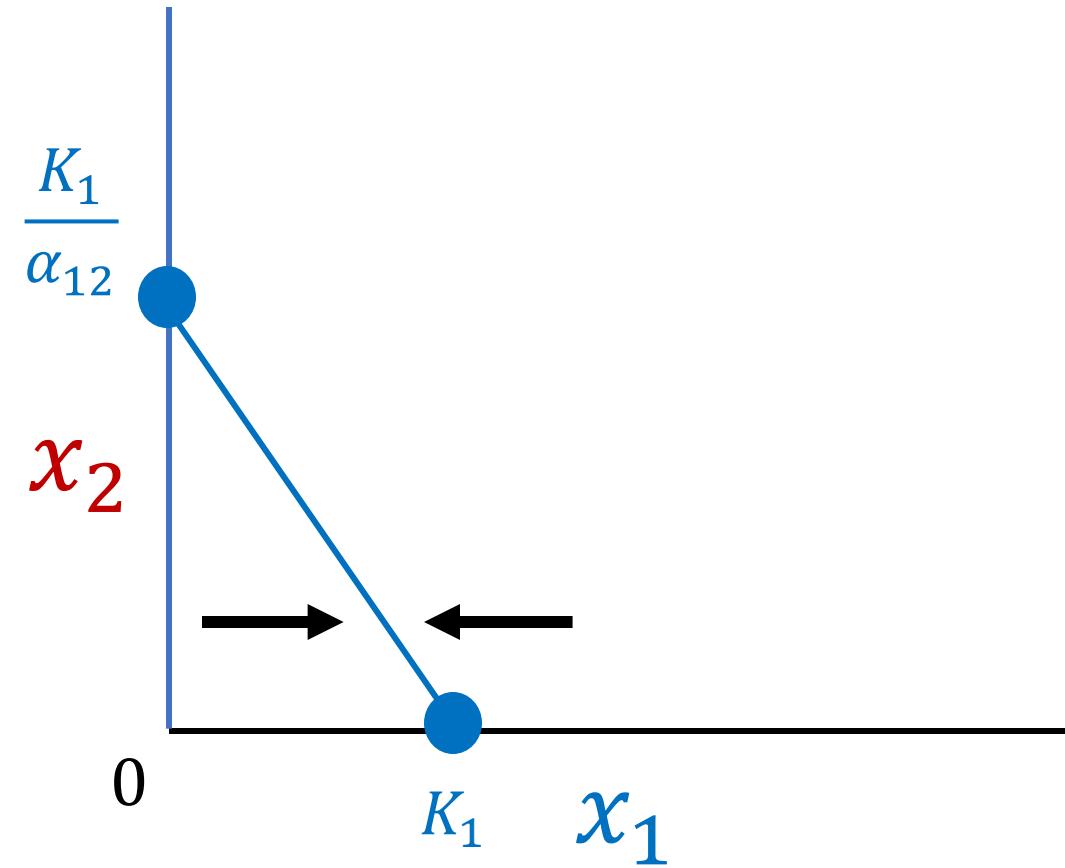
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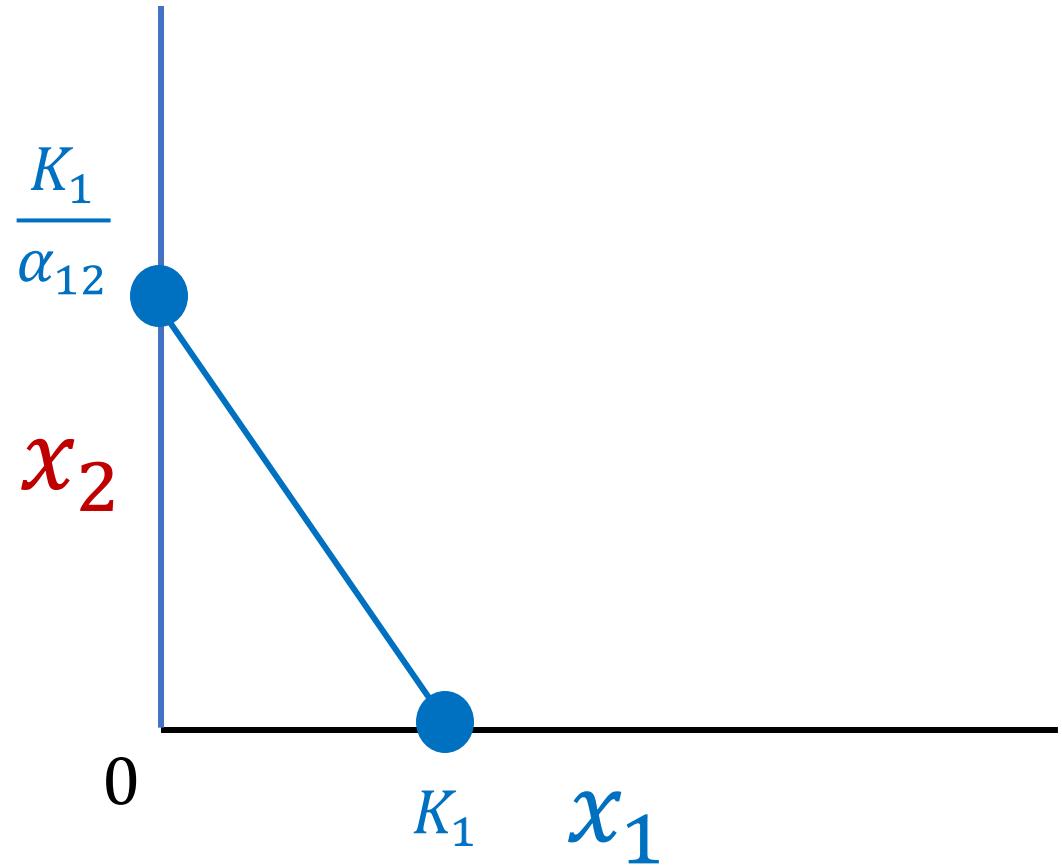
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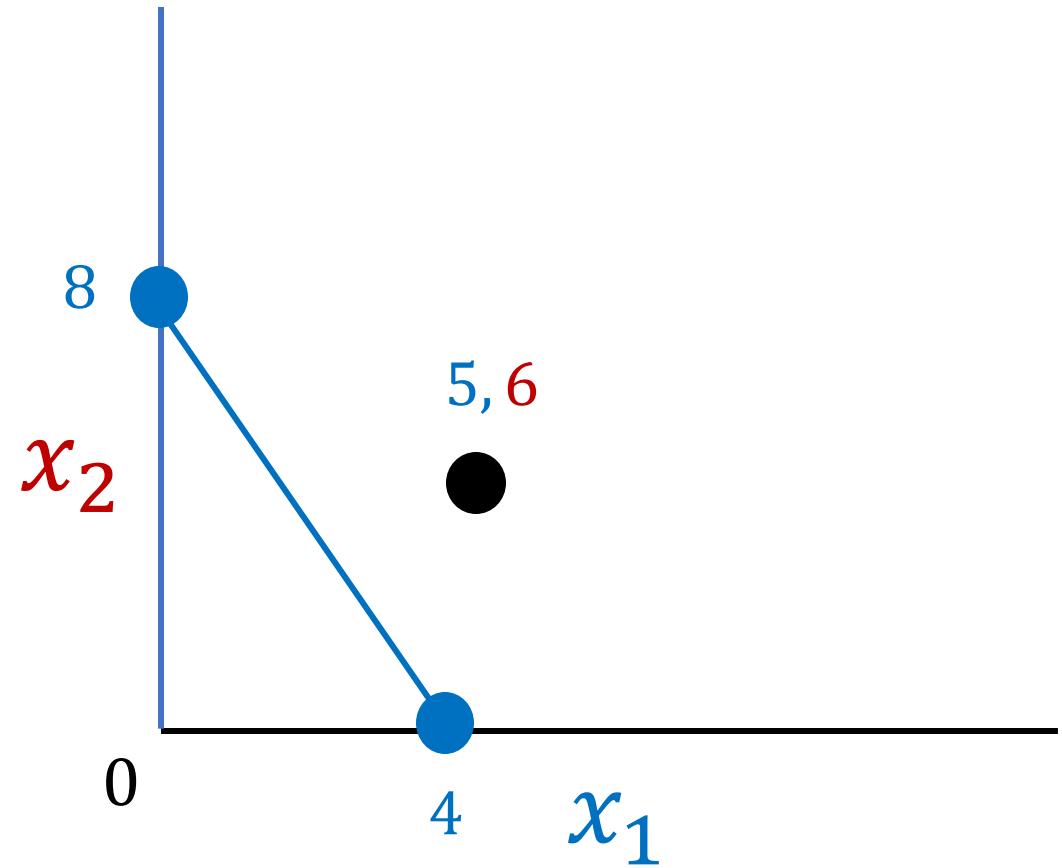
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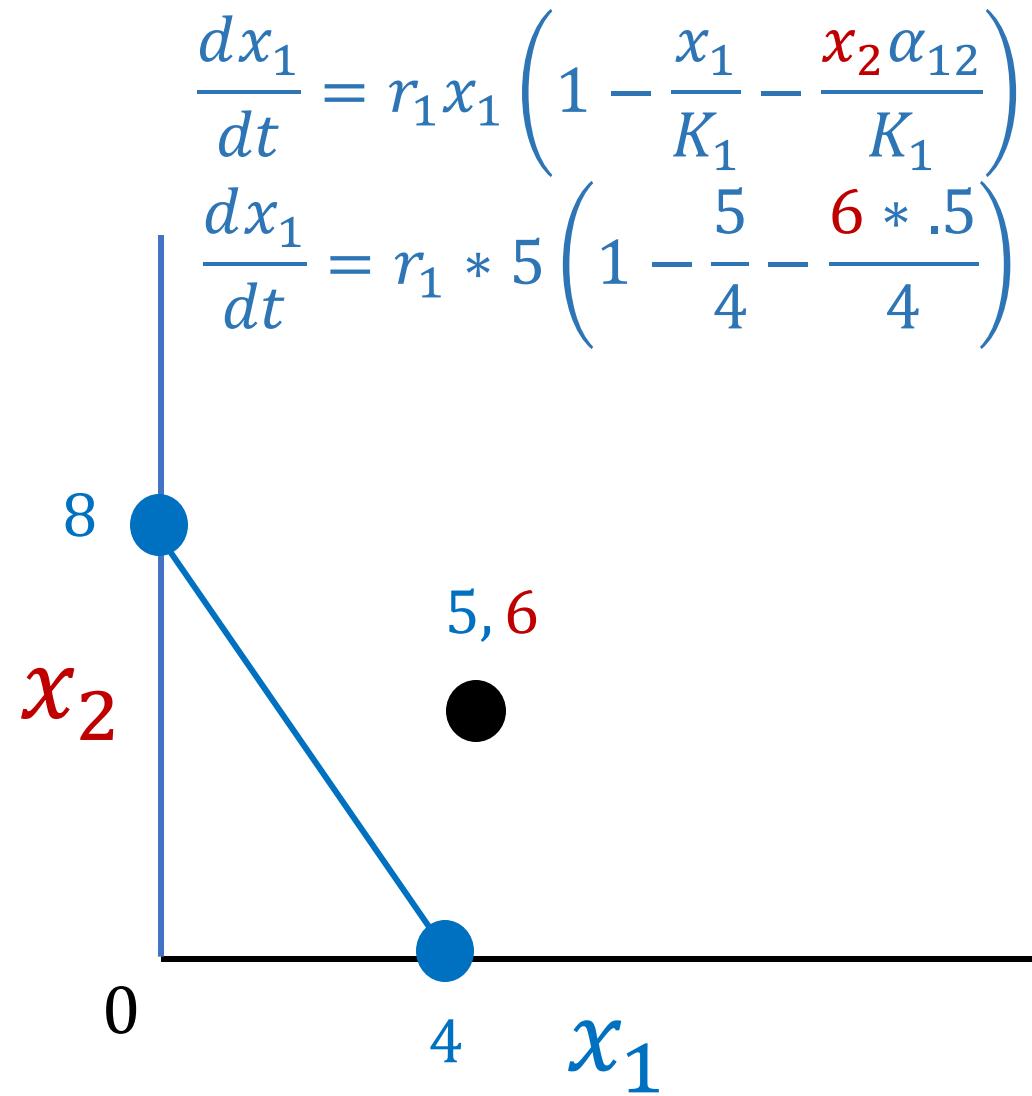
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- $K_1 = 4 ; \alpha_{12} = .5$

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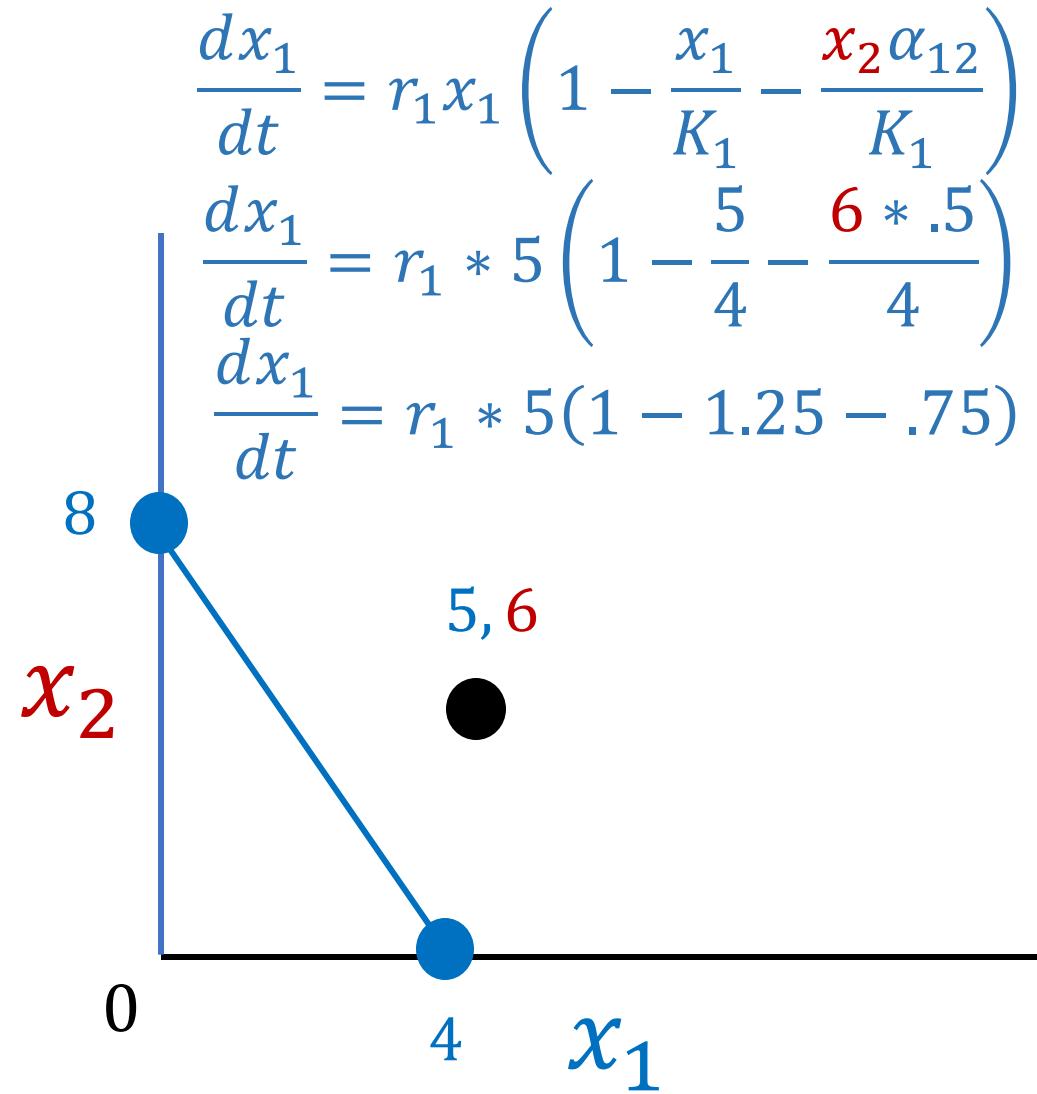
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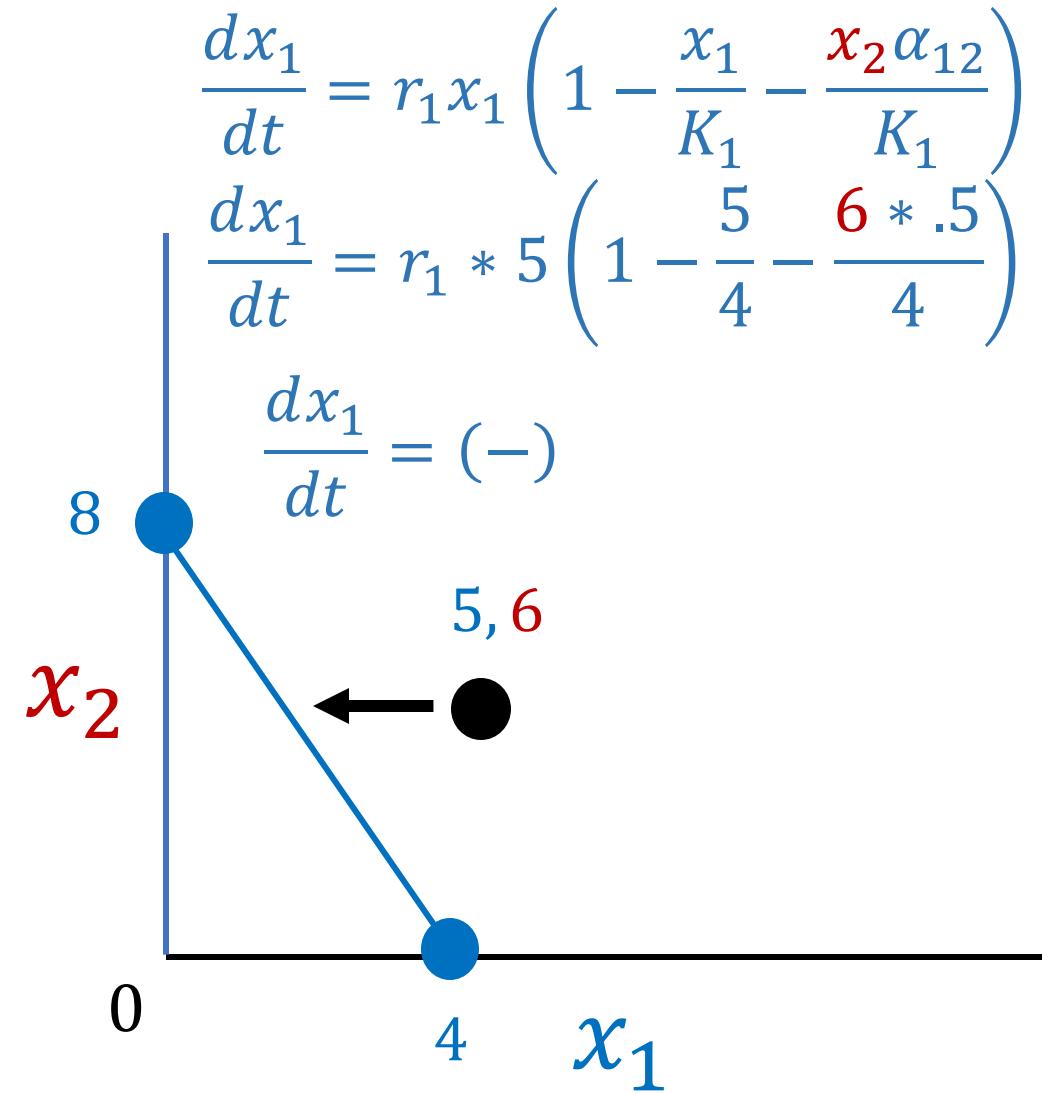
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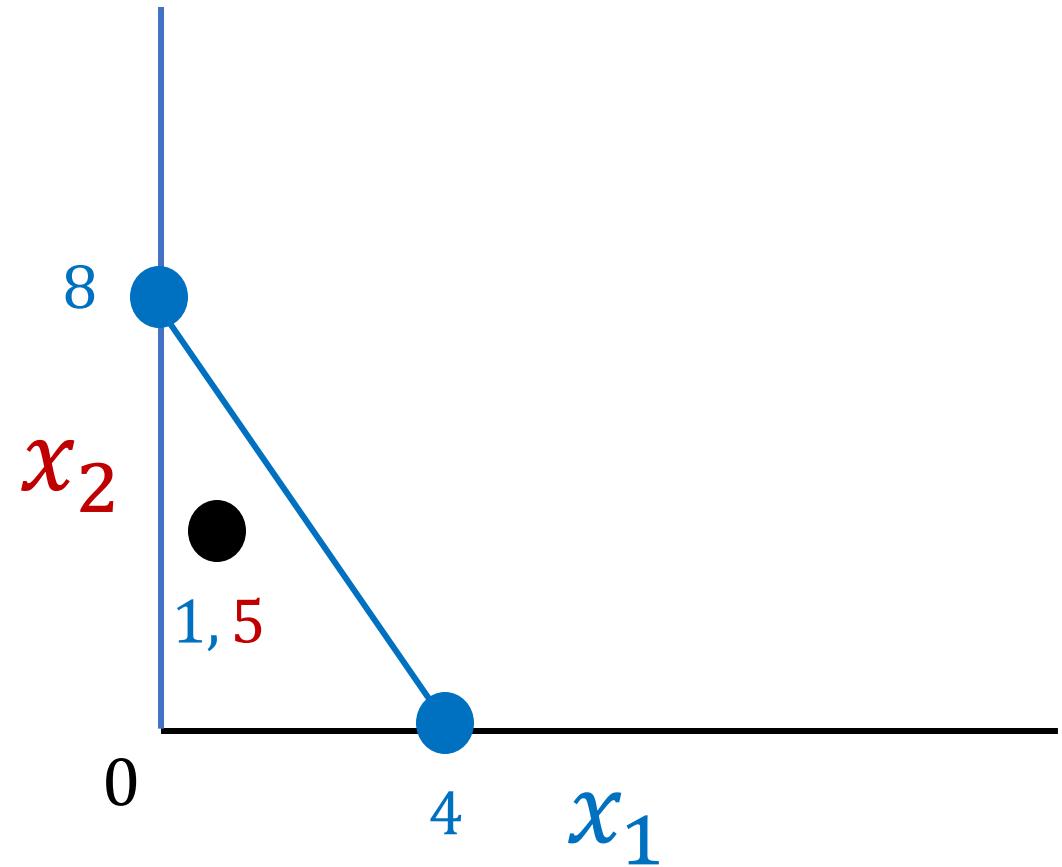
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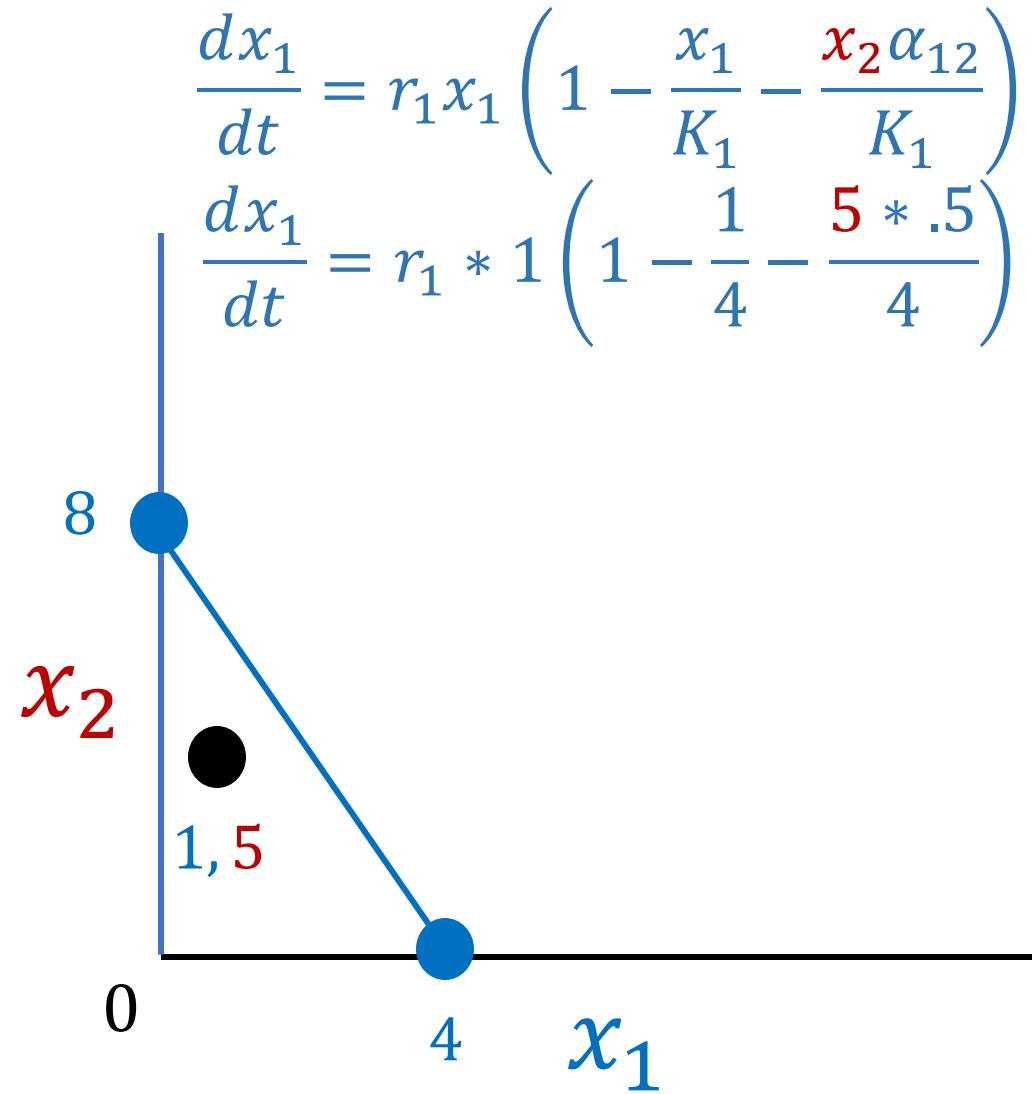
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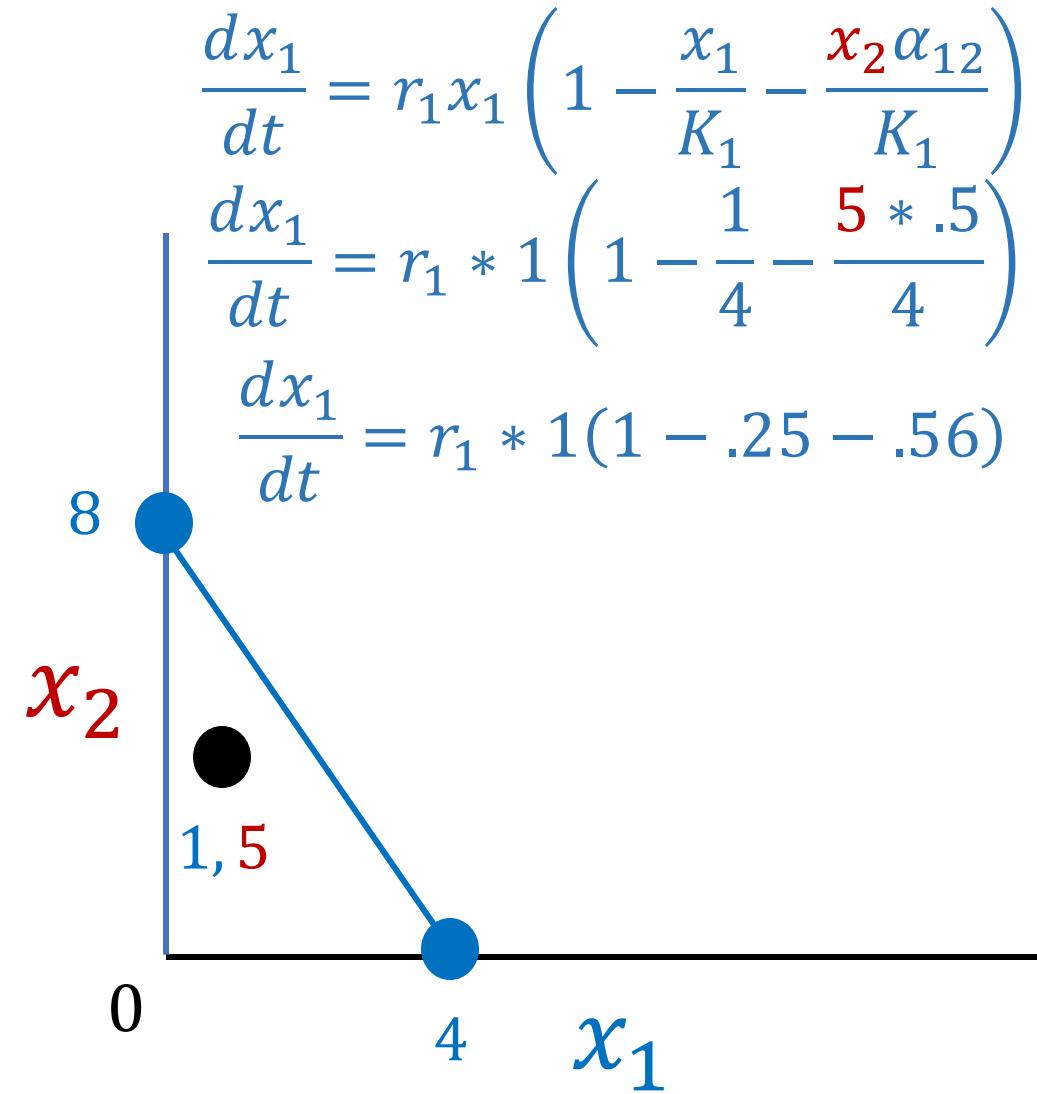
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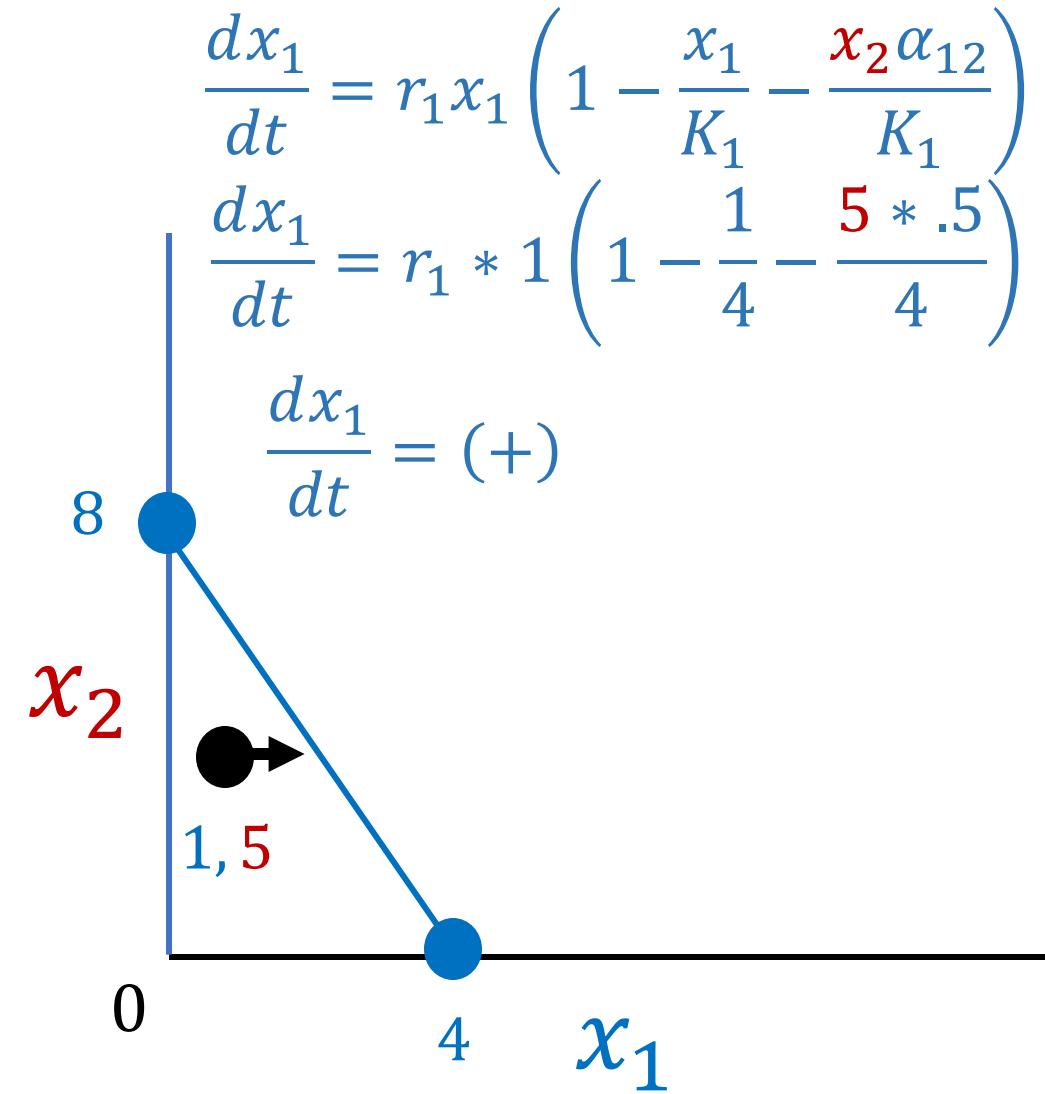
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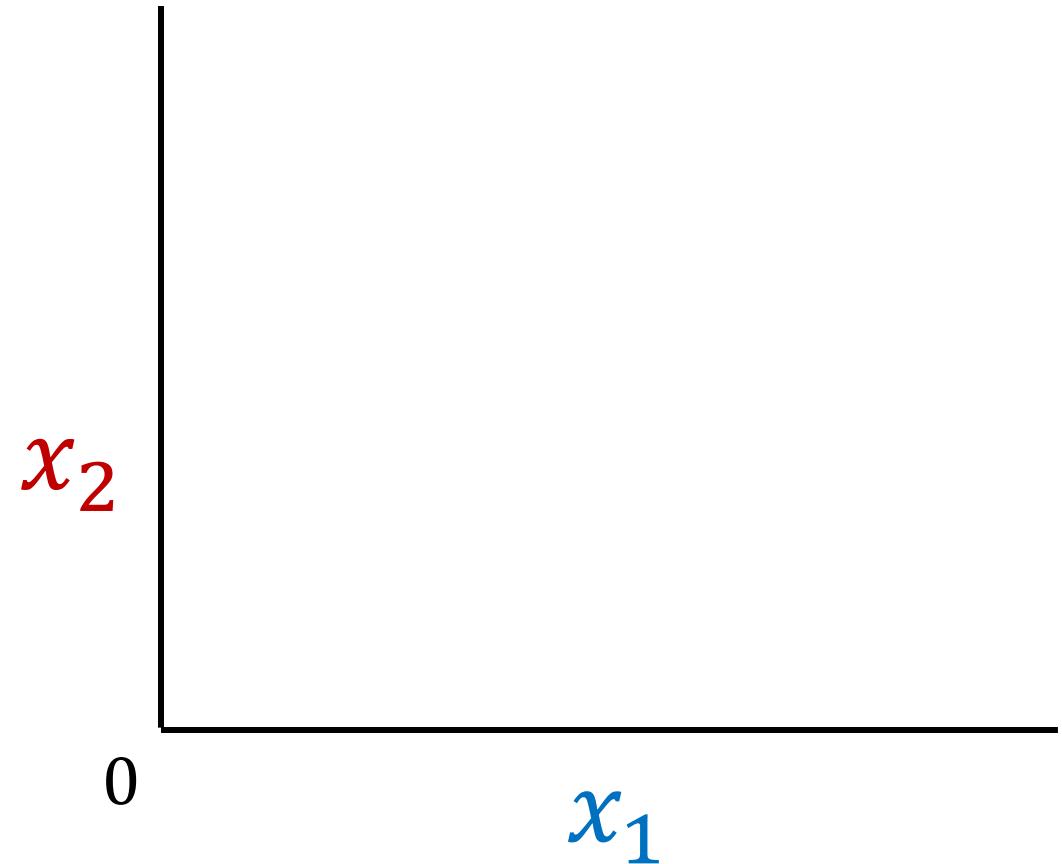
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## Nullclines (or isoclines) of the Lotka-Volterra competition model

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

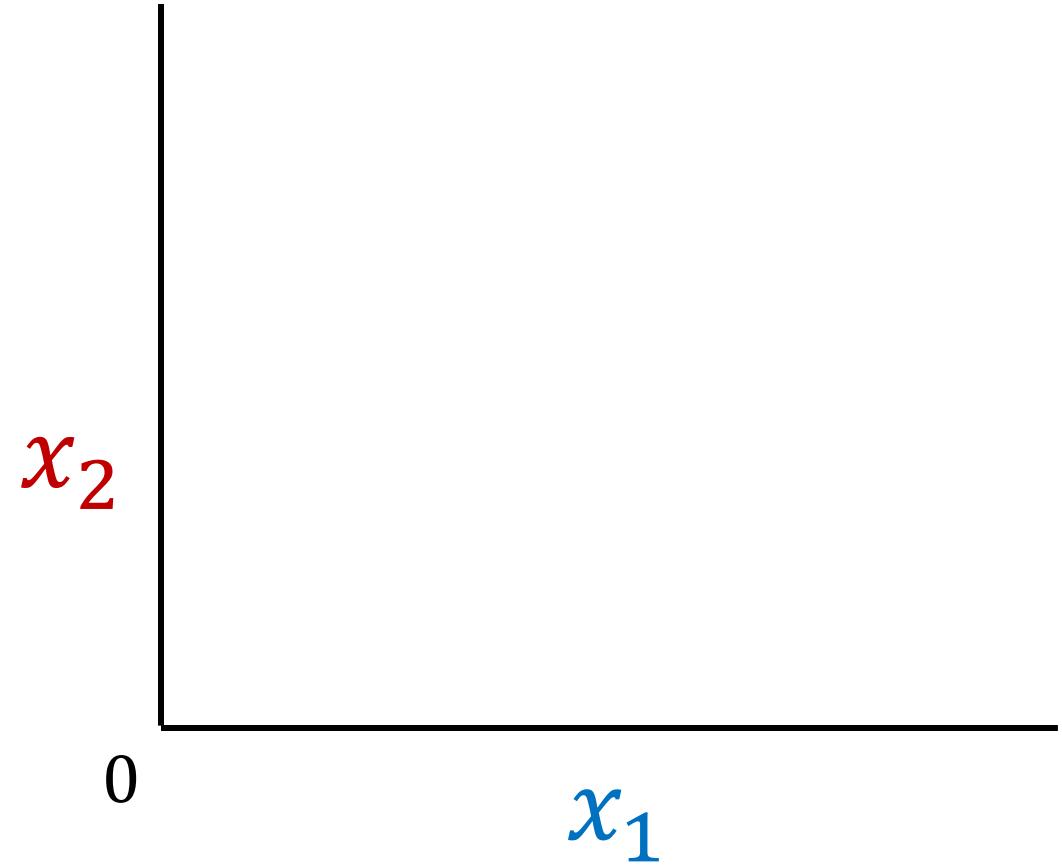
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These are the lines that correspond to conditions when the rate of change for one species is 0.

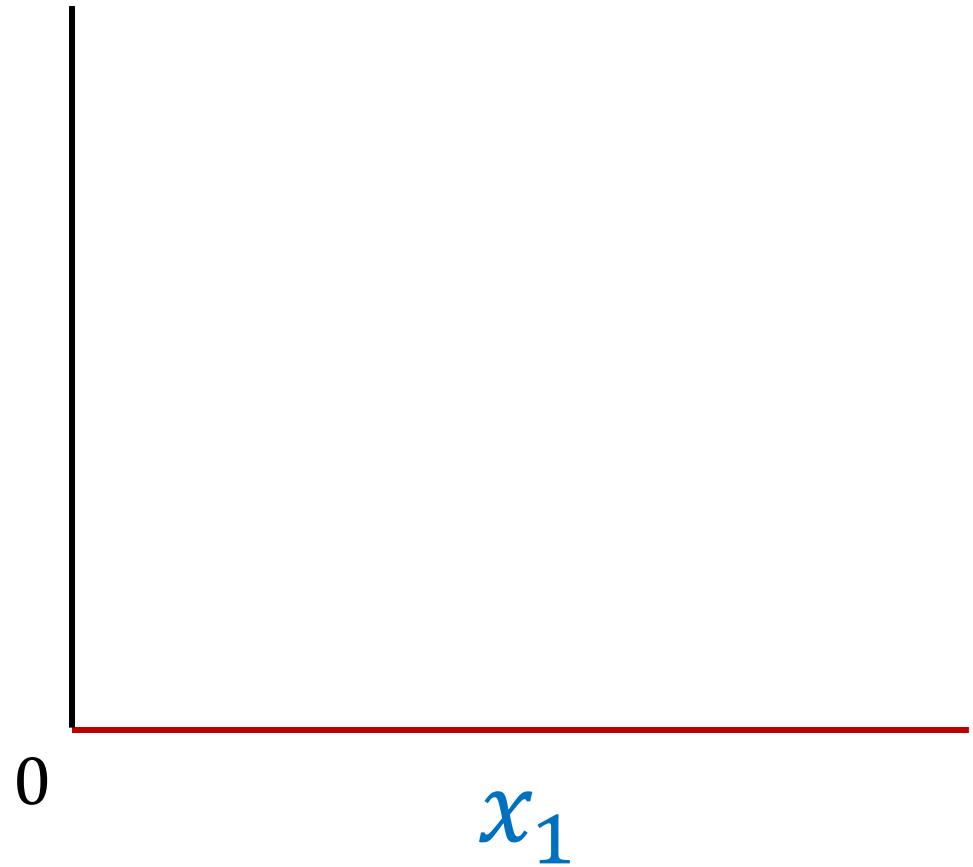
- Nullclines for species 2 occur at all conditions for which  $\frac{dx_2}{dt} = 0$

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

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first nullcline at  $x_2 = 0$



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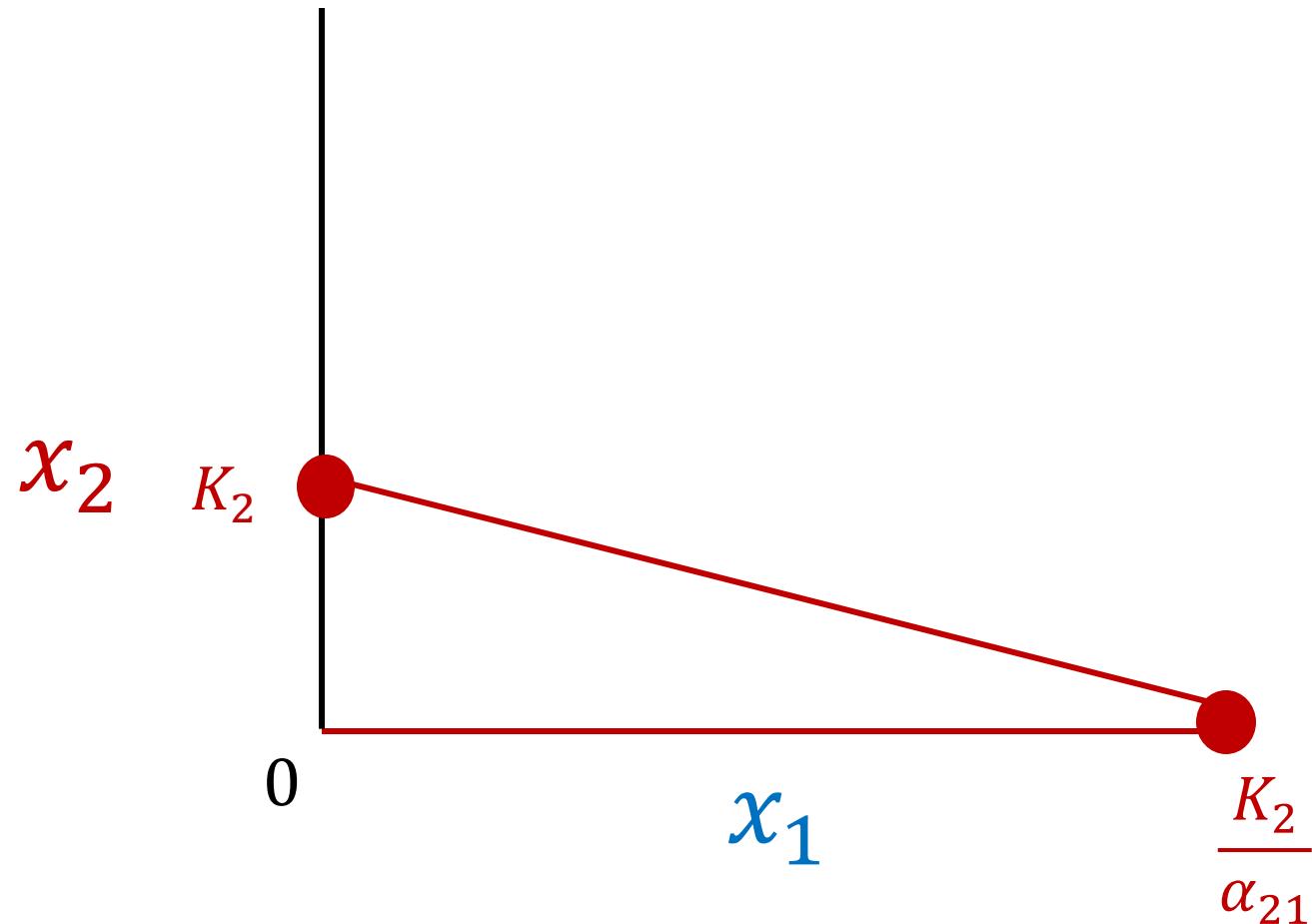
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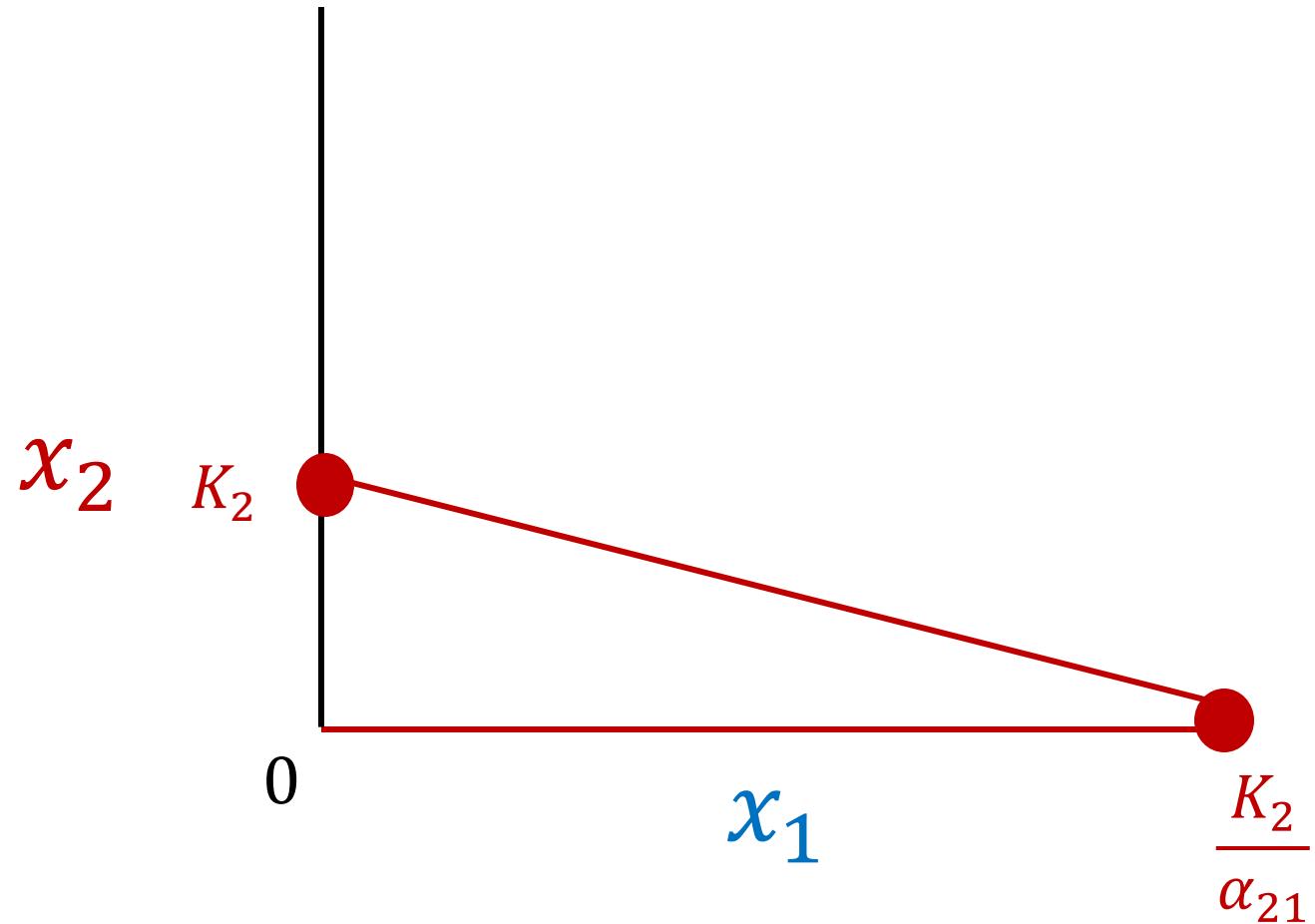
first nullcline at  $x_2 = 0$

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



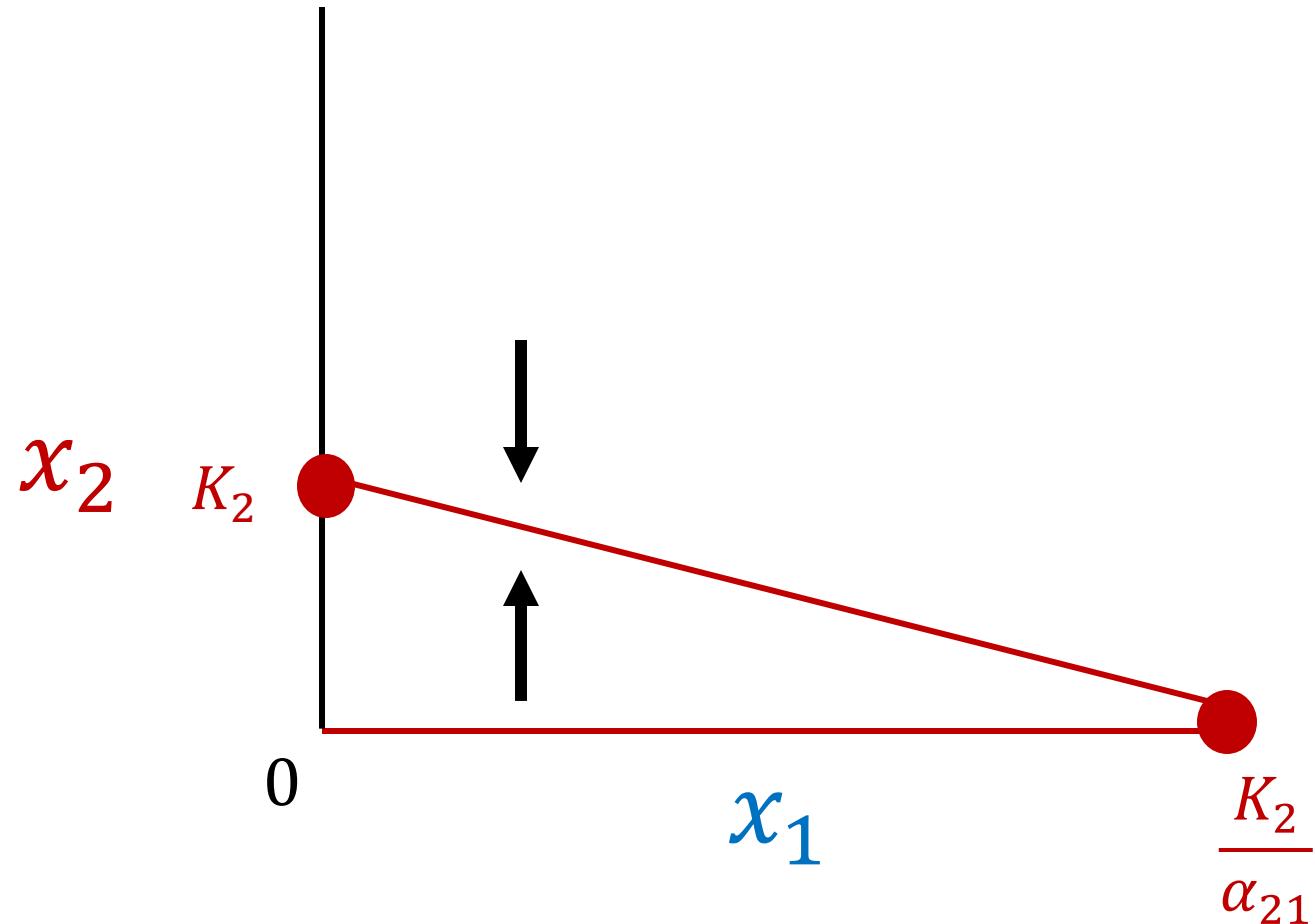
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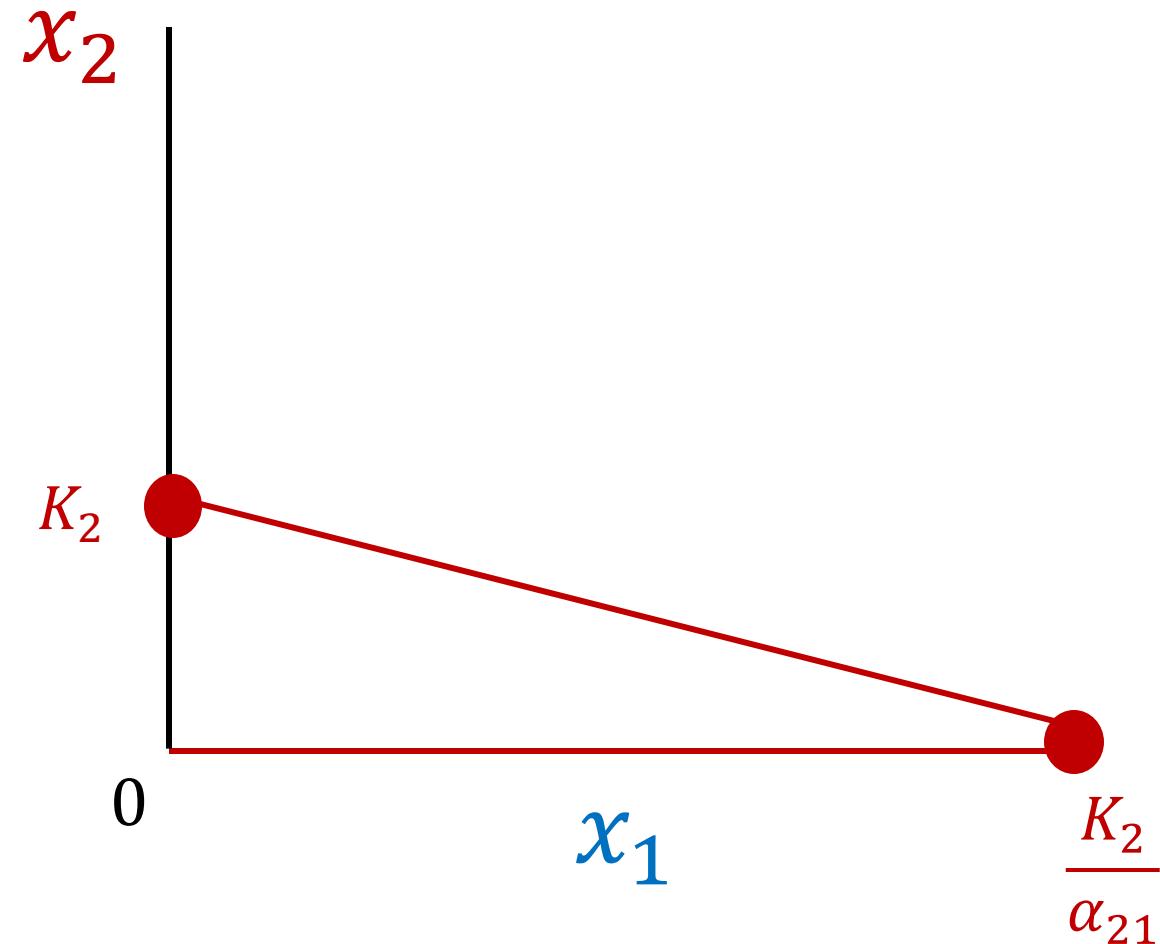
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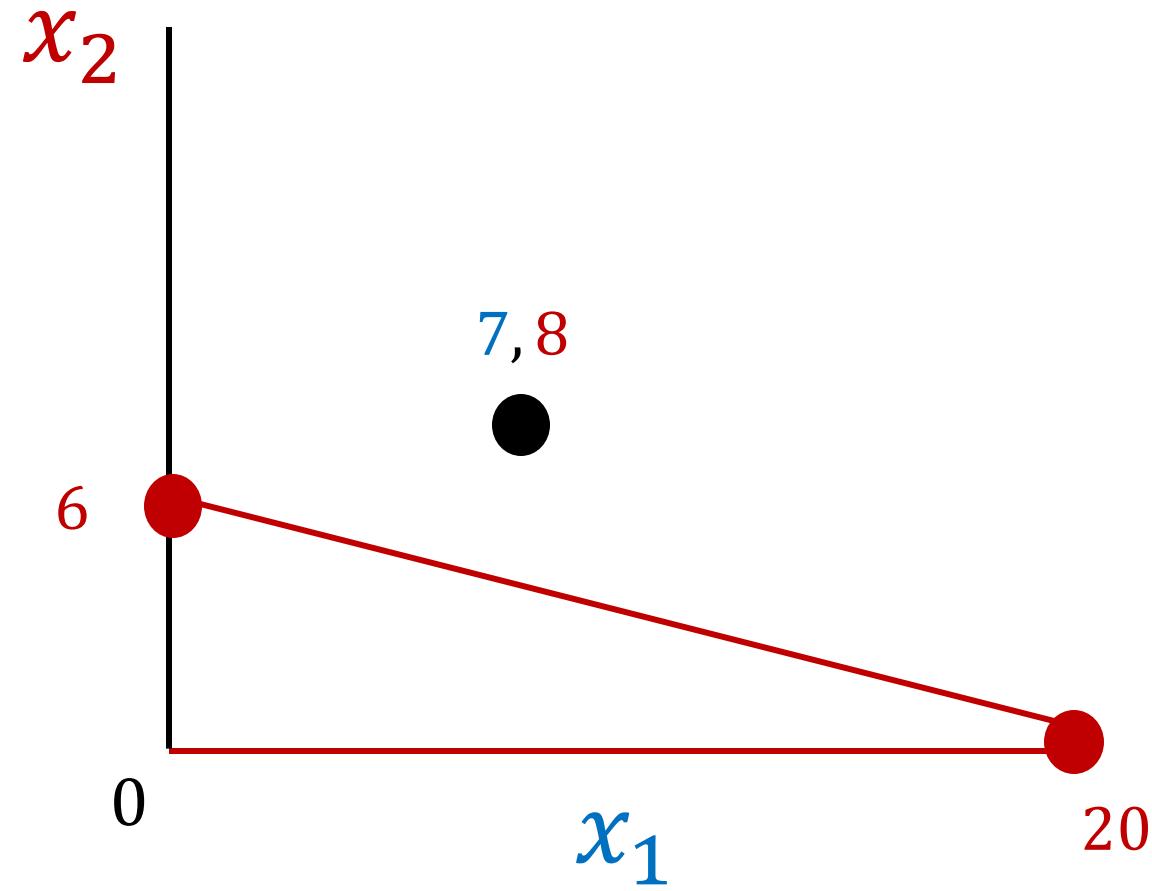
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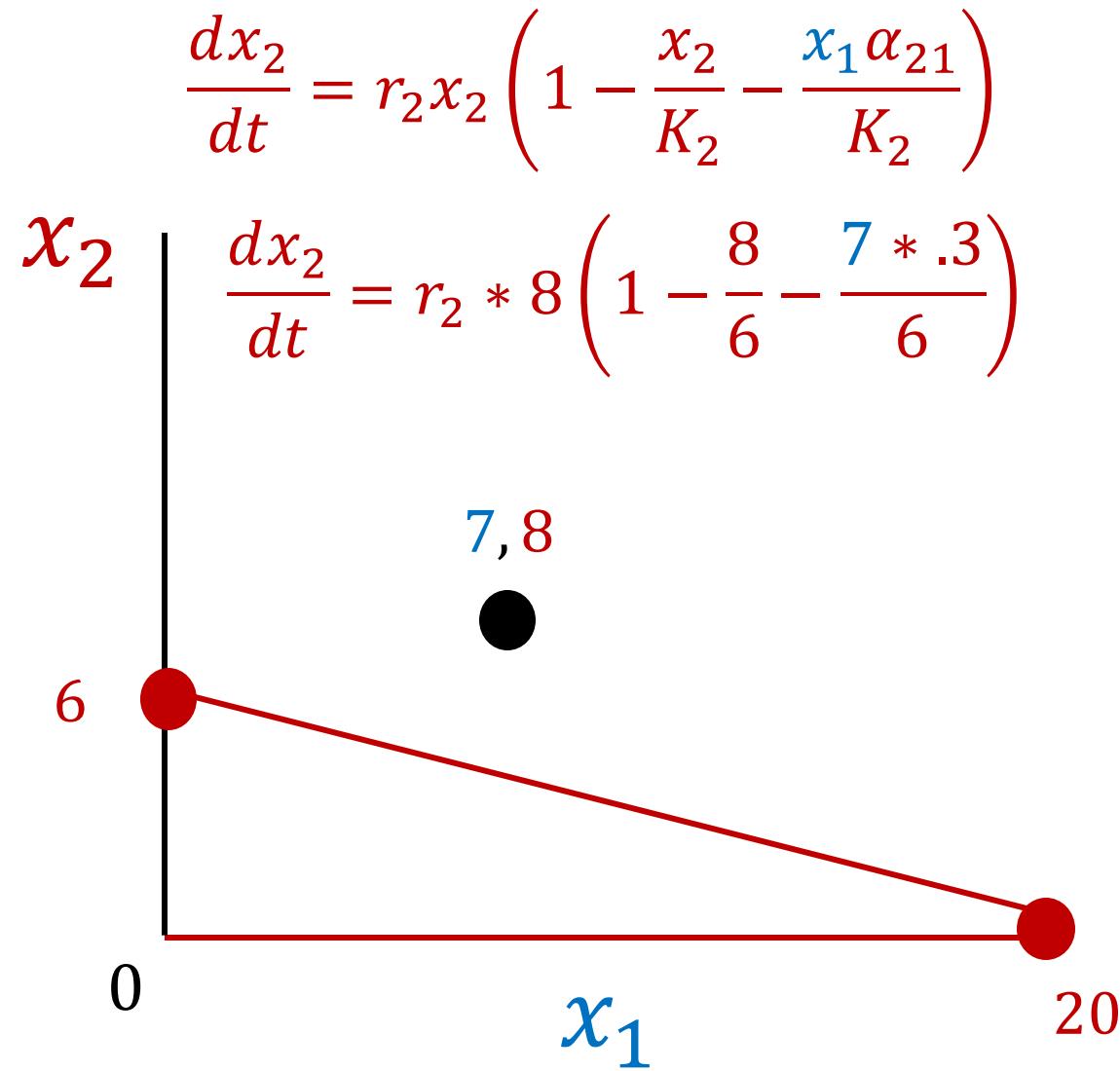
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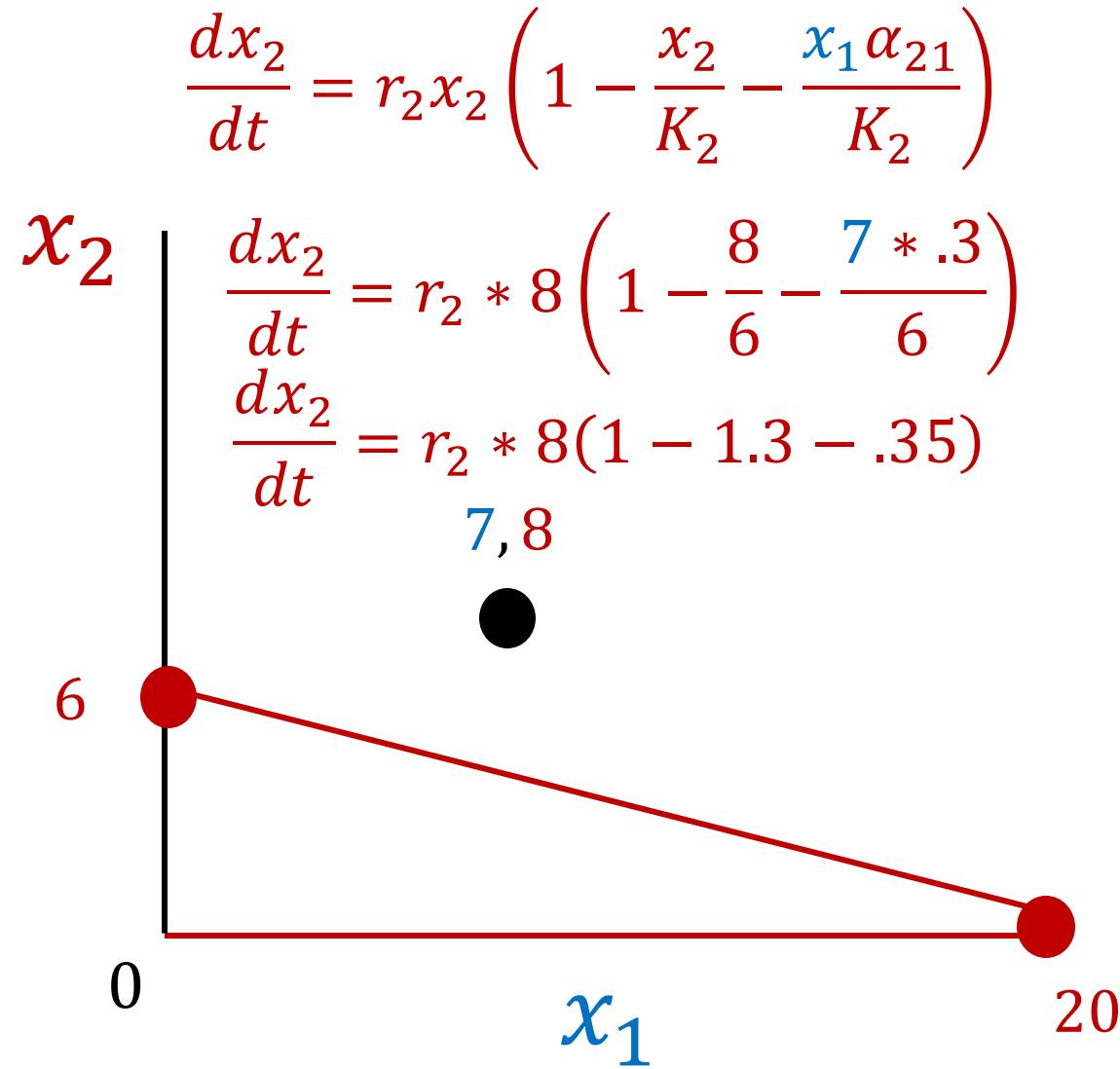
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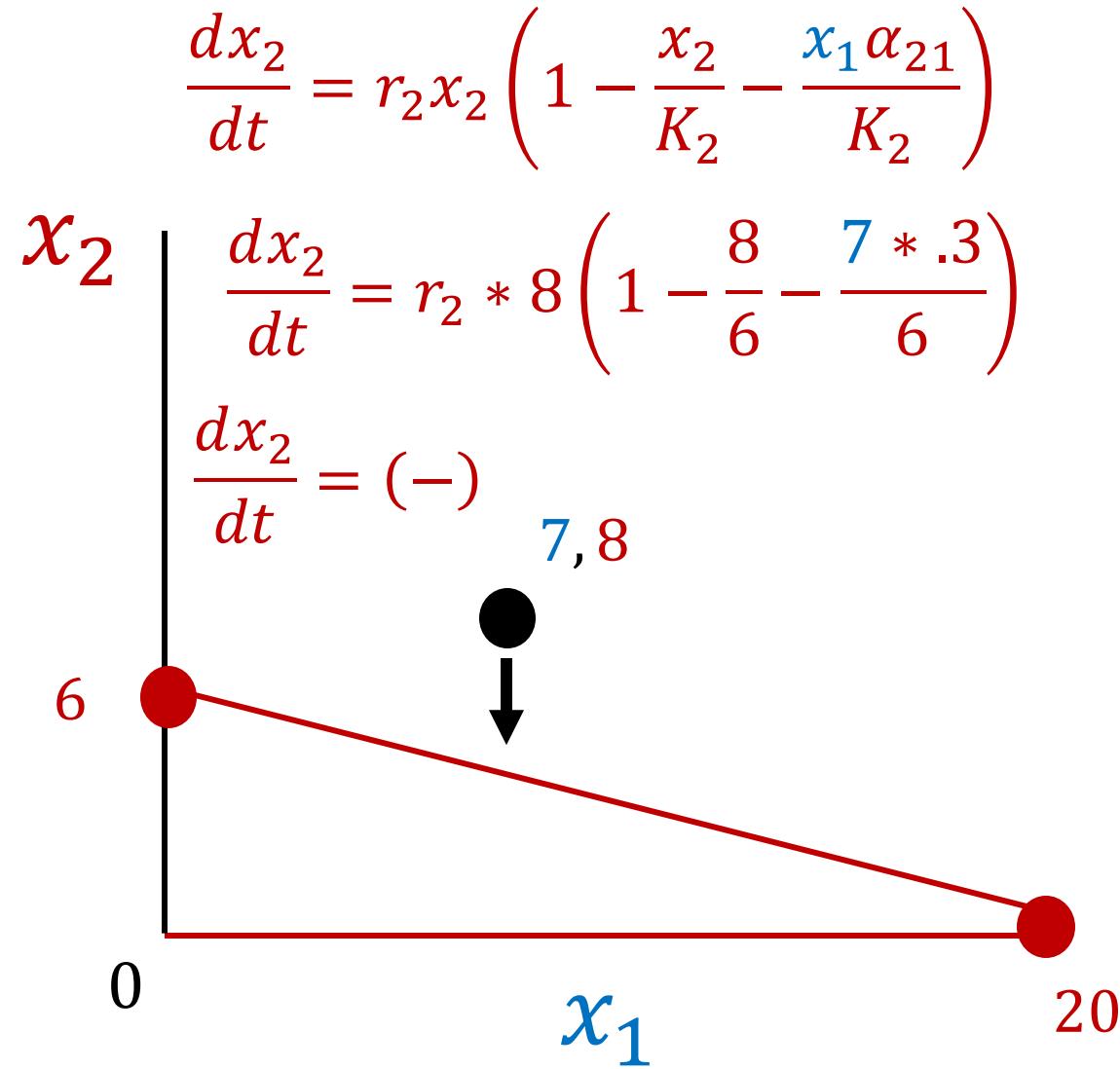
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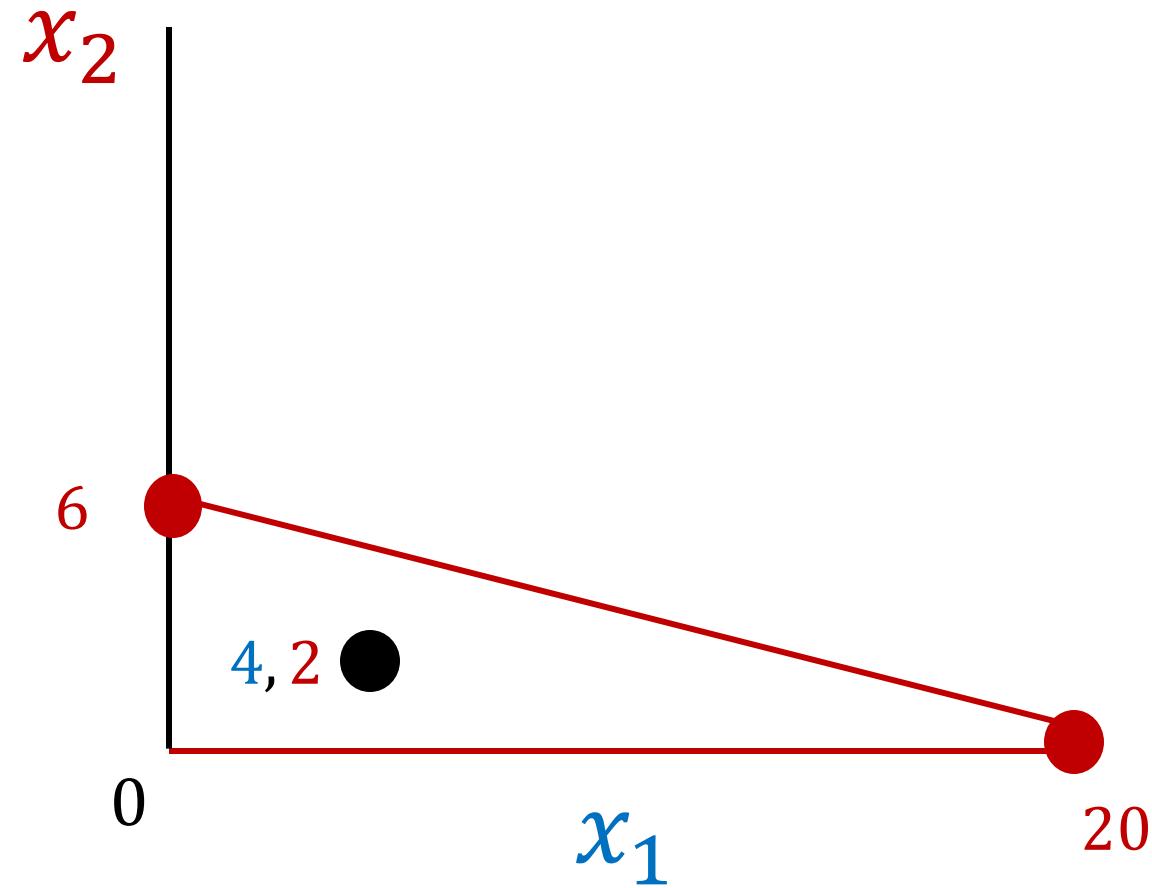
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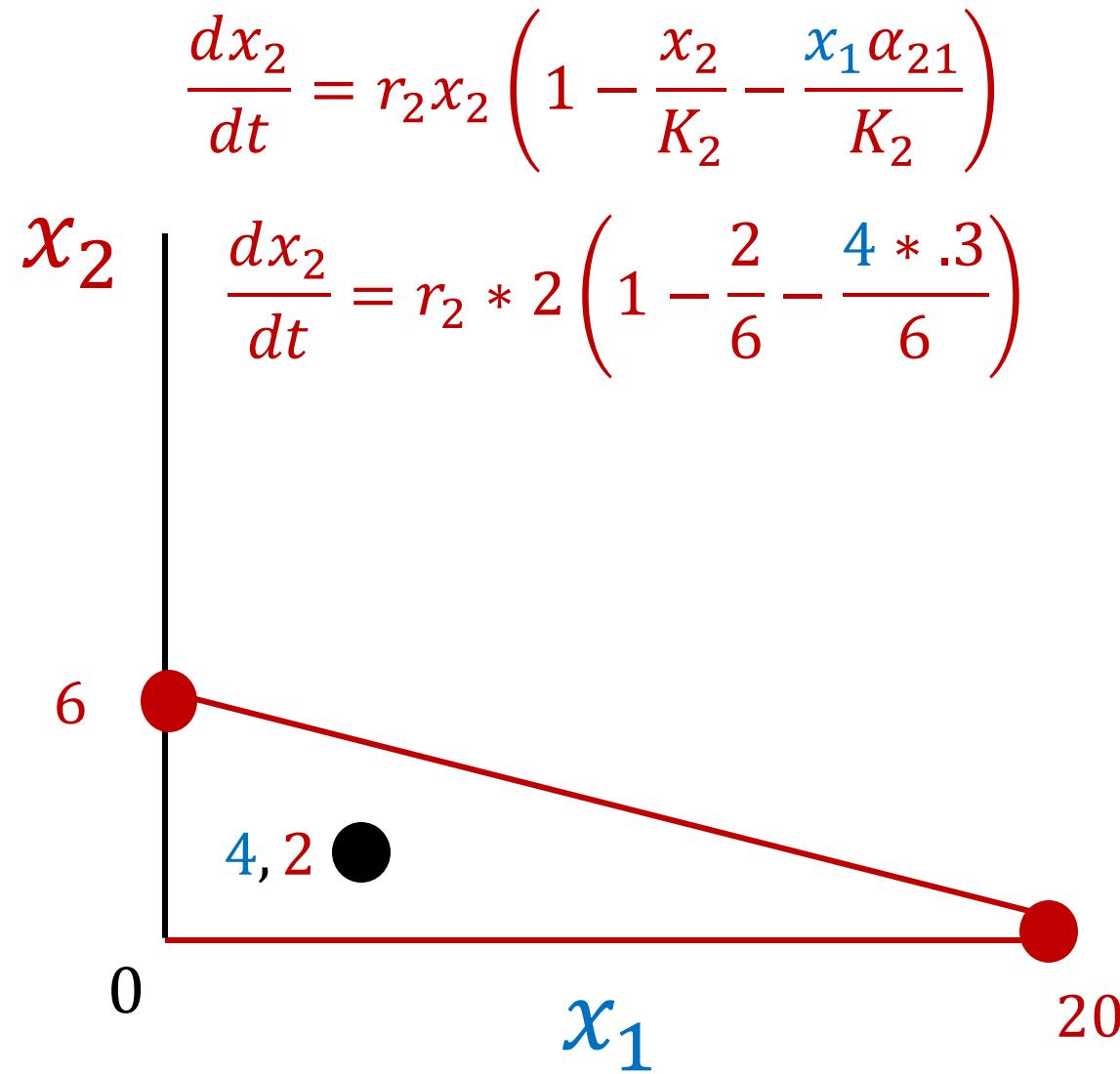
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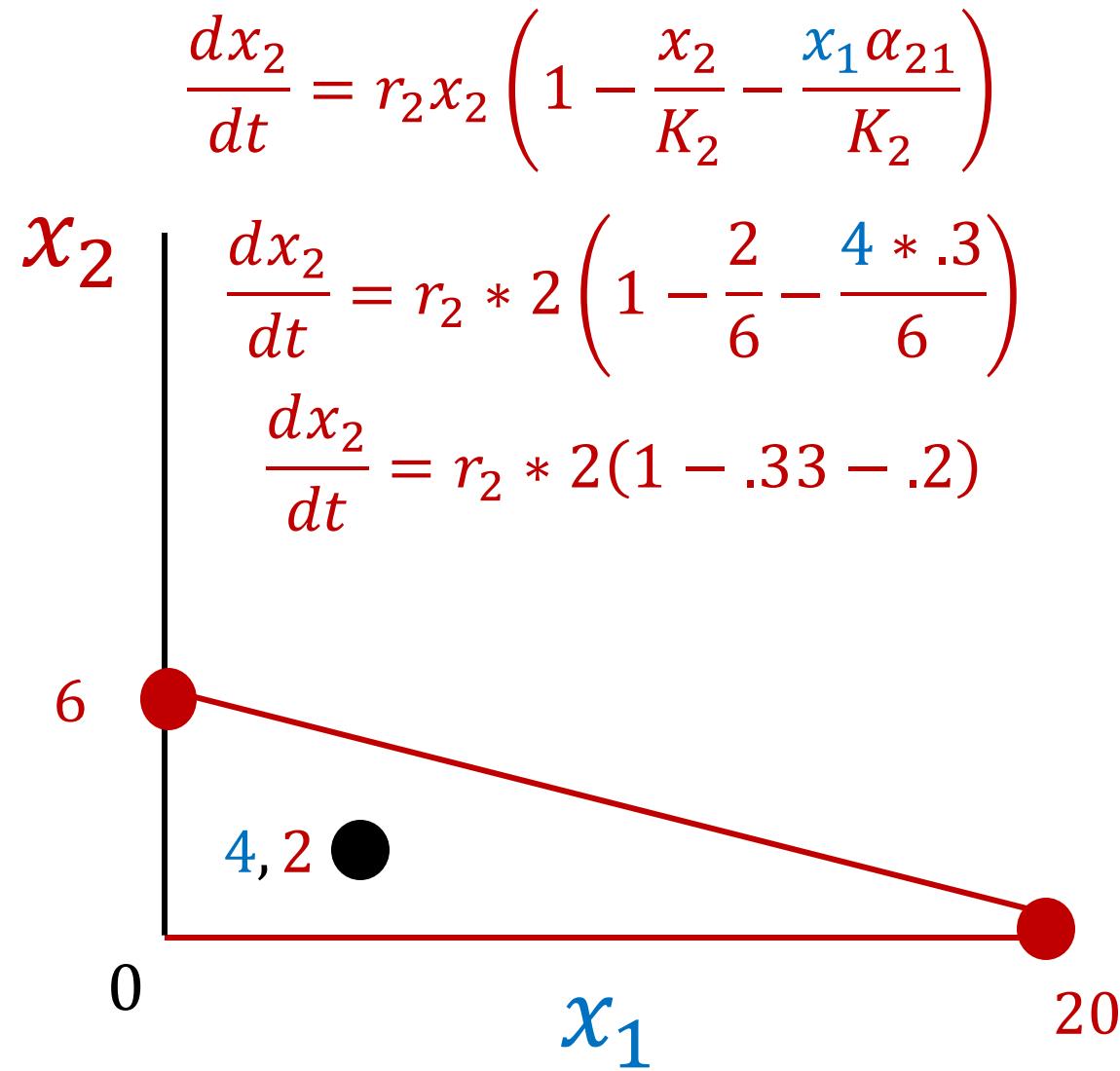
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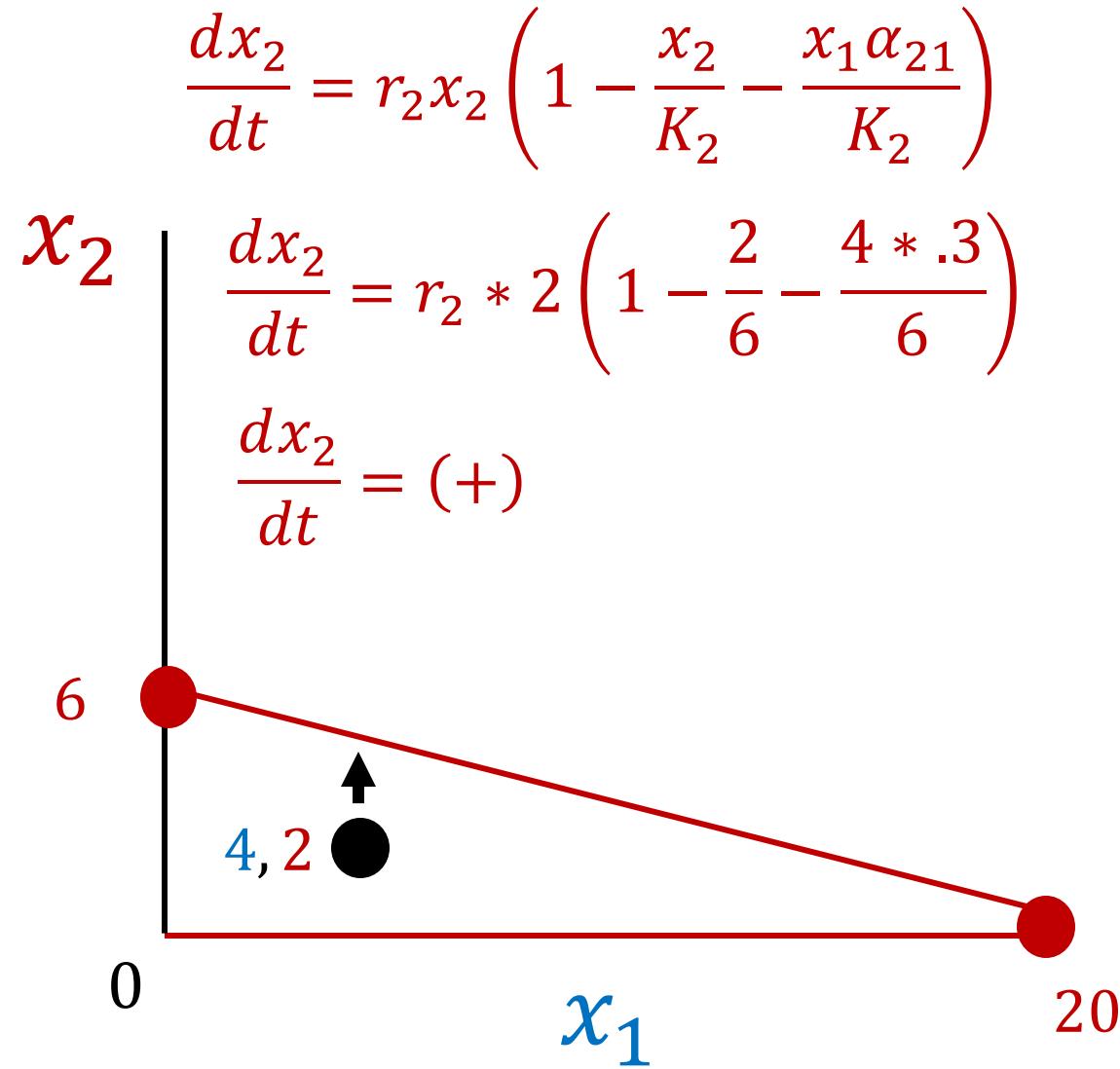
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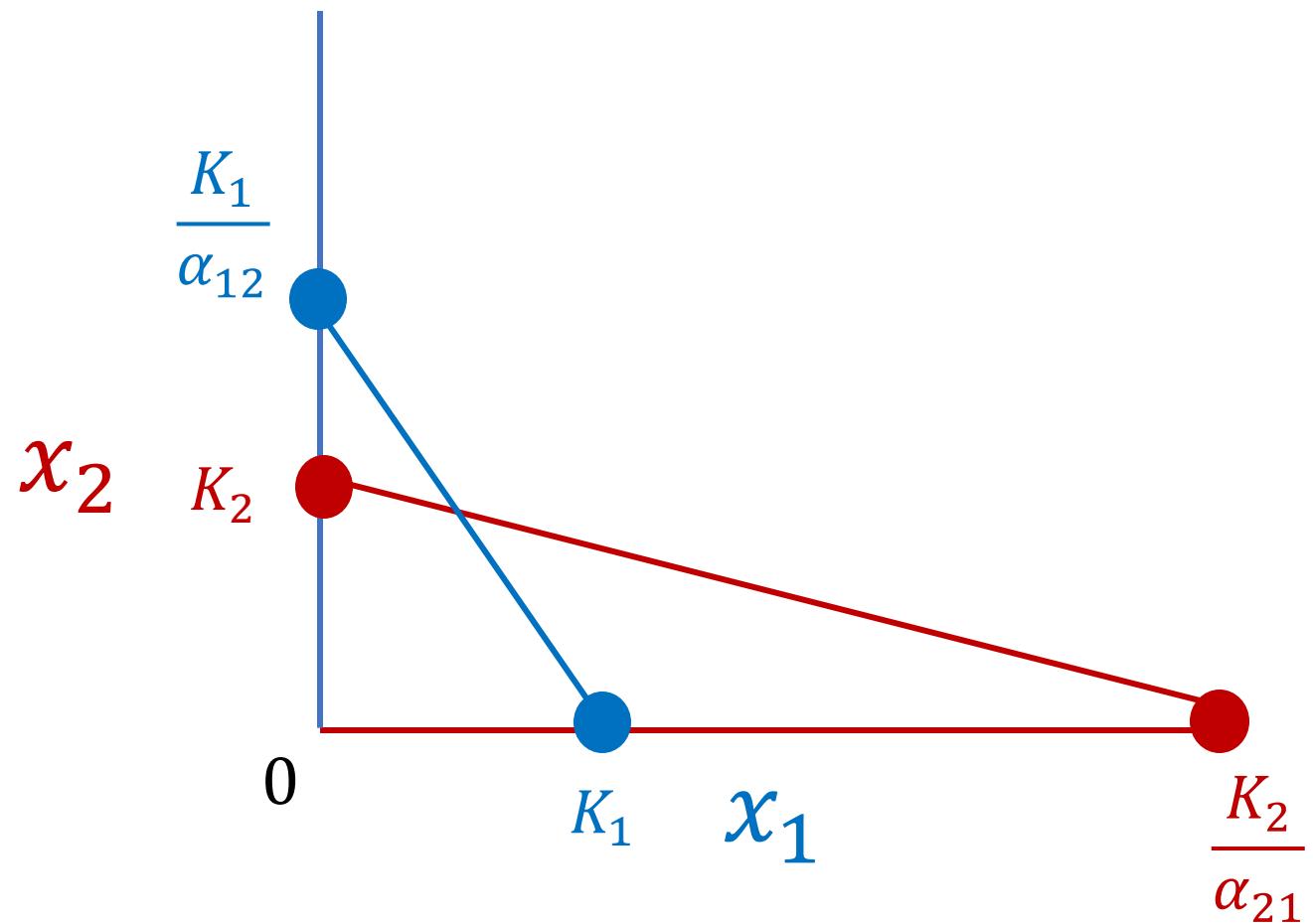


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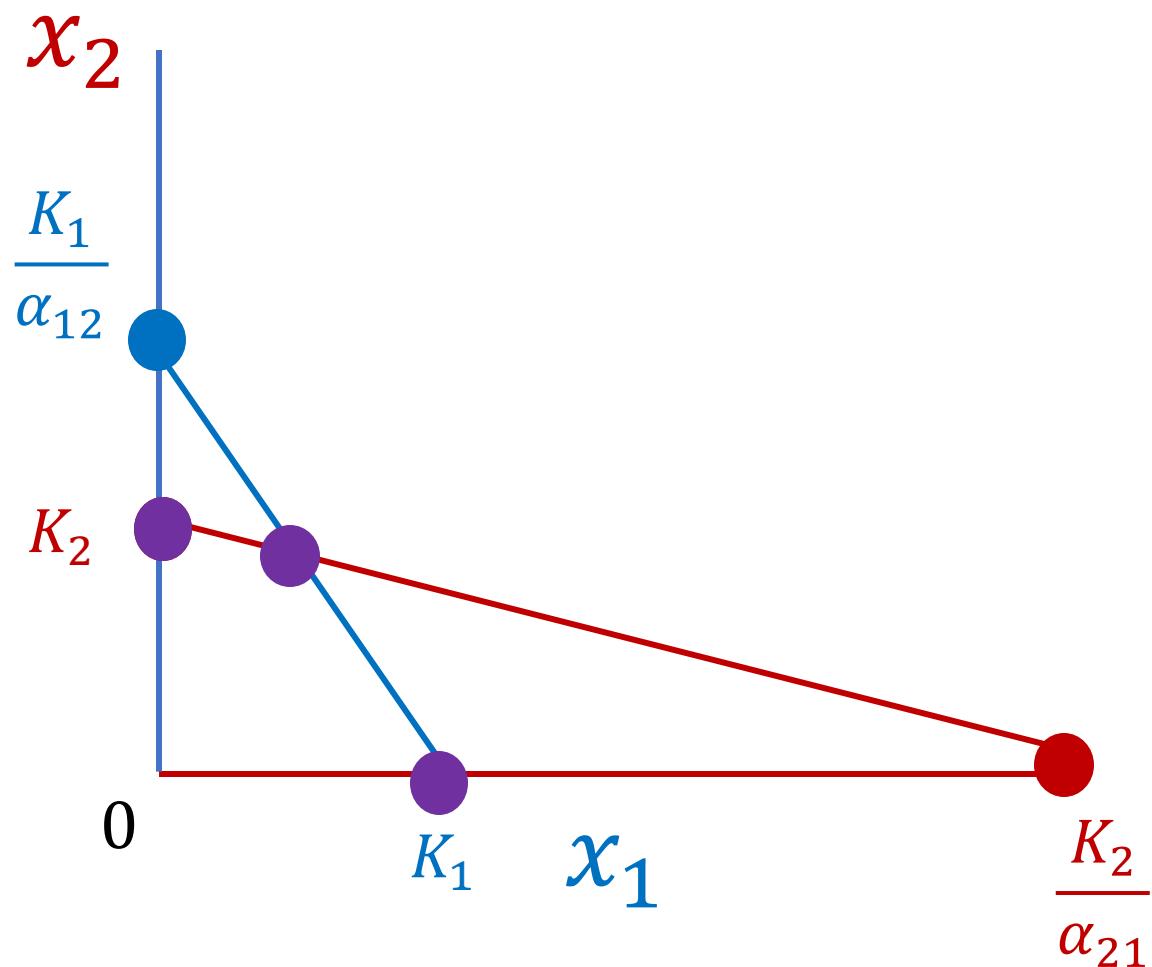


Given different combinations of  $x_1$  and  $x_2$  what is the outcome of competition?

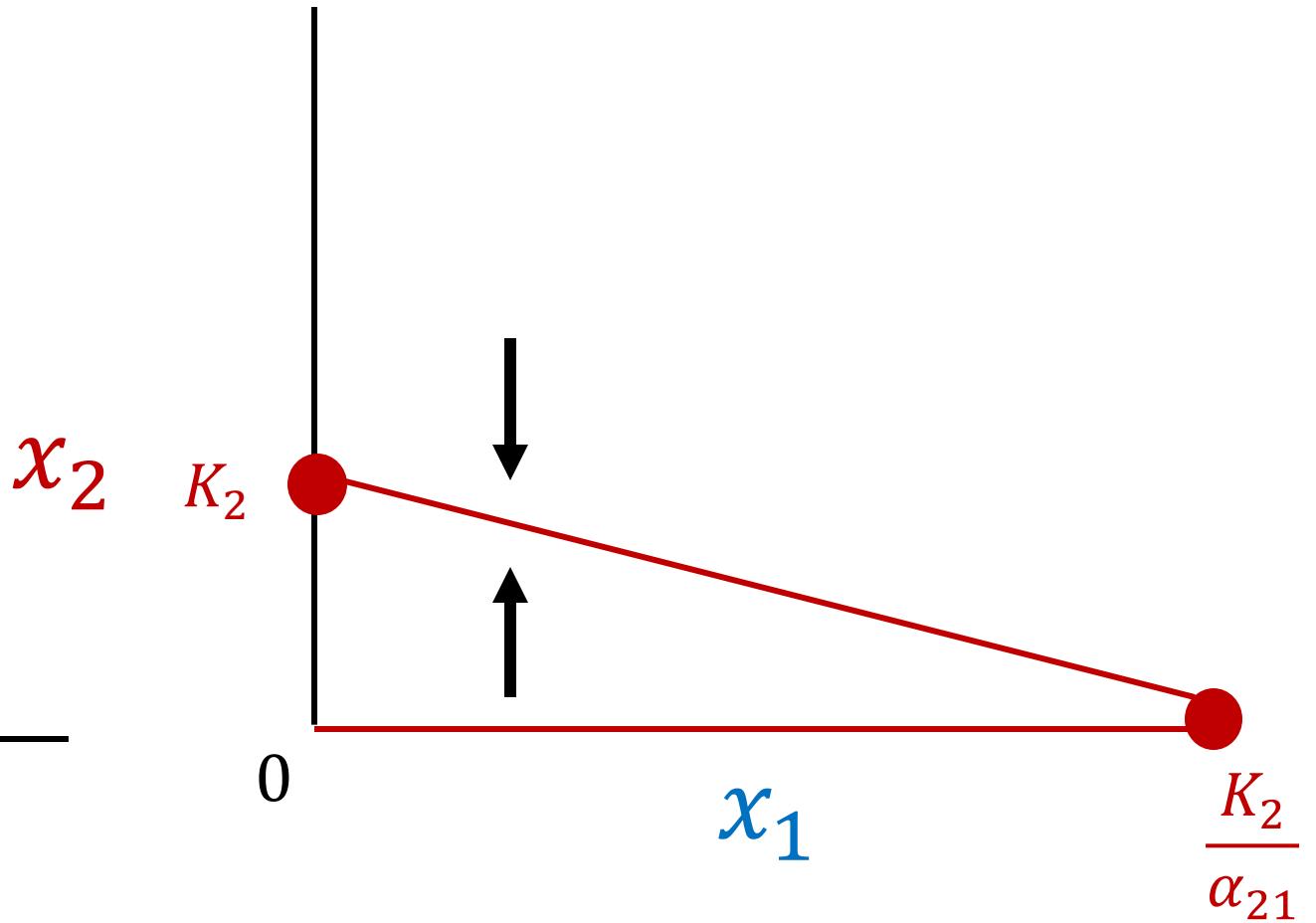
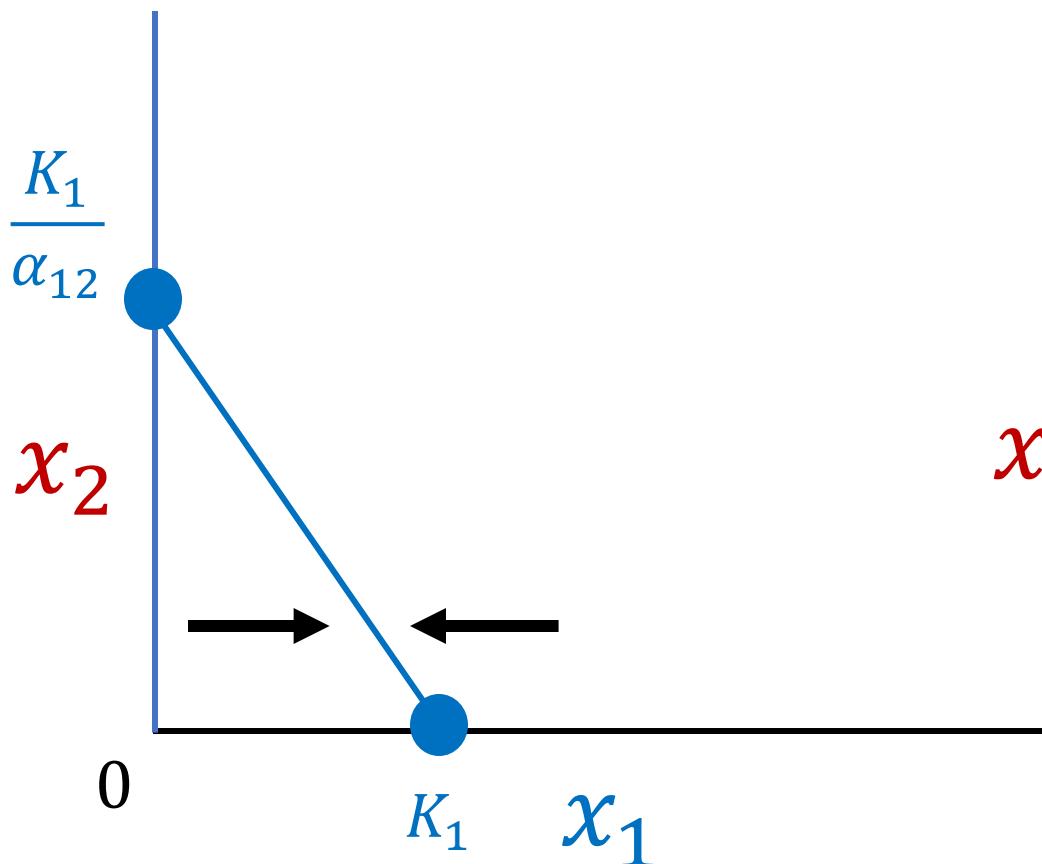


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System will converge to one of its equilibria, depending on the values of the competition and carrying capacity parameters.



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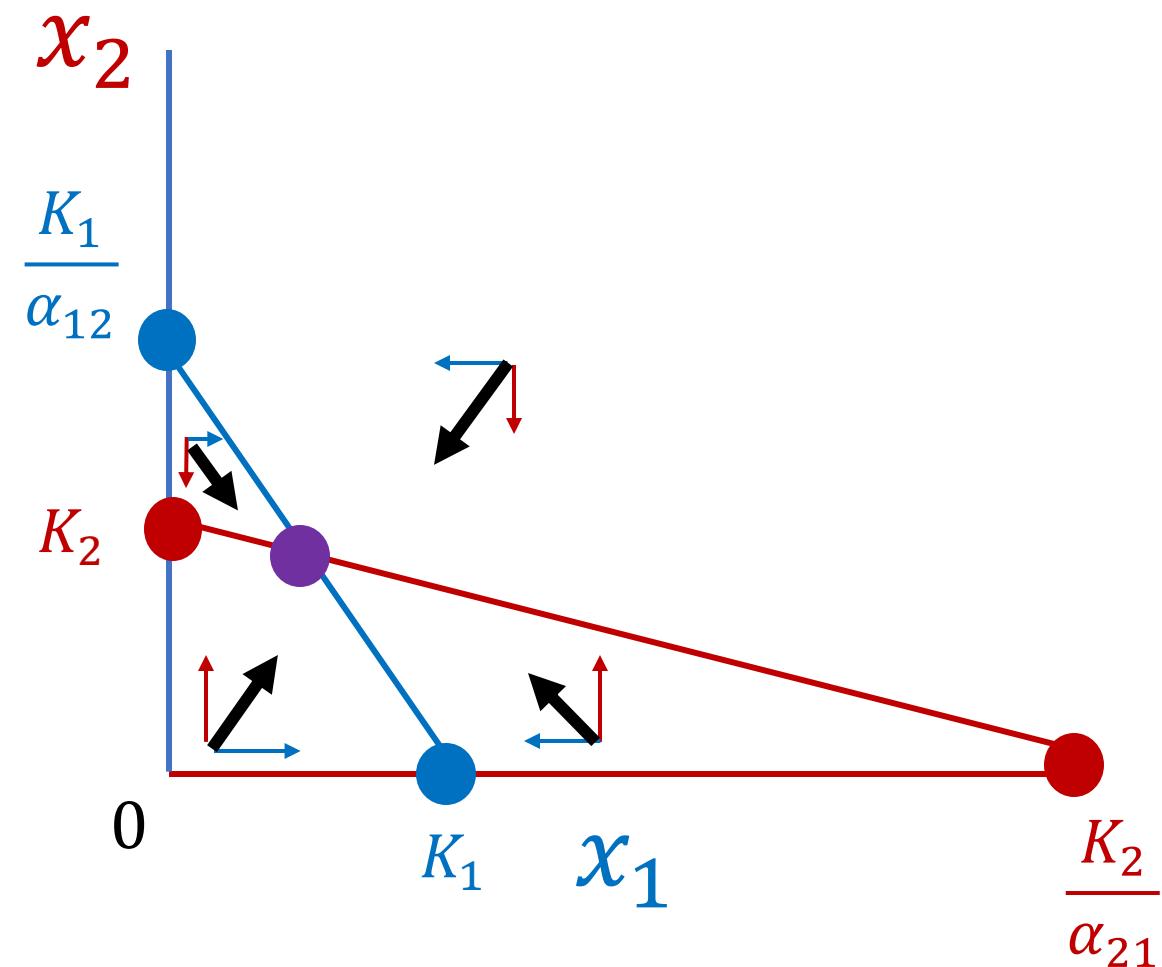


We can use vector addition from the individual nullclines to determine the outcome of competition.

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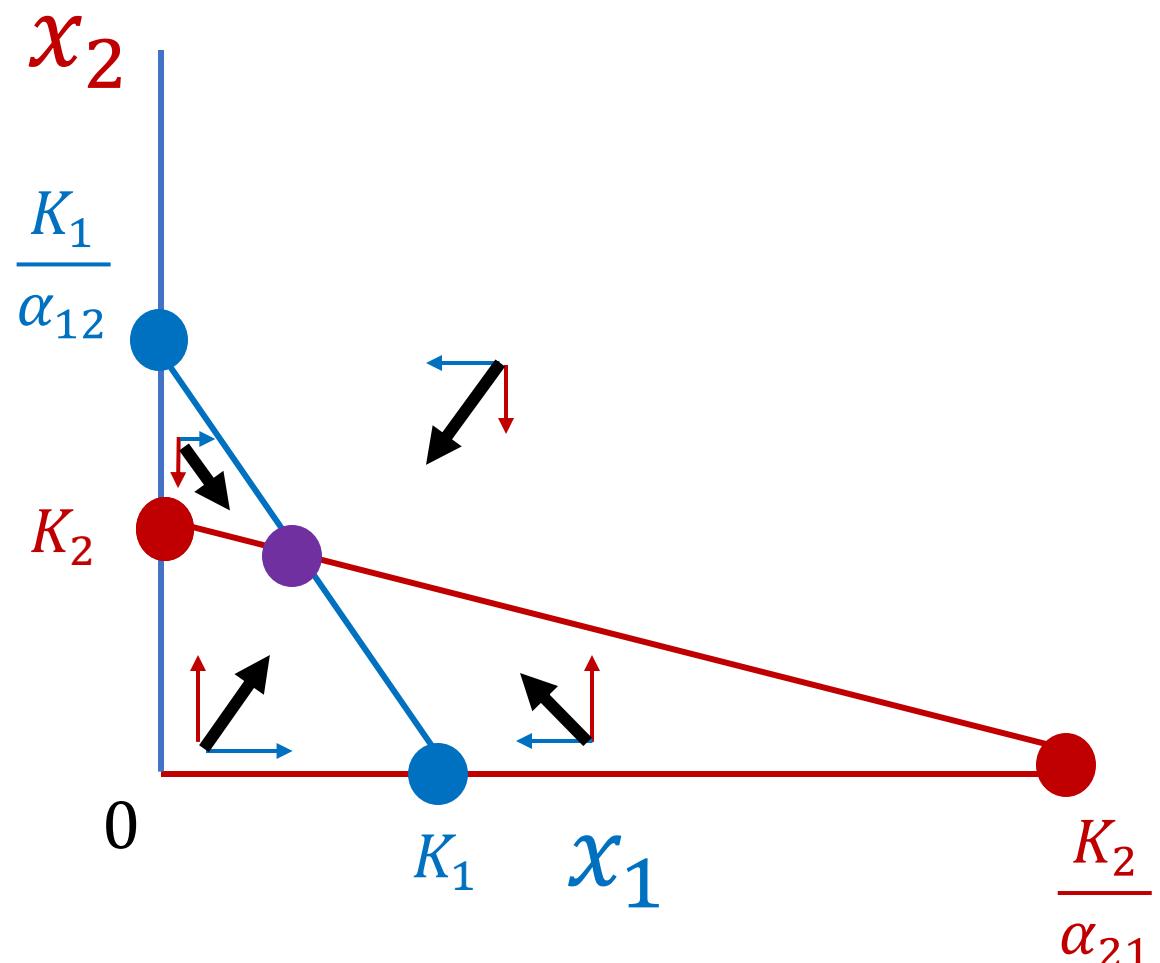
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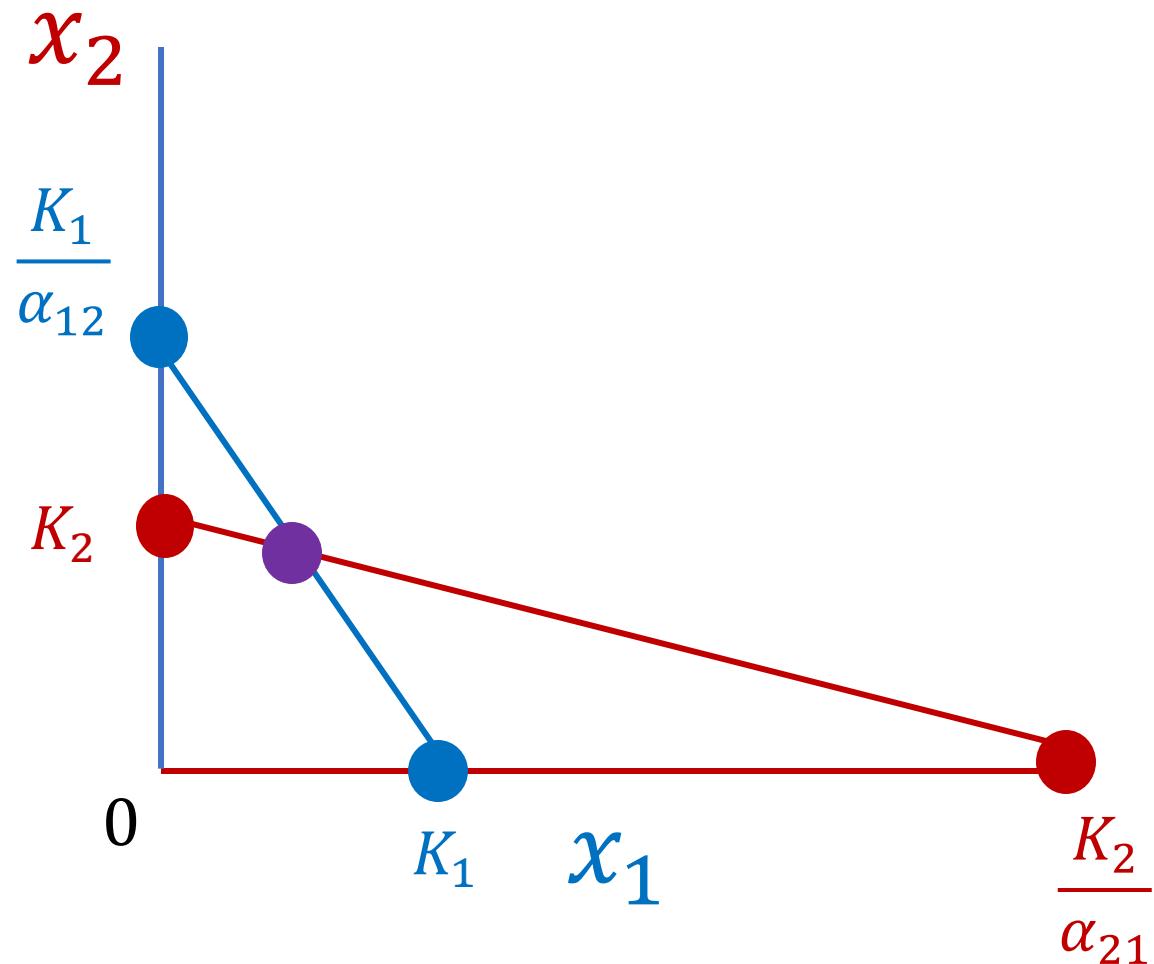
This configuration is a **stable equilibrium**, indicating **stable coexistence** at:

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



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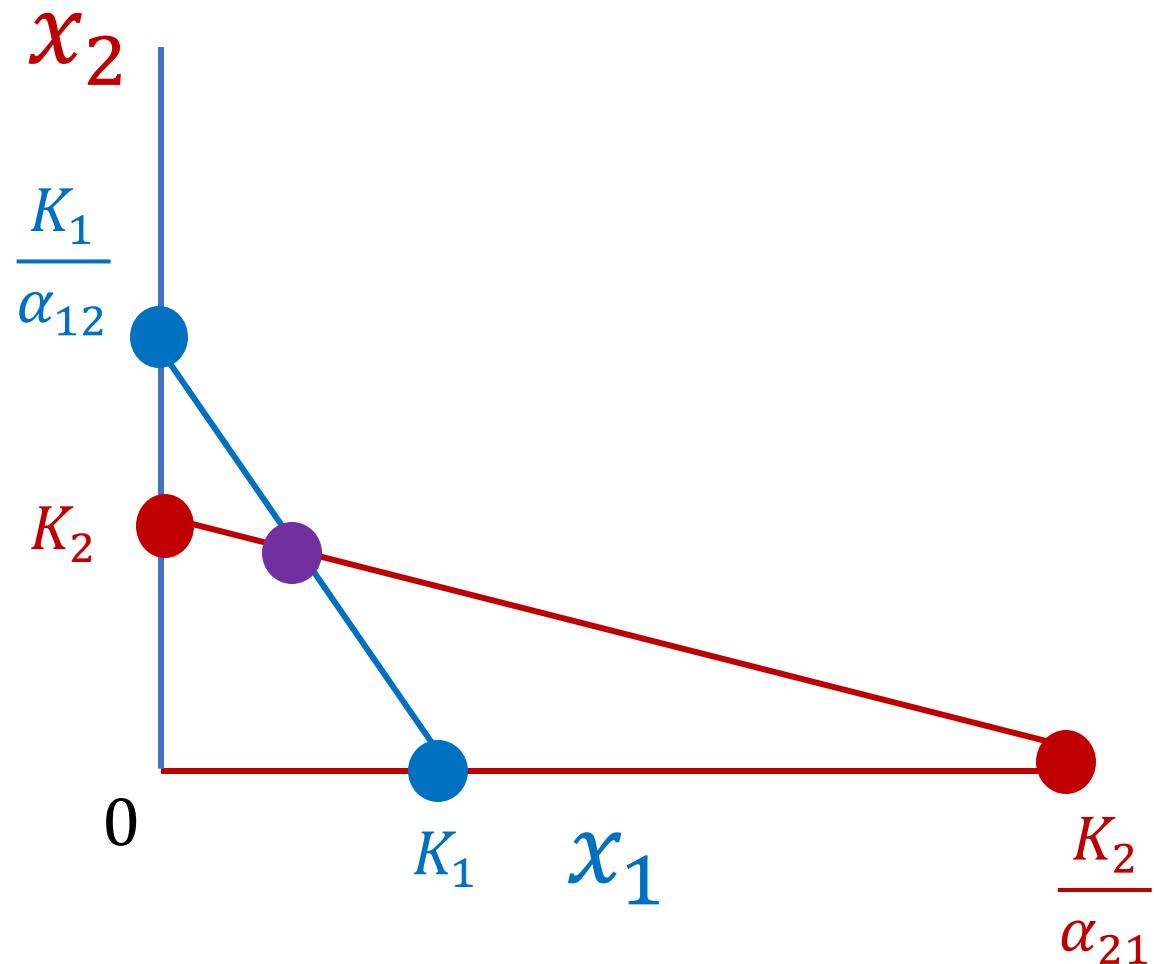
Like before, we can also solve  $\frac{dx_1}{dt}$  at different combinations of  $x_1$  and  $x_2$  to test the direction the  $x_1$  population will move during competition (always along the x-axis).



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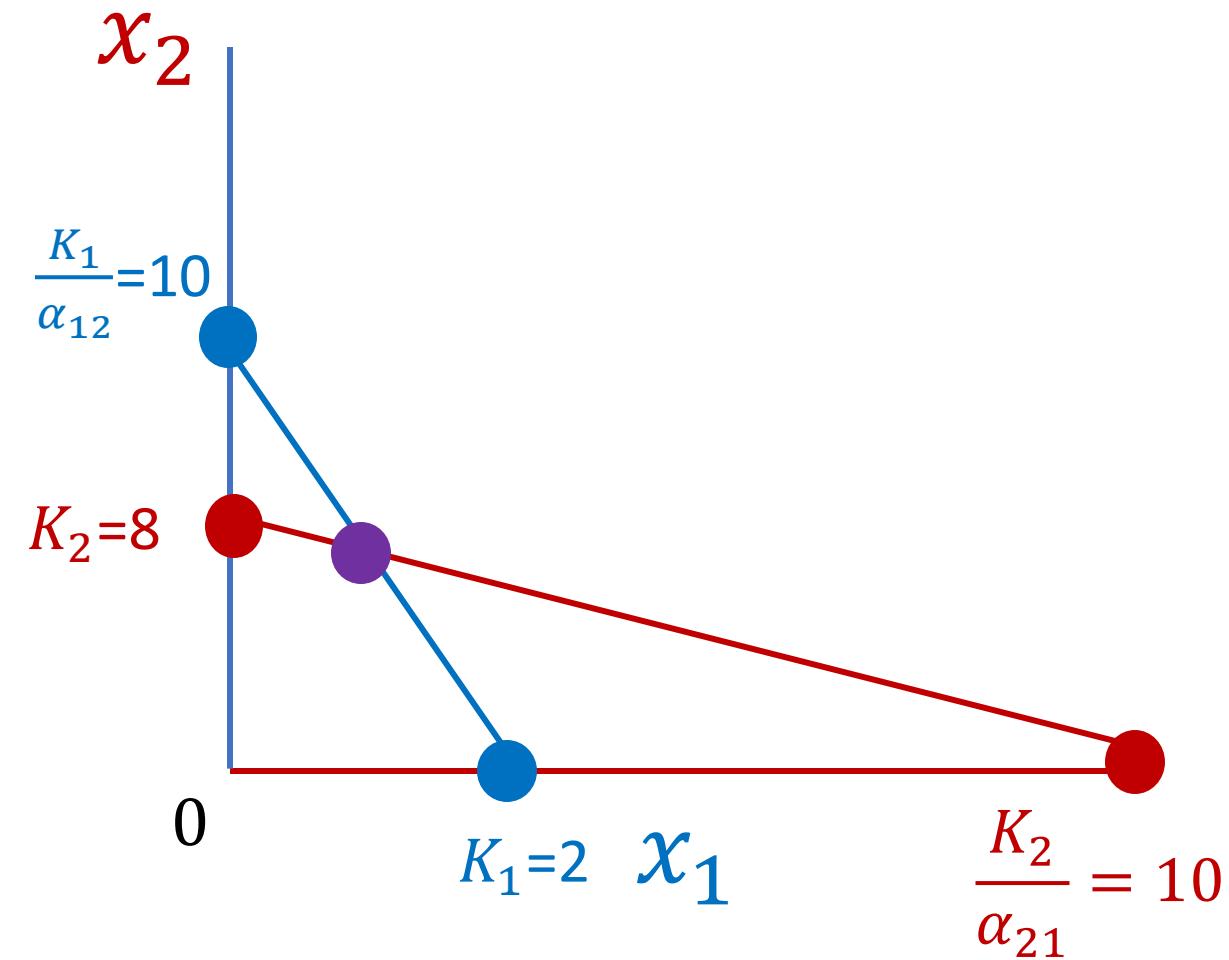


Given different combinations of  $x_1$  and  $x_2$  what is the outcome of competition?

Let's try it!

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

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



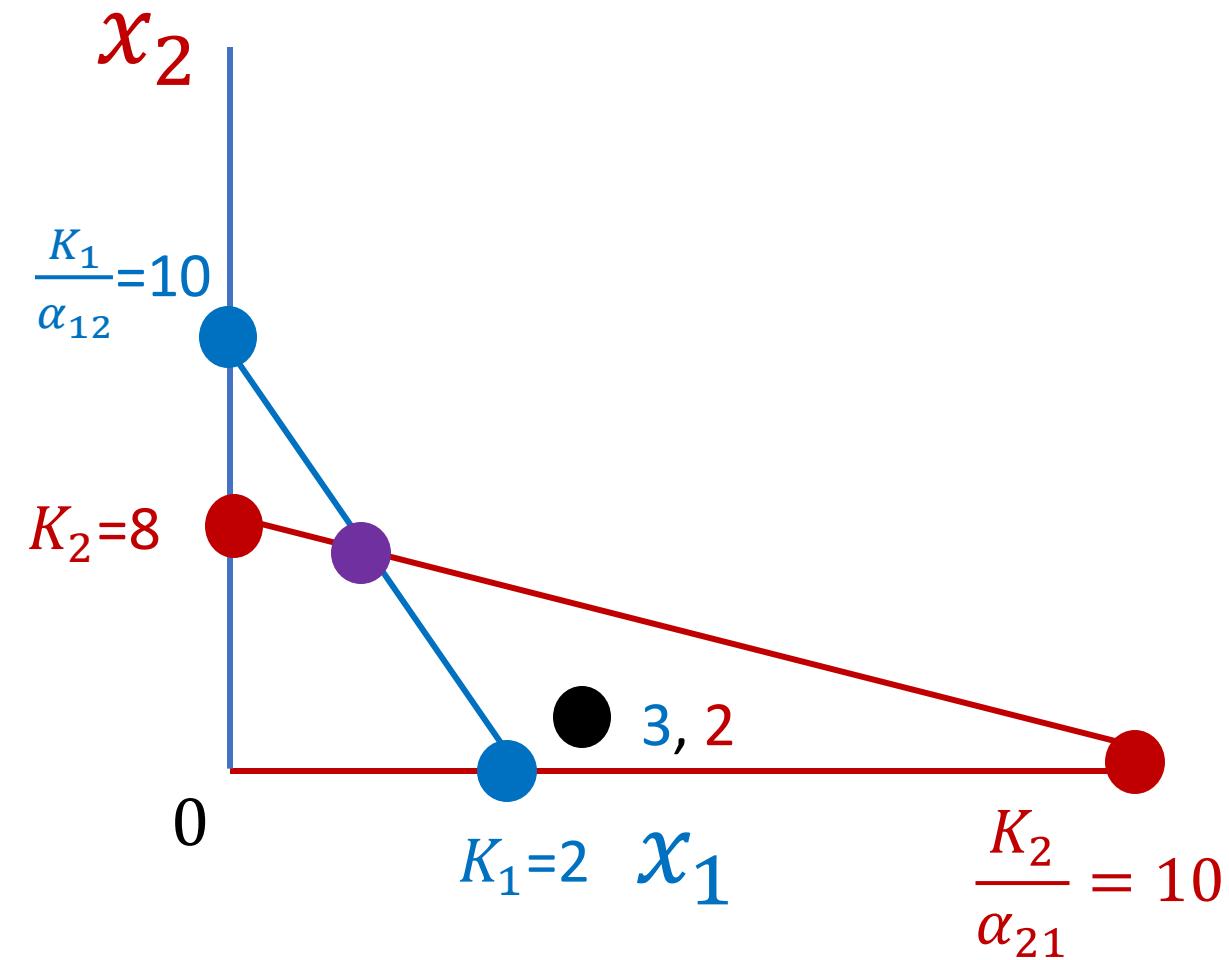
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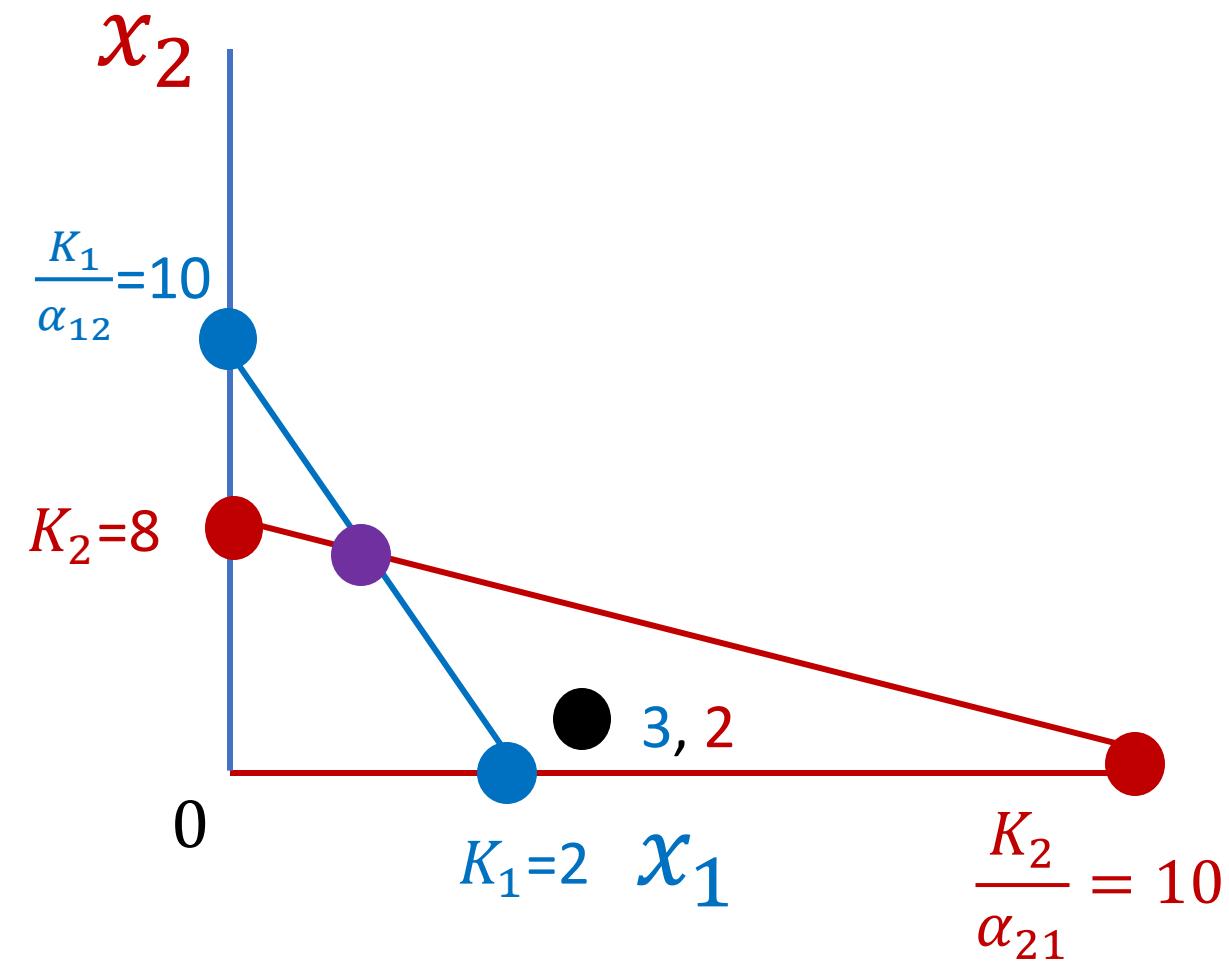
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$$\frac{dx_1}{dt} = r_1 * 3 \left( 1 - \frac{3}{2} - \frac{2 * .3}{2} \right)$$



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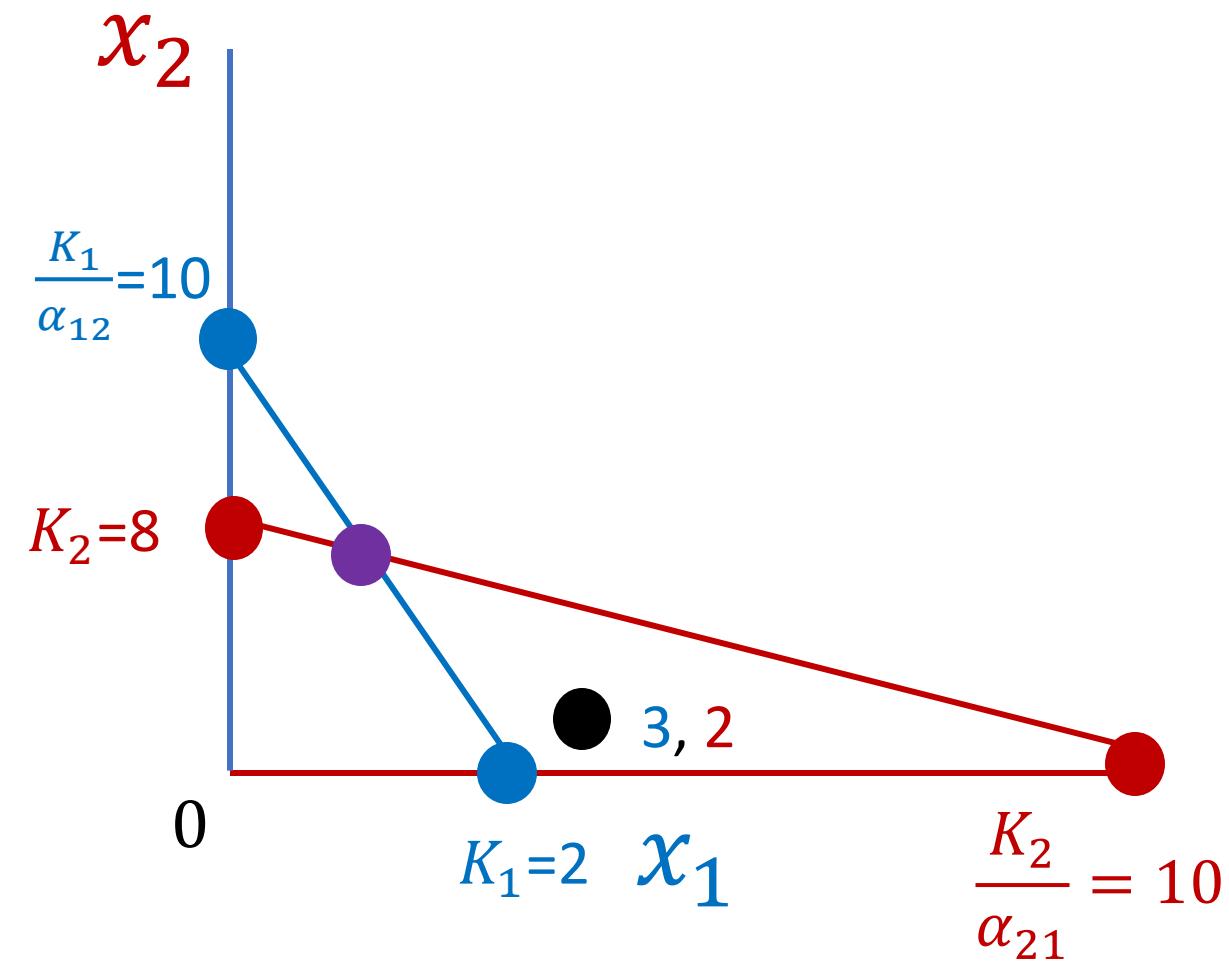
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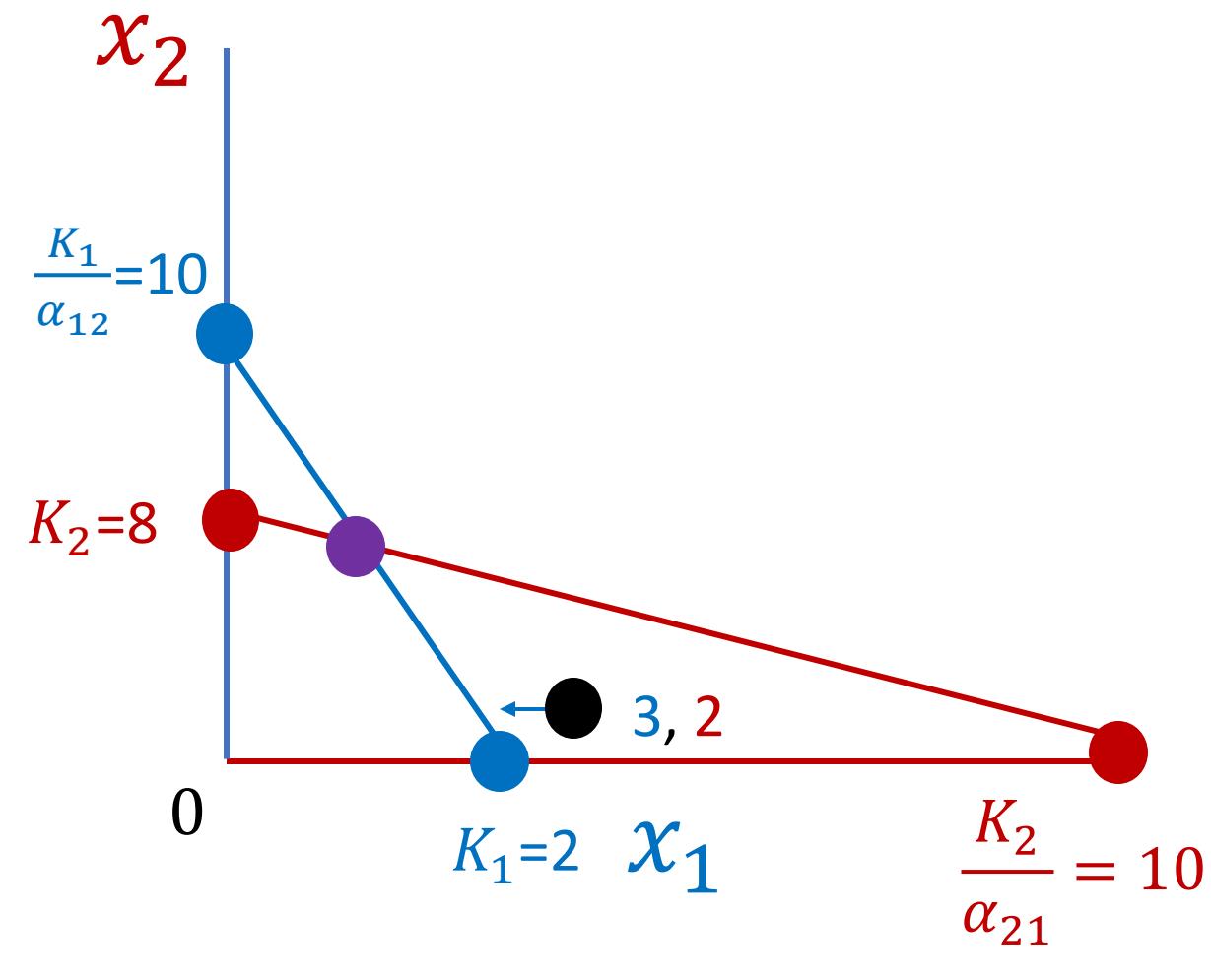
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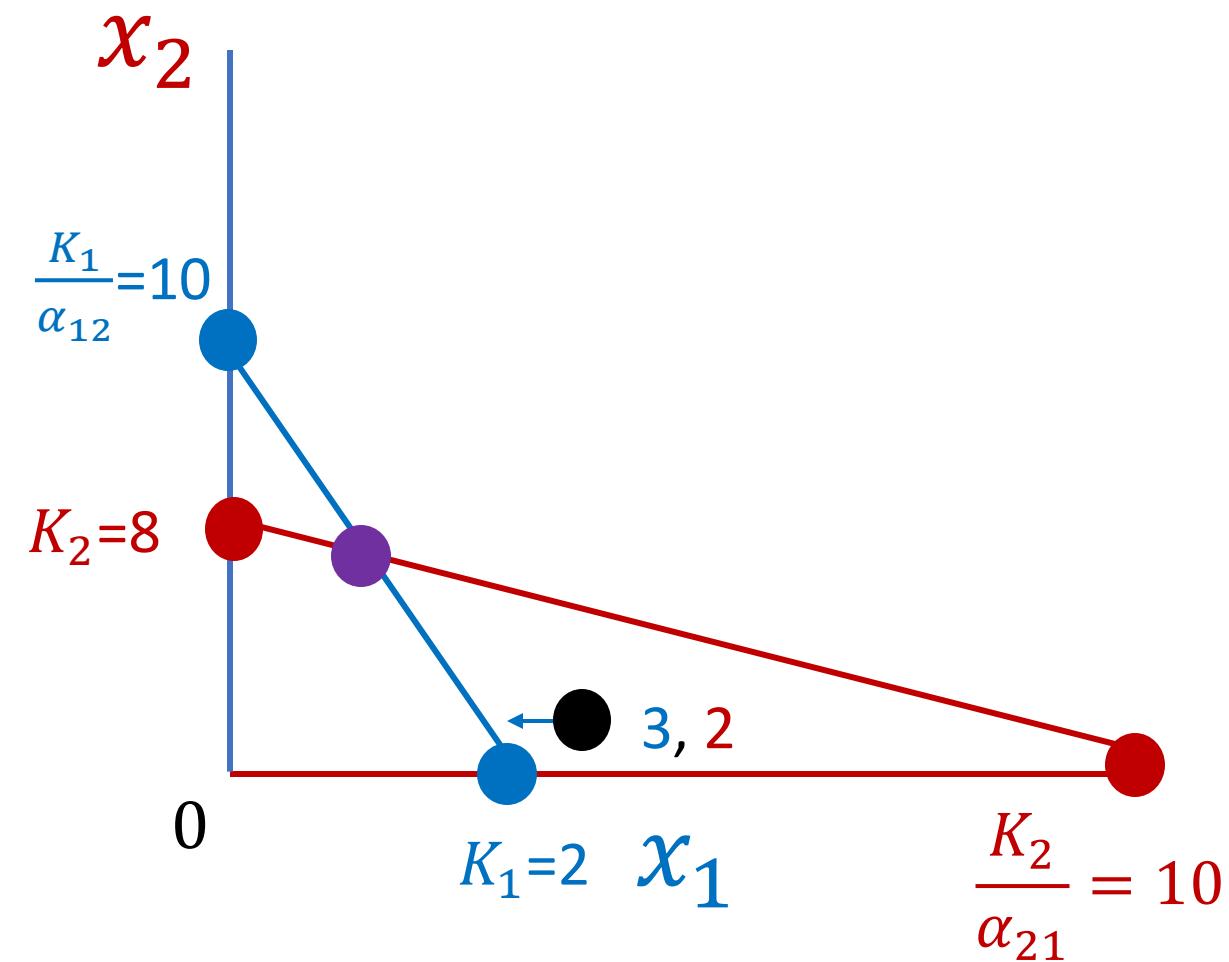
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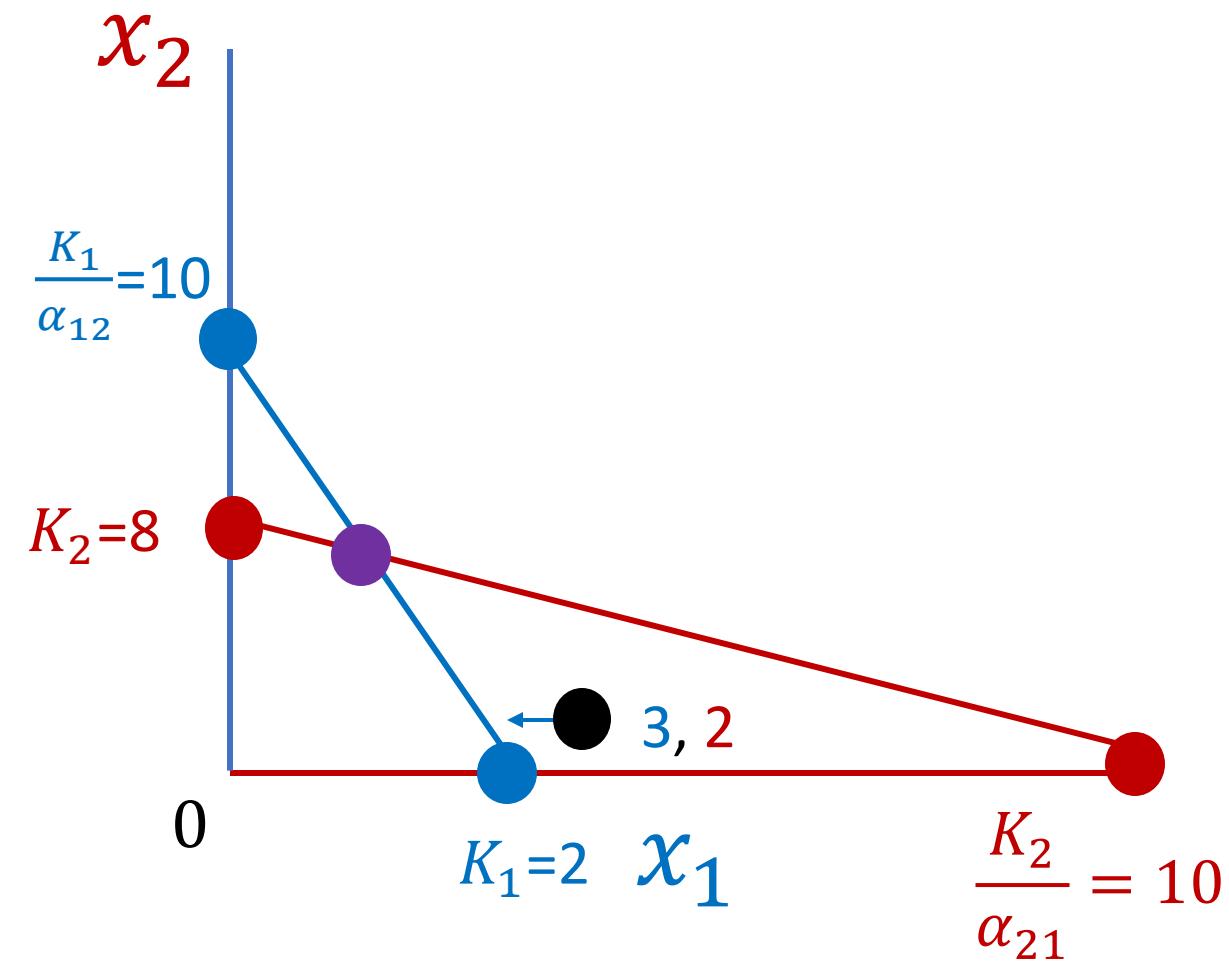
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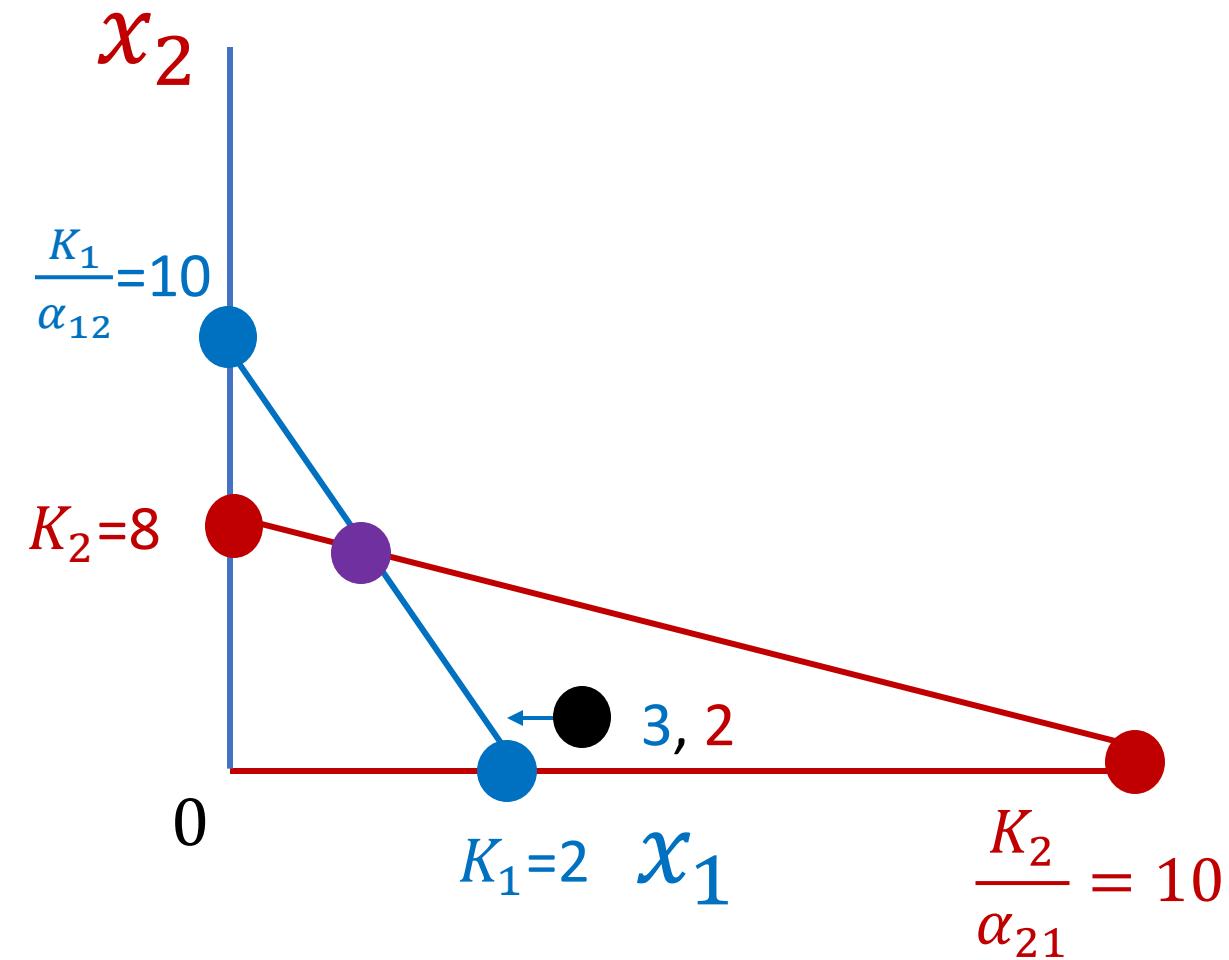
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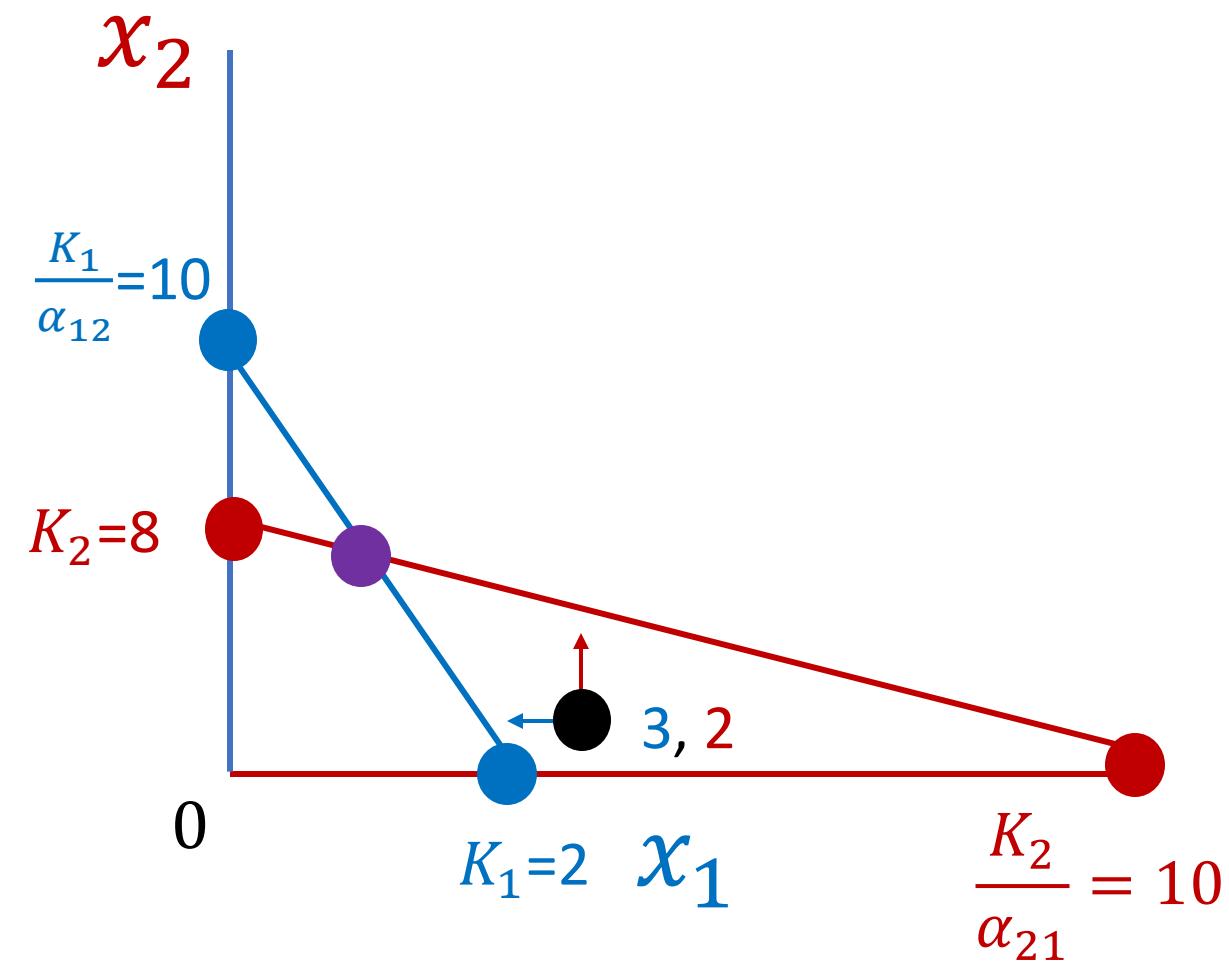
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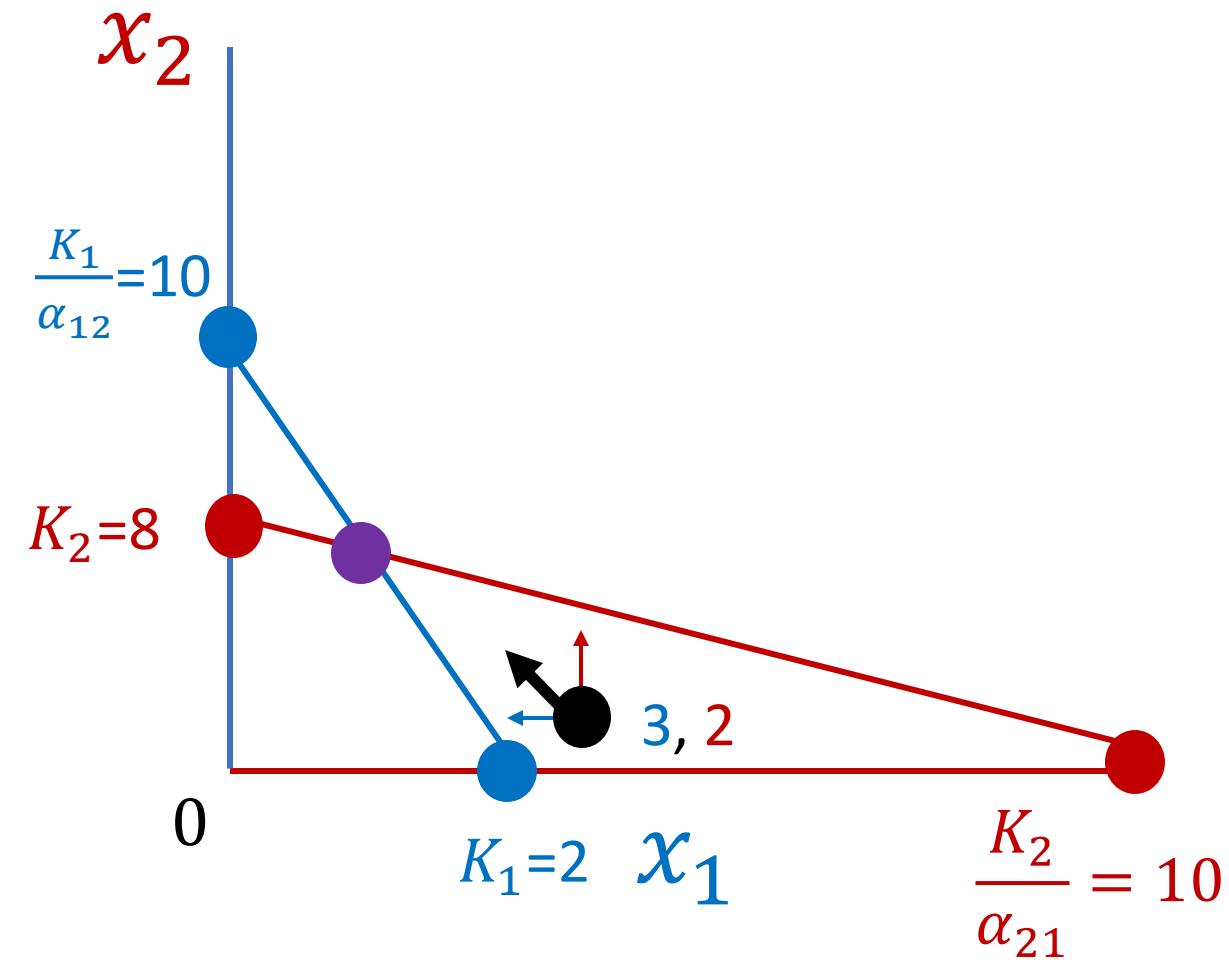
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Results replicate graphical approach!

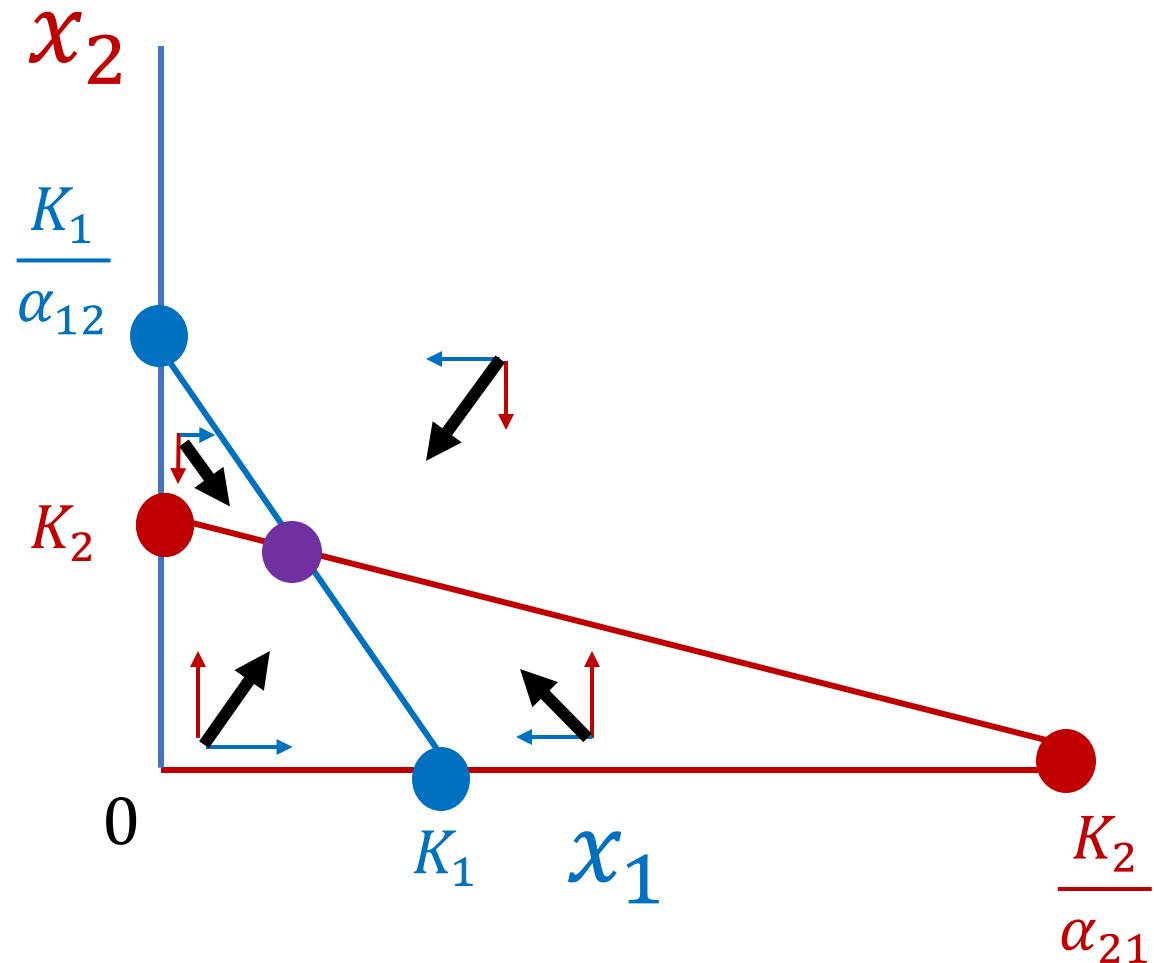


# Four possible outcomes for competition

**Case 1:**

**Stable equilibrium**, with **coexistence** at:

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



# Four possible outcomes for competition

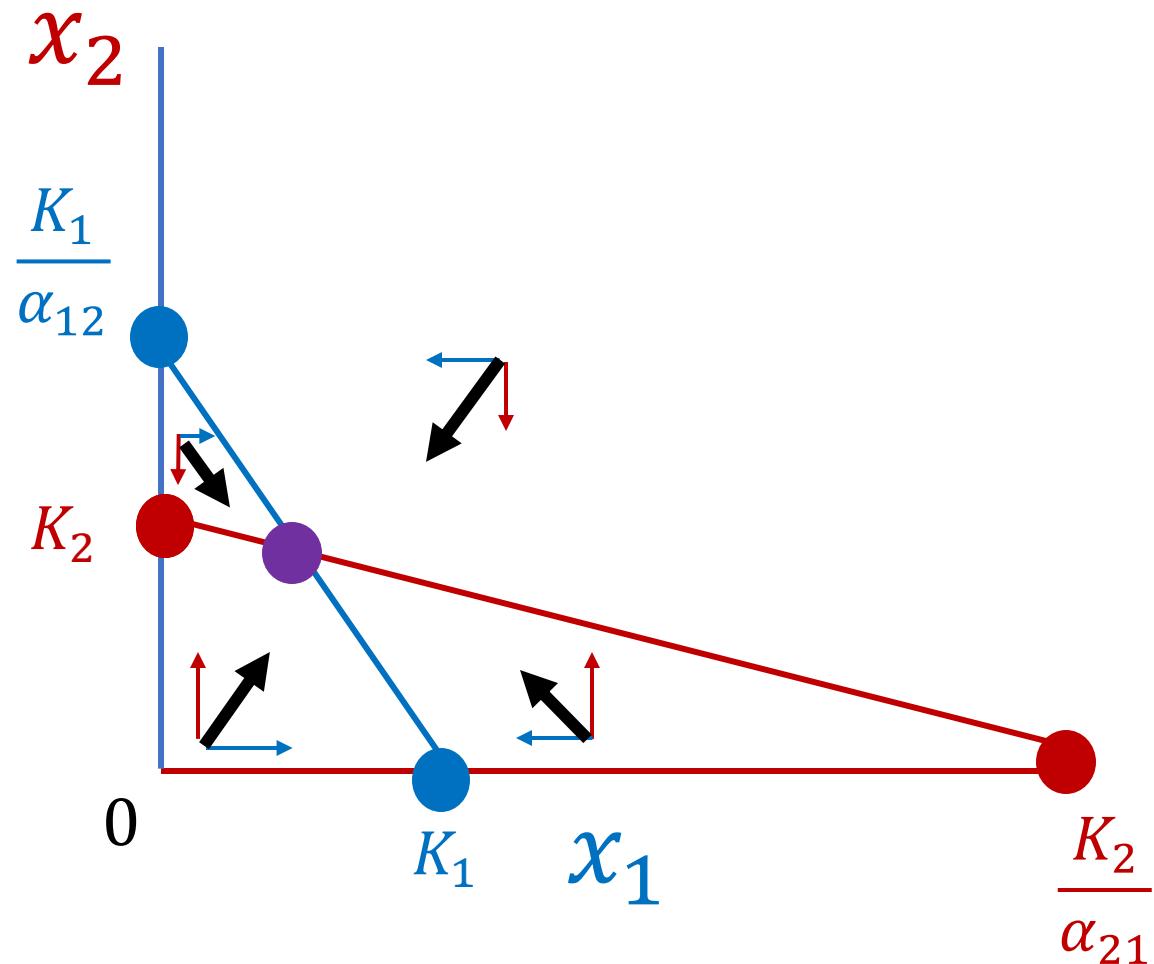
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$$\frac{K_1}{\alpha_{12}} > K_2 \text{ & } \frac{K_2}{\alpha_{21}} > K_1$$

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



# Four possible outcomes for competition

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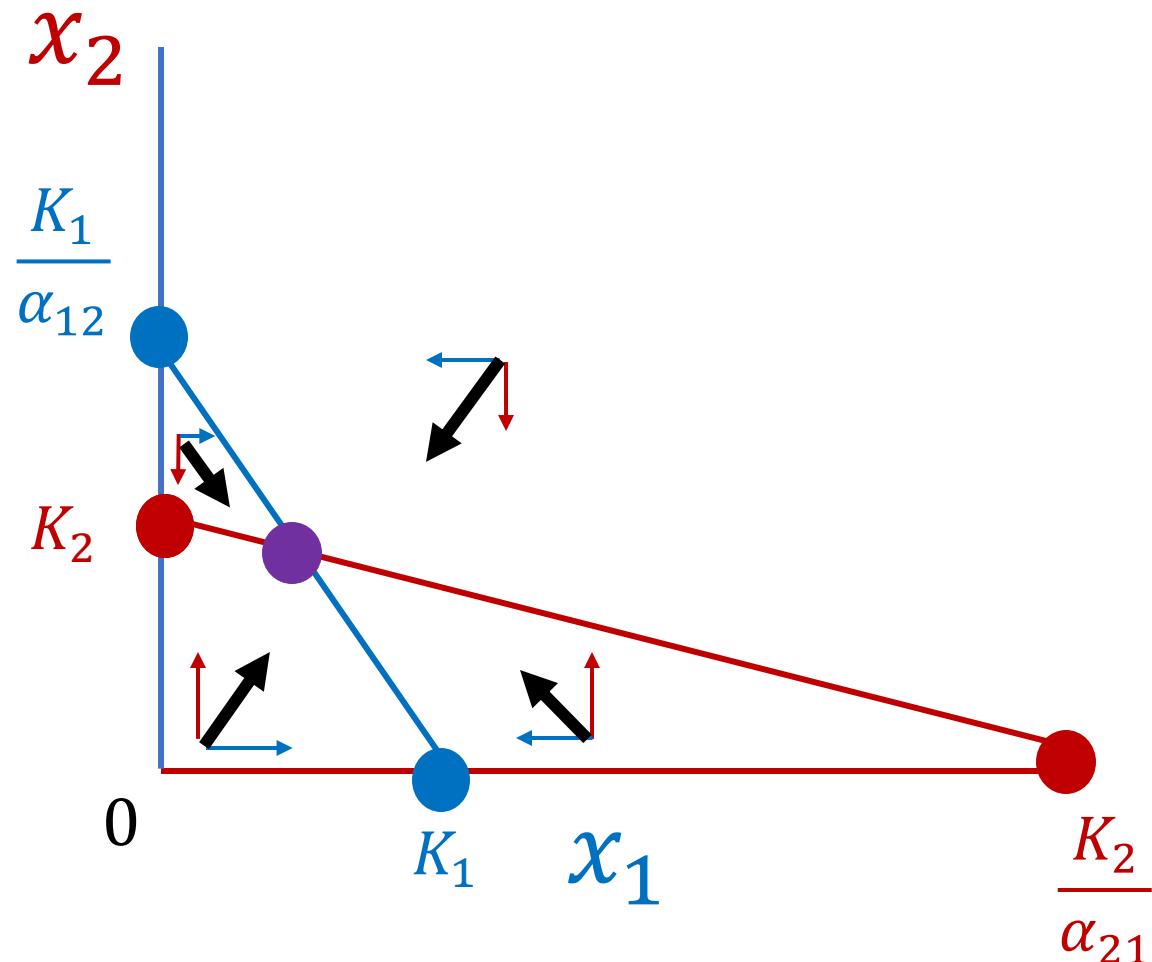
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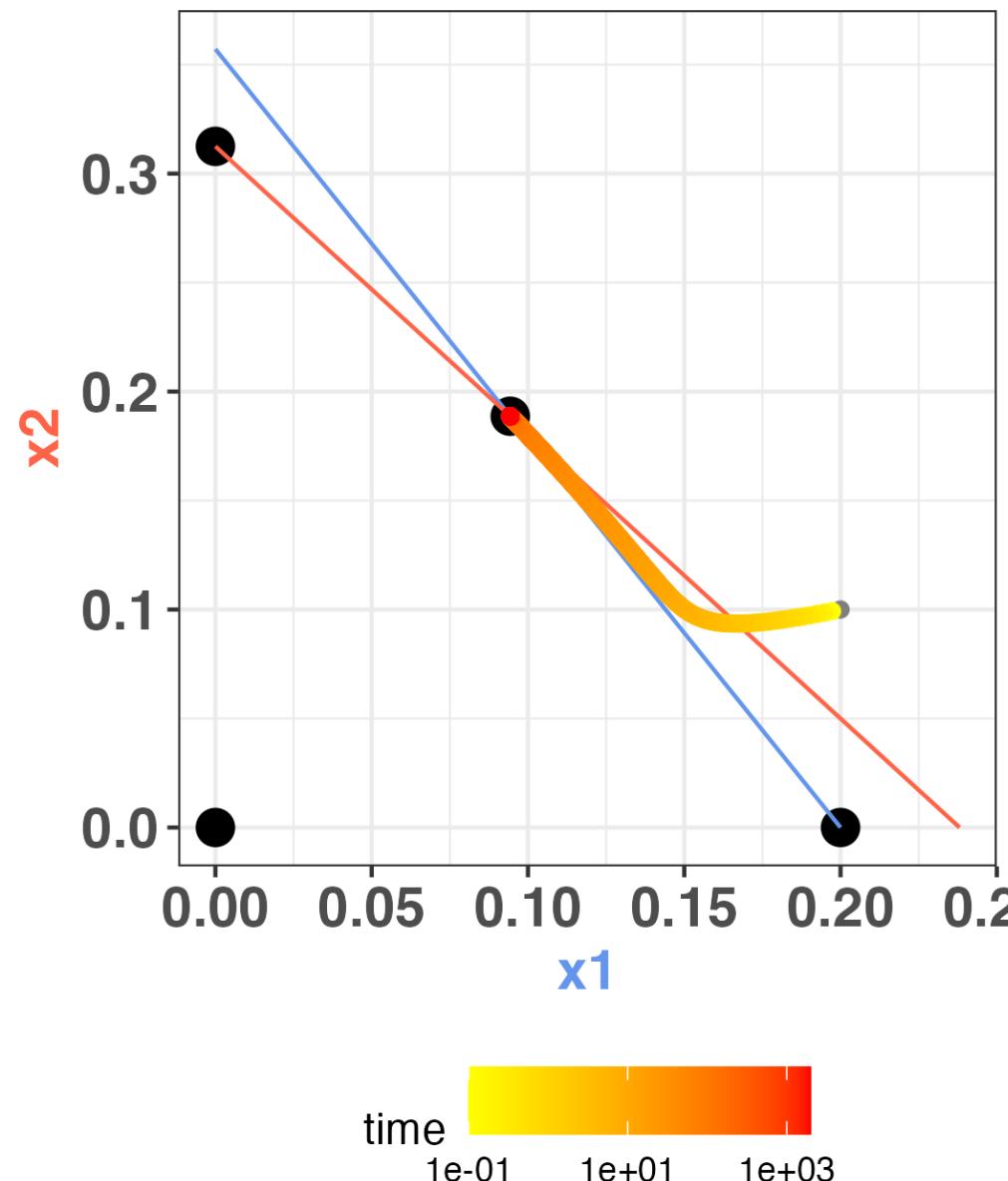
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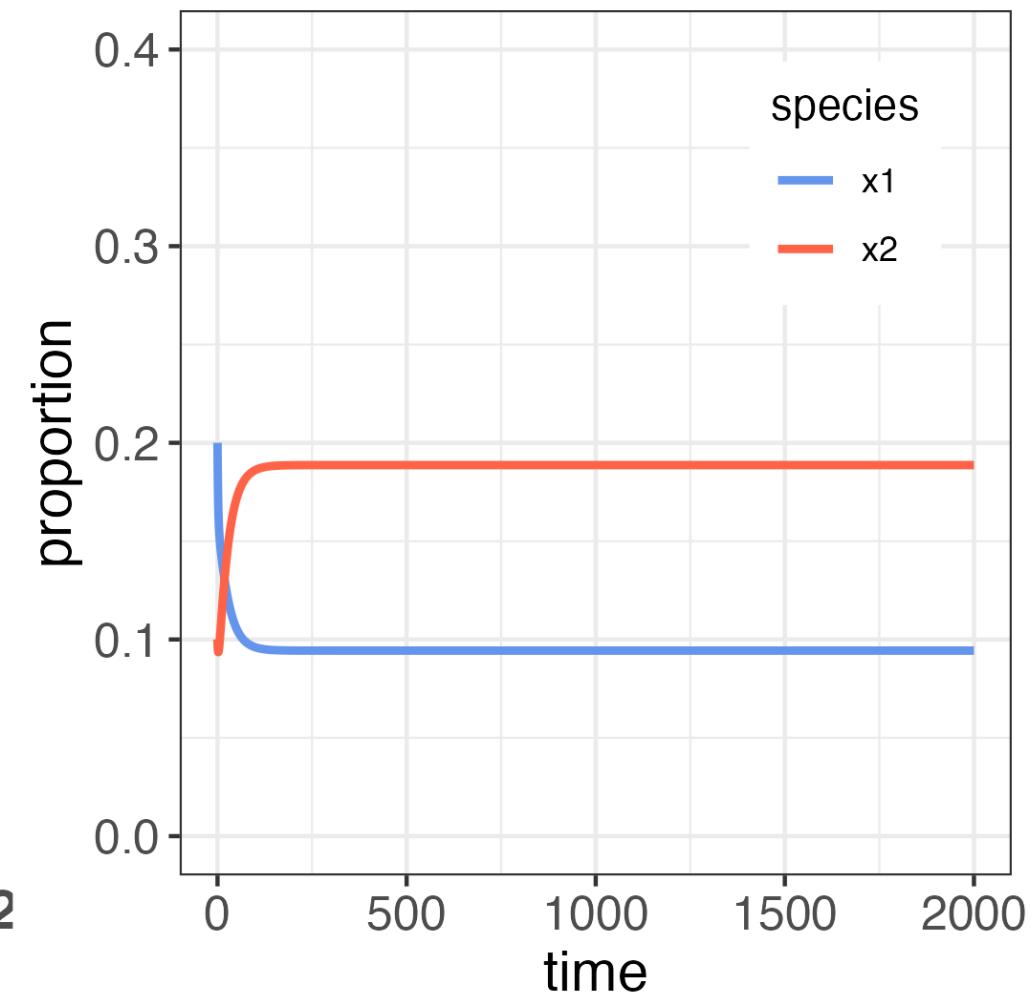
- Species coexist stably but **below carrying capacity** for each individual population.
- Intraspecific** competition is stronger than **interspecific** competition.



**Case 1:**  
**Stable equilibrium, with coexistence:**



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

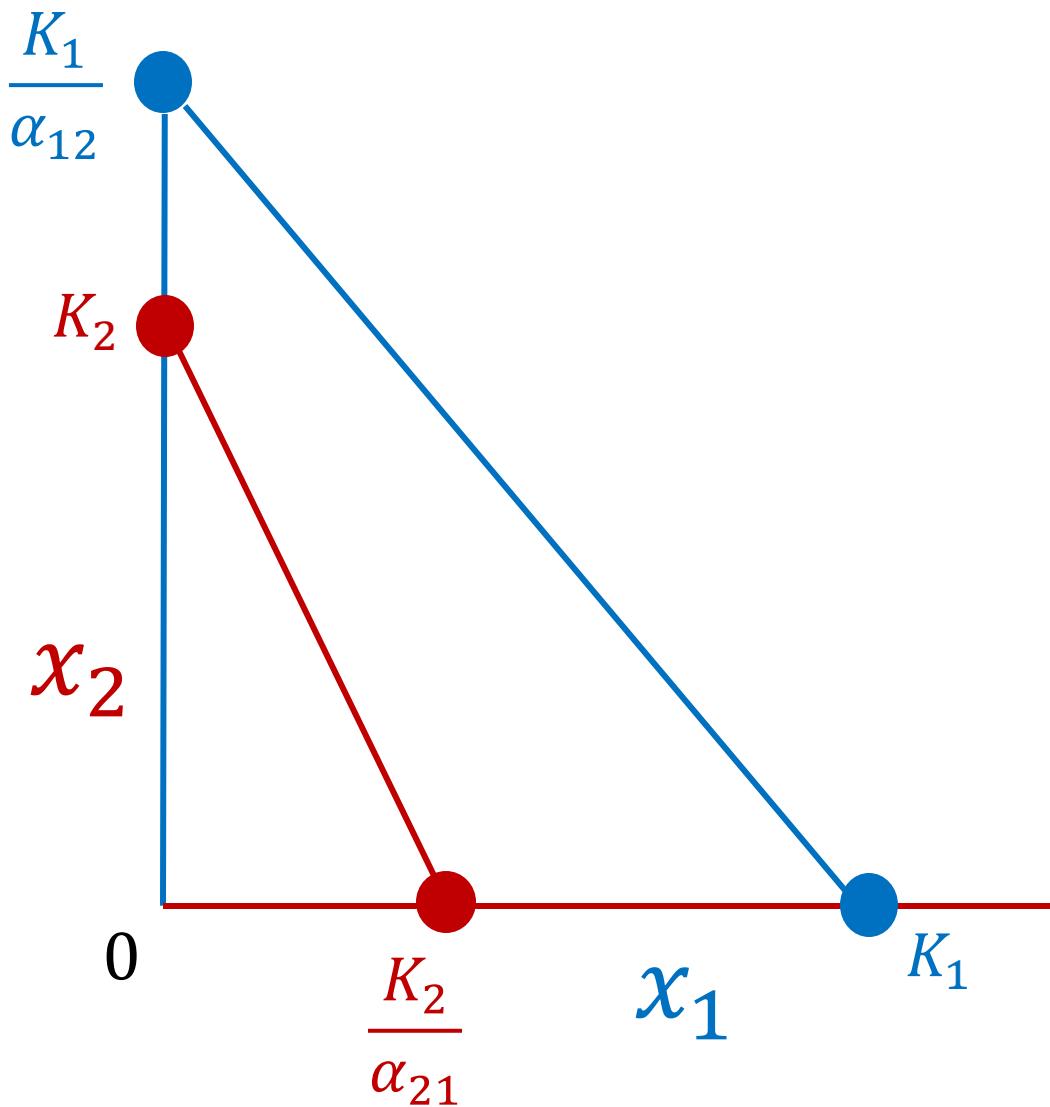


# Four possible outcomes for competition

**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

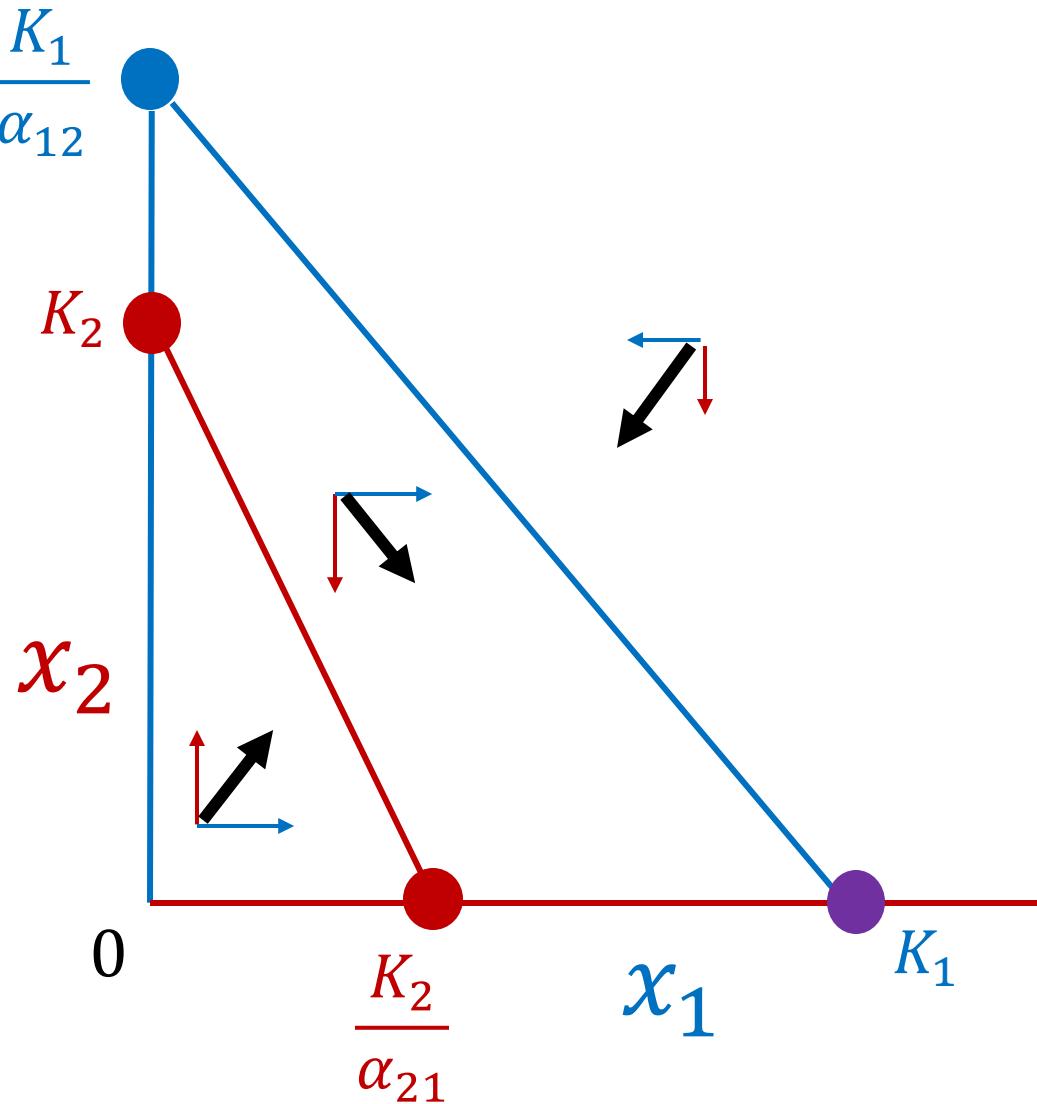
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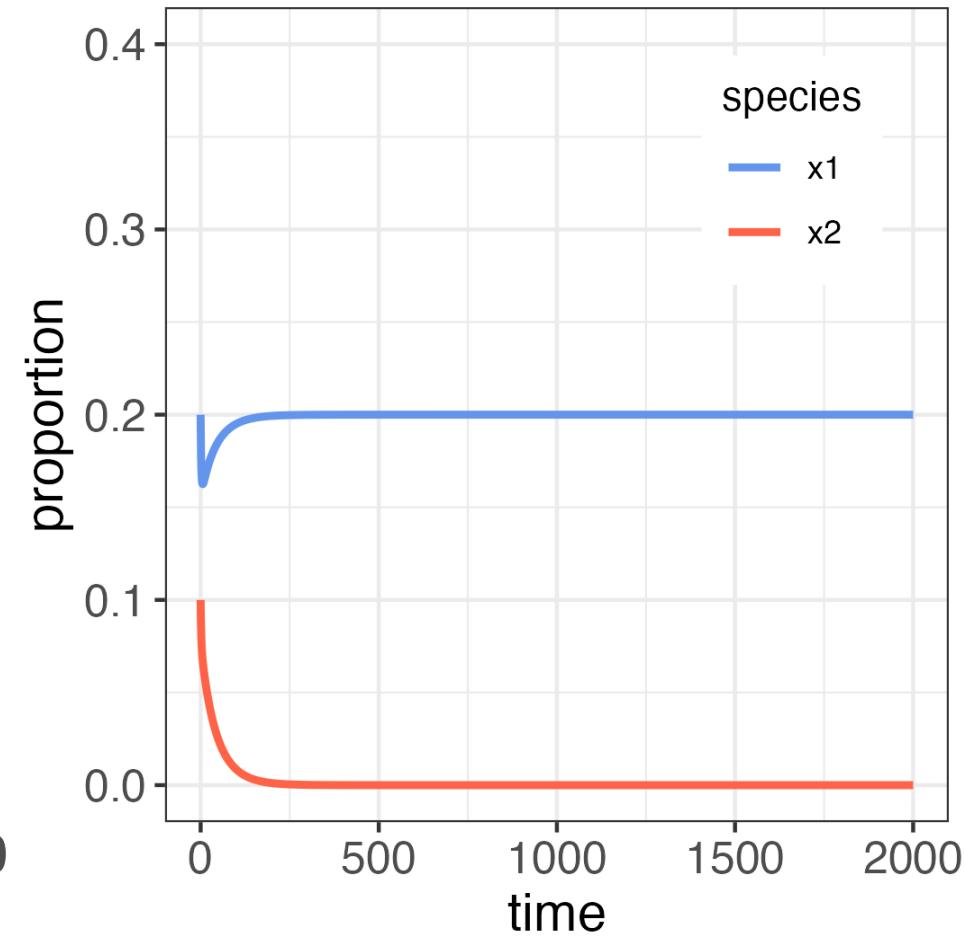
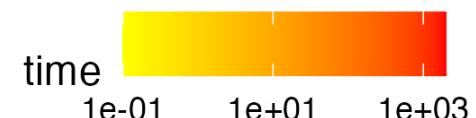
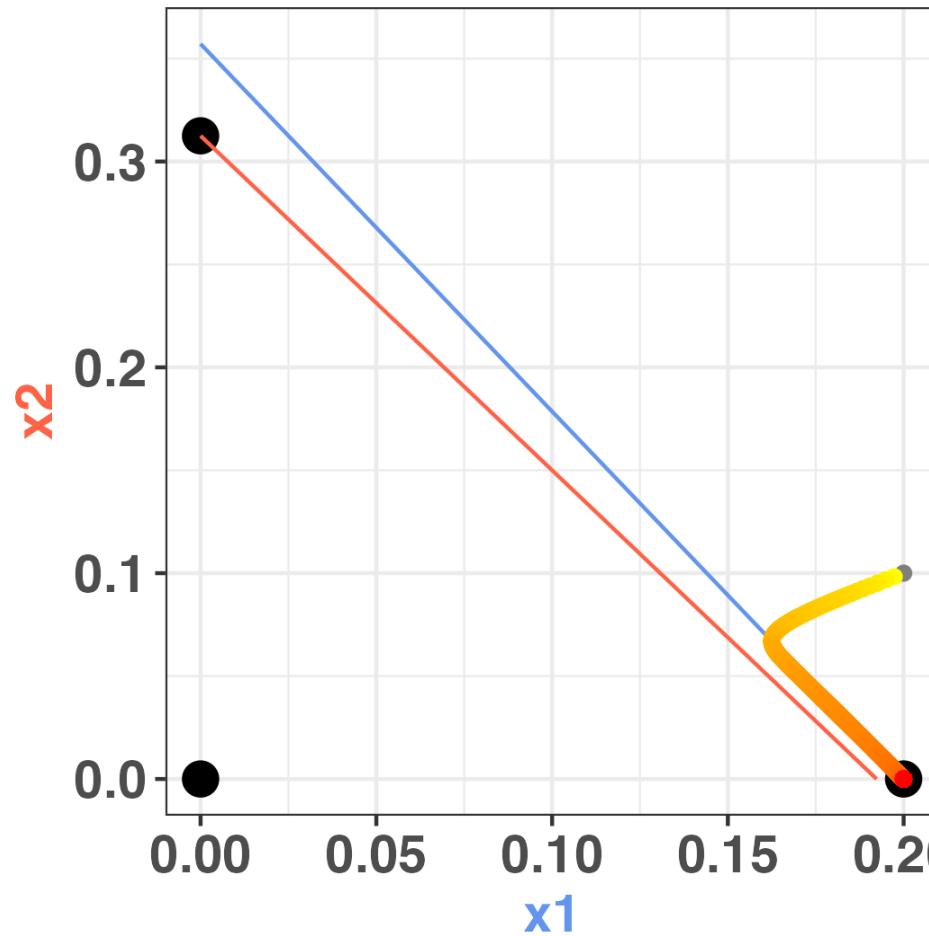
System collapses to equilibrium:

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



**Case 2:**  
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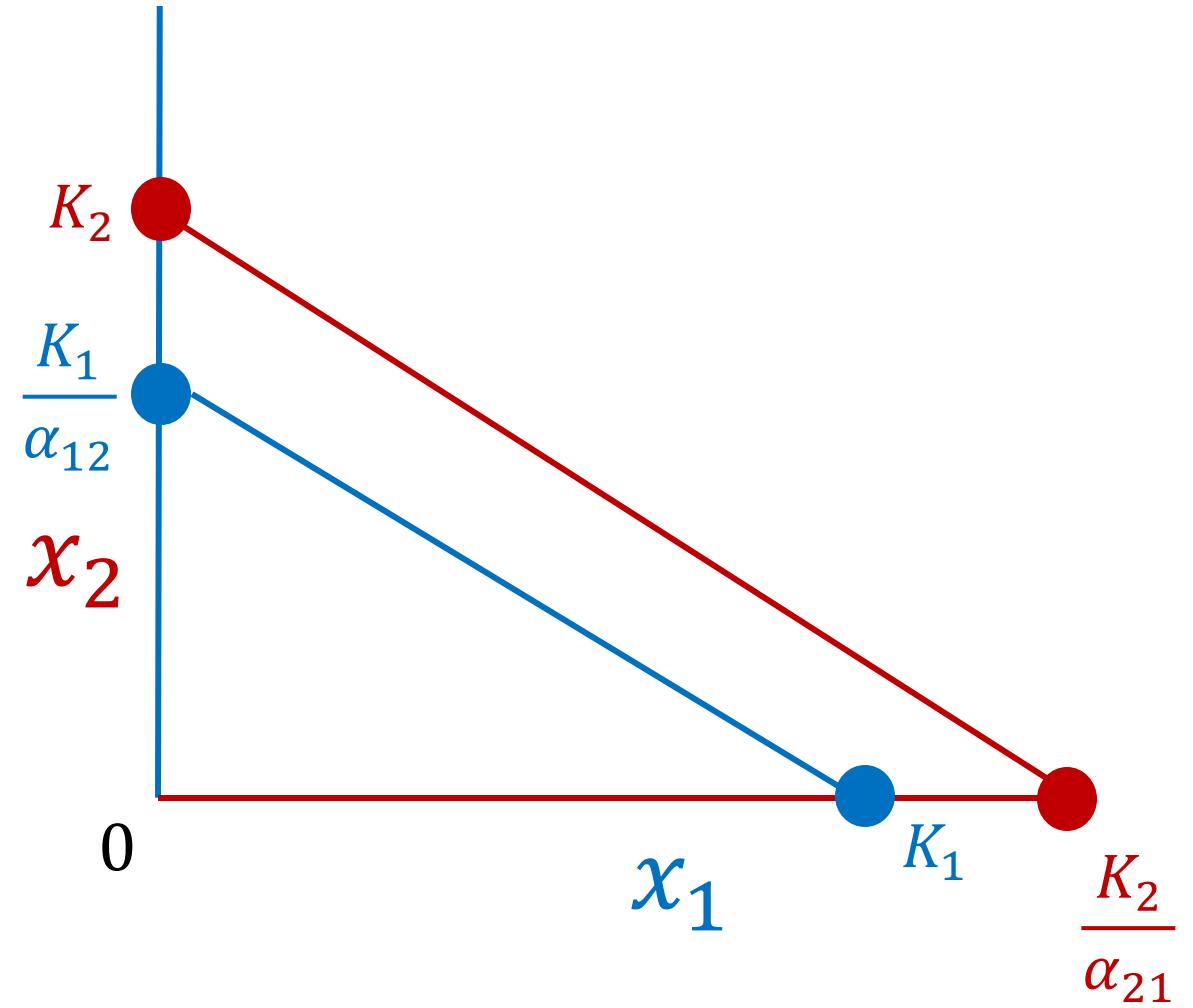


# Four possible outcomes for competition

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

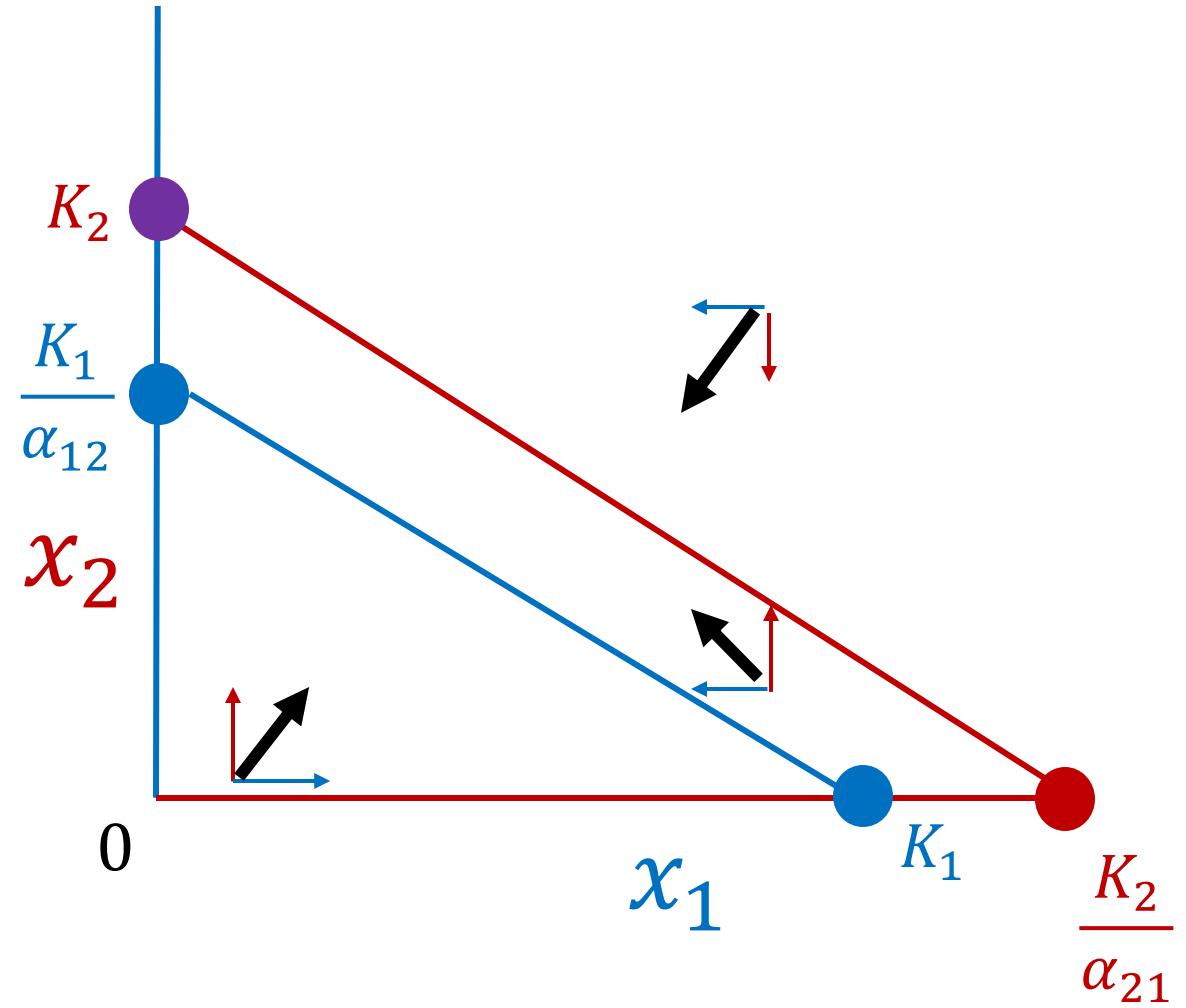
Case 3:

Species 2 outcompetes species 1

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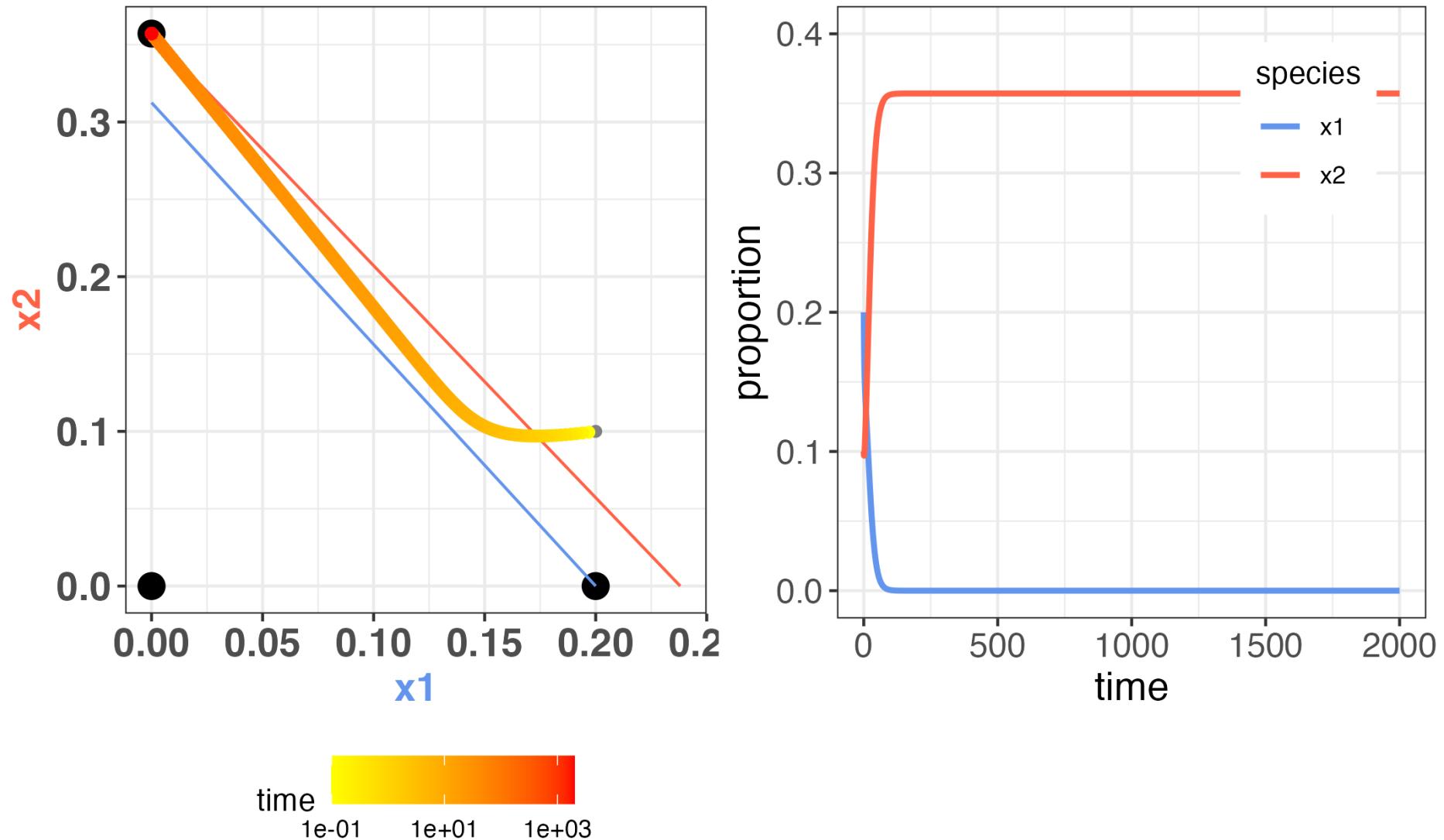
System collapses to equilibrium:

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



**Case 3:**  
**Species 2 outcompetes species 1**

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

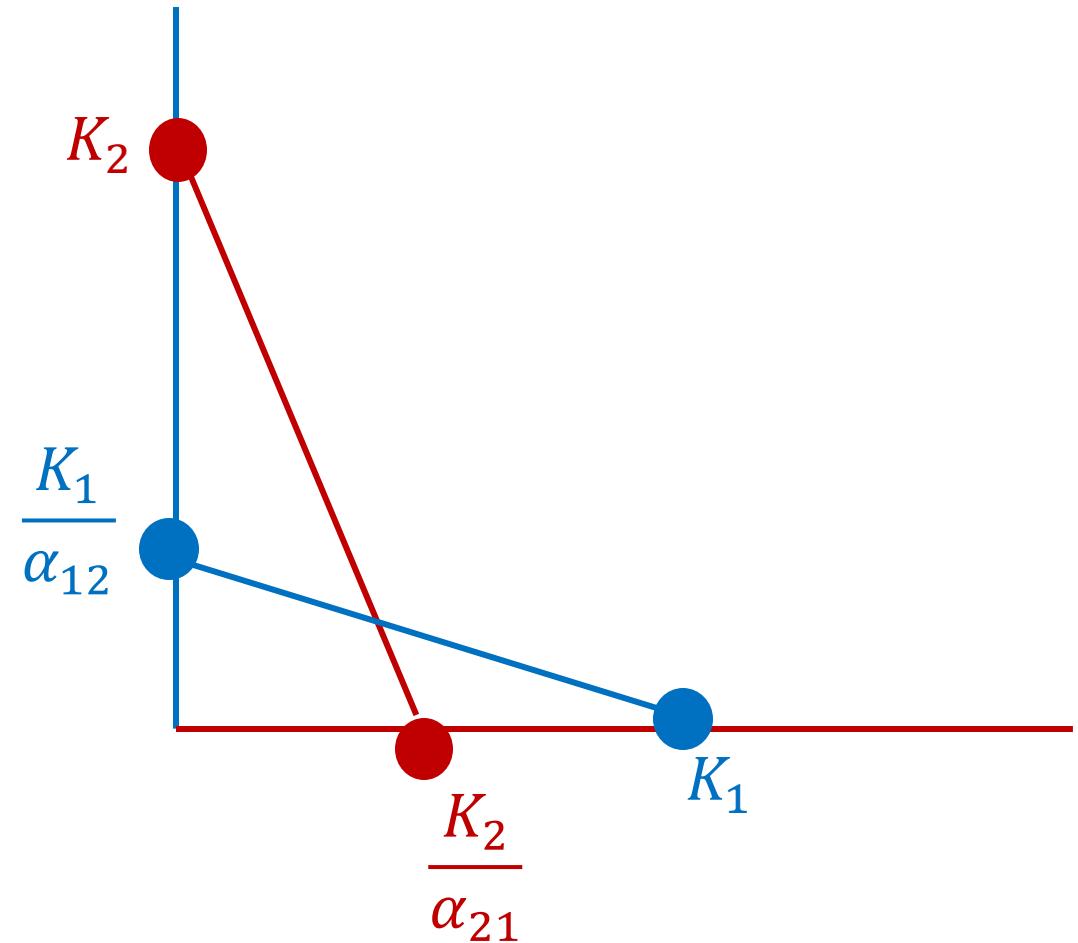


# Four possible outcomes for competition

## Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.



# Four possible outcomes for competition

## Case 4: Precedence

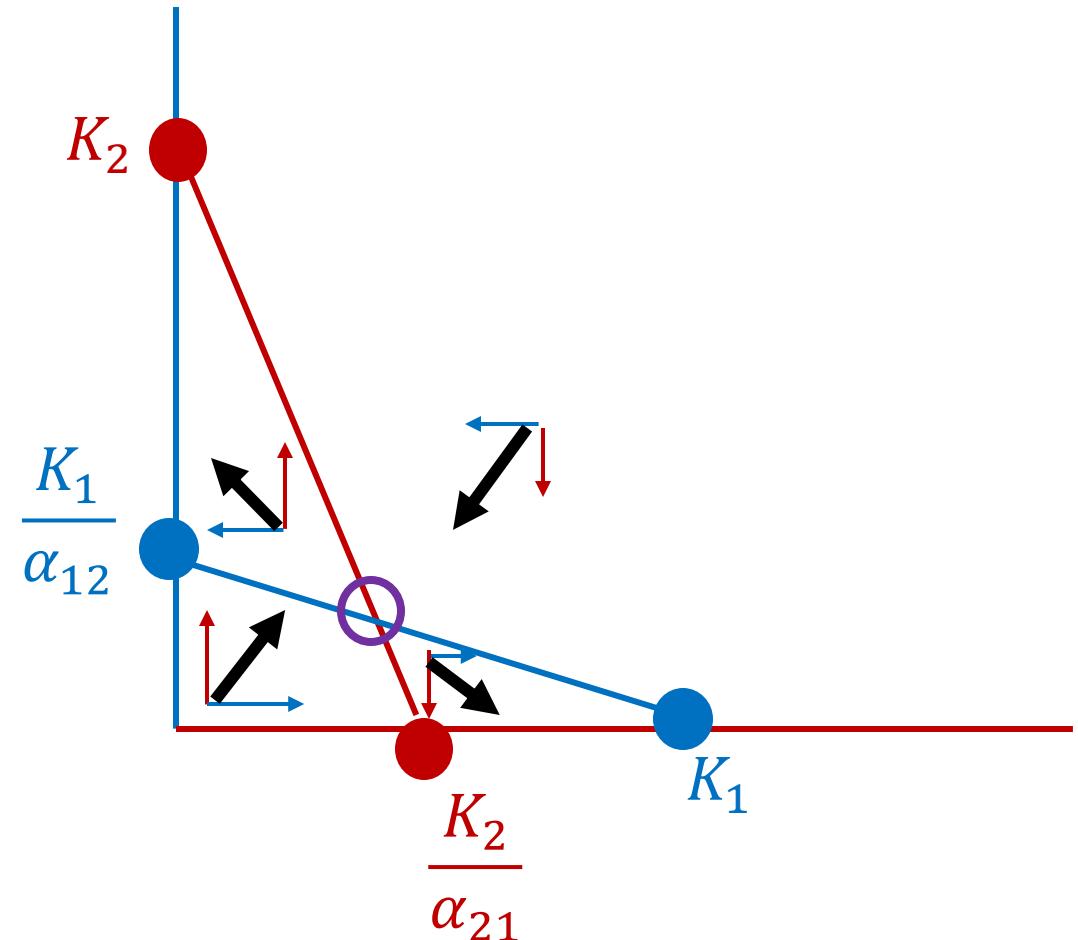
Aggressive interspecific competition.

Outcome depends on starting conditions.

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

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

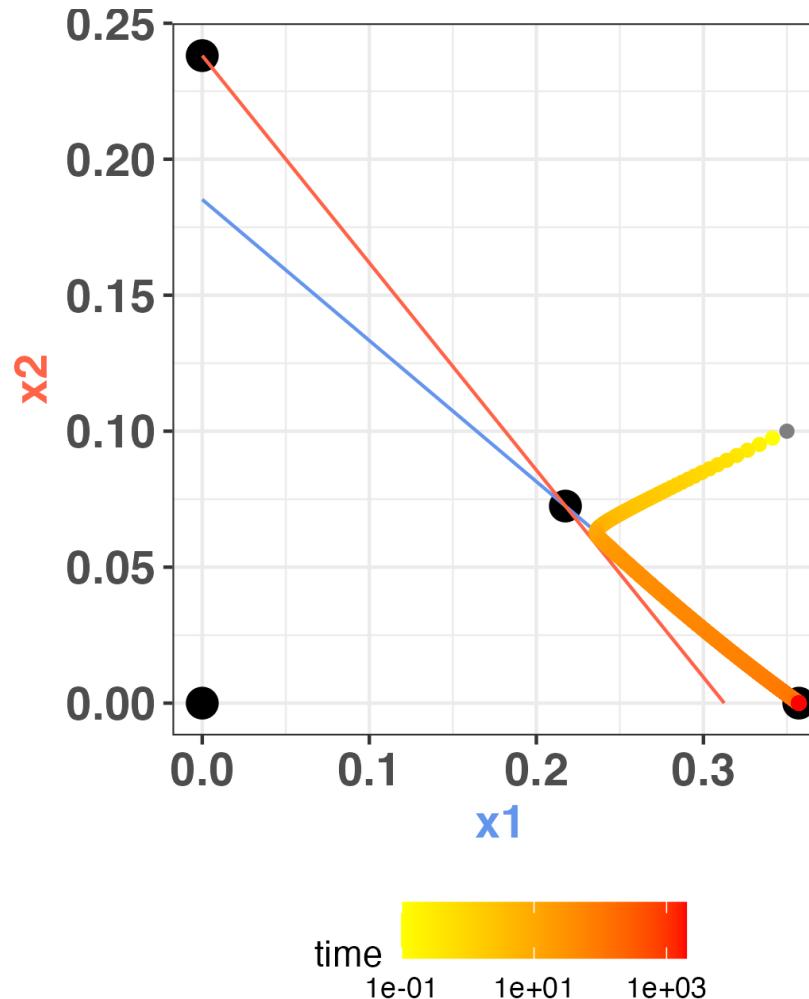
- **System will move towards either single species equilibria** ( $x_1^* = 0$ ;  $x_2^* = K_2$  OR  $x_1^* = K_1$ ;  $x_2^* = 0$ ), depending on starting conditions.
- Under extremely unrealistic starting conditions, system will sit at an **unstable equilibrium** that will collapse in either direction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



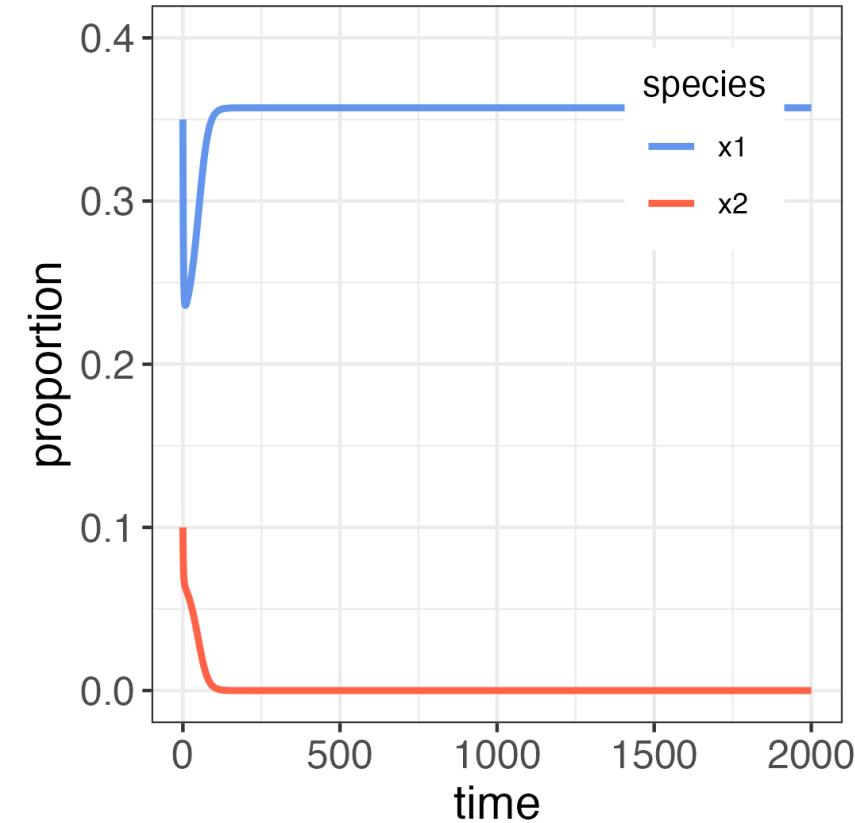
## Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.



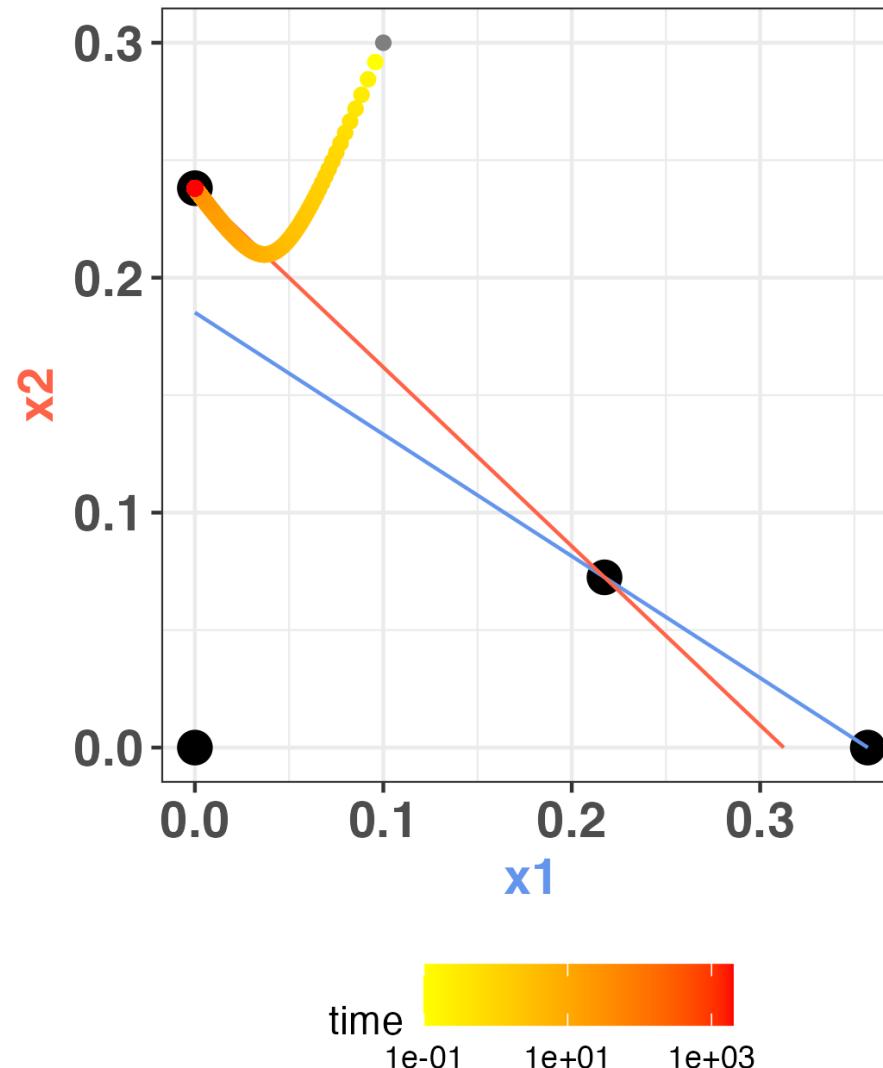
Here, **x1 outcompetes x2**



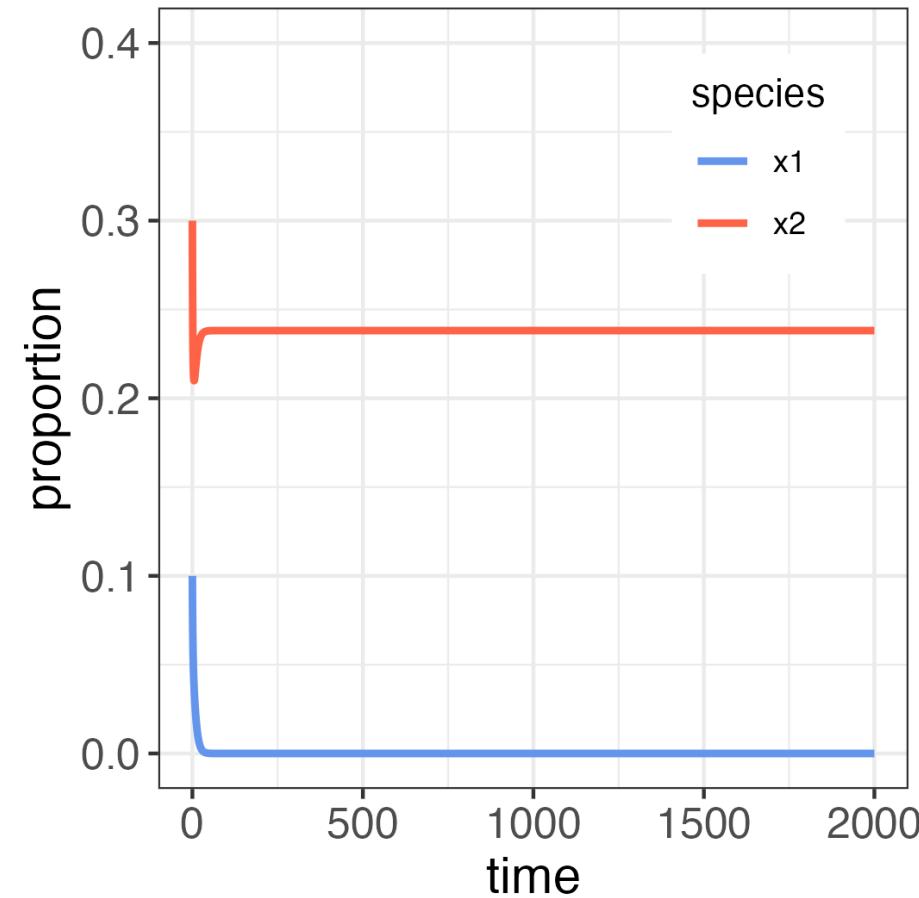
## Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.



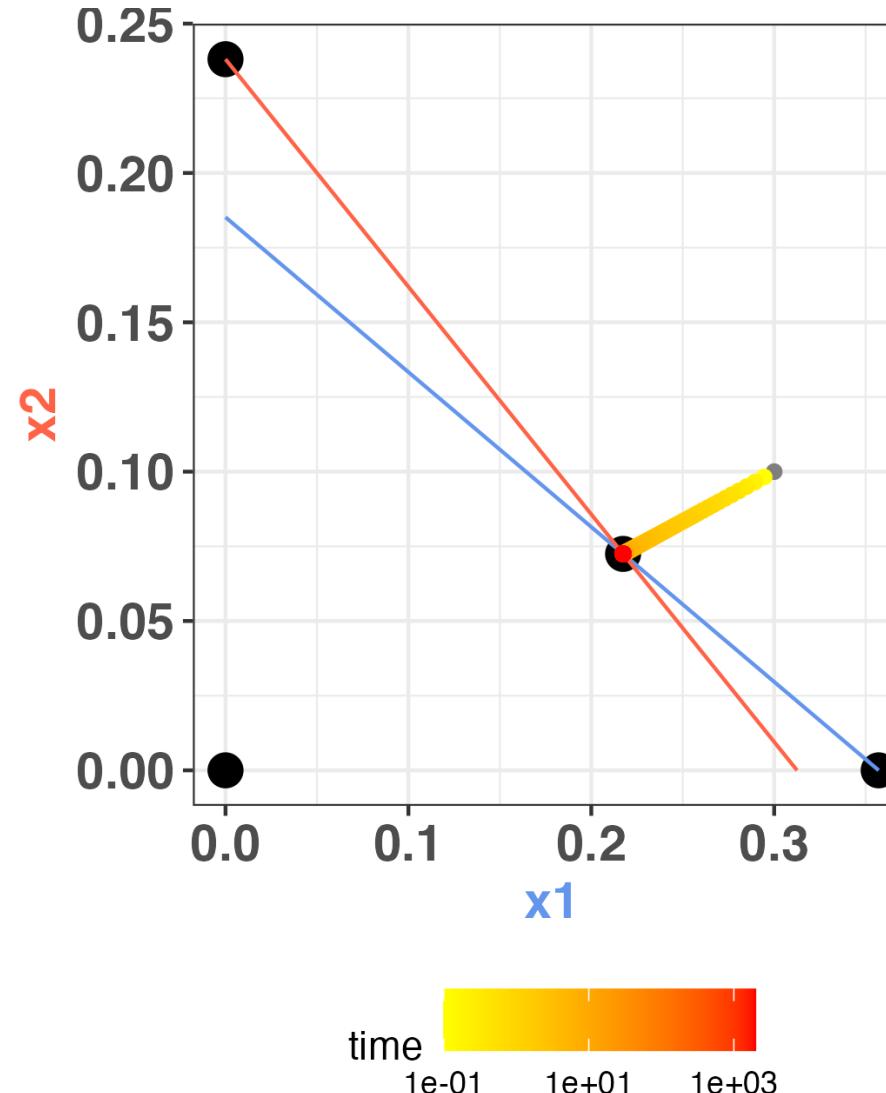
Here,  **$x_2$  outcompetes  $x_1$**



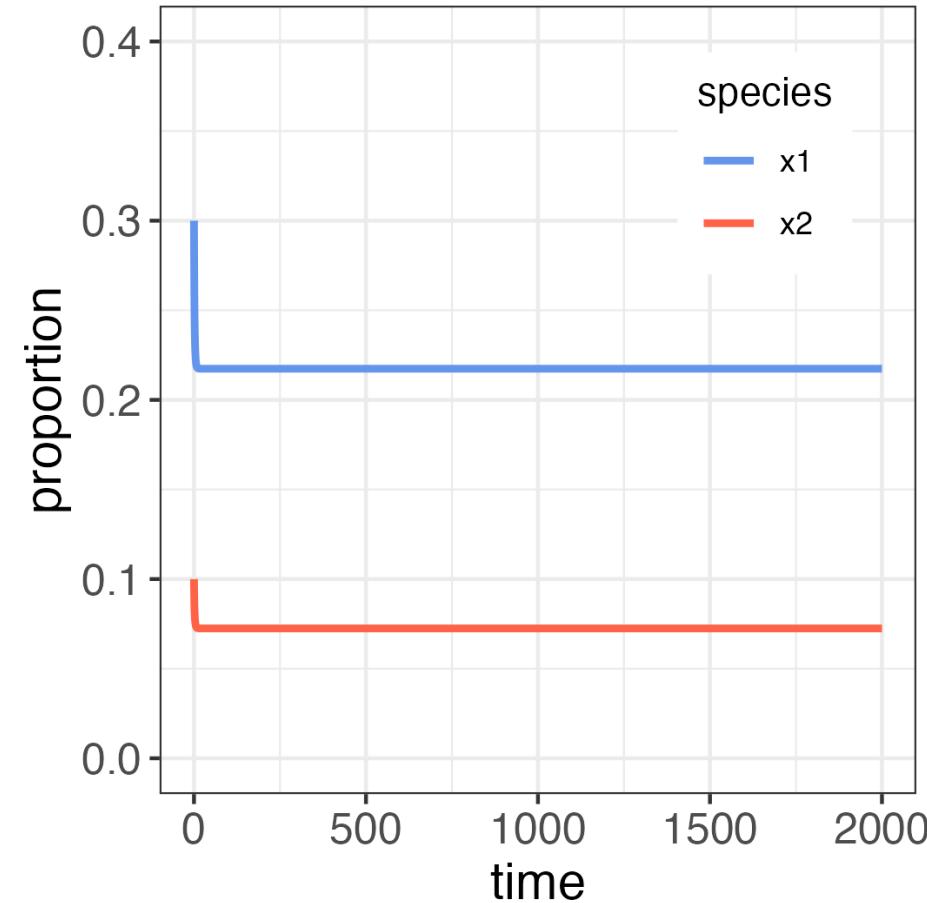
## Case 4: Precedence

Aggressive interspecific competition.

Outcome depends on starting conditions.

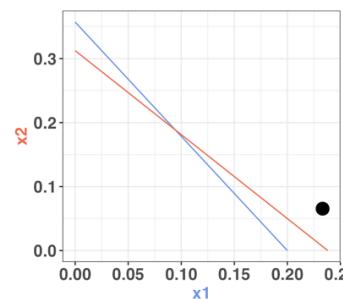


Here, **coexistence**





**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 x<sub>2</sub> will outcompete x<sub>1</sub>, so we will e... 21%
- B Species x<sub>1</sub> will outcompete x<sub>2</sub>, so we will e... 34%
- C Both species will coexist at the sta... 32%
- D The outcome depends on the initial conditions. 13%

Power



Instructions

Responses

Correctness

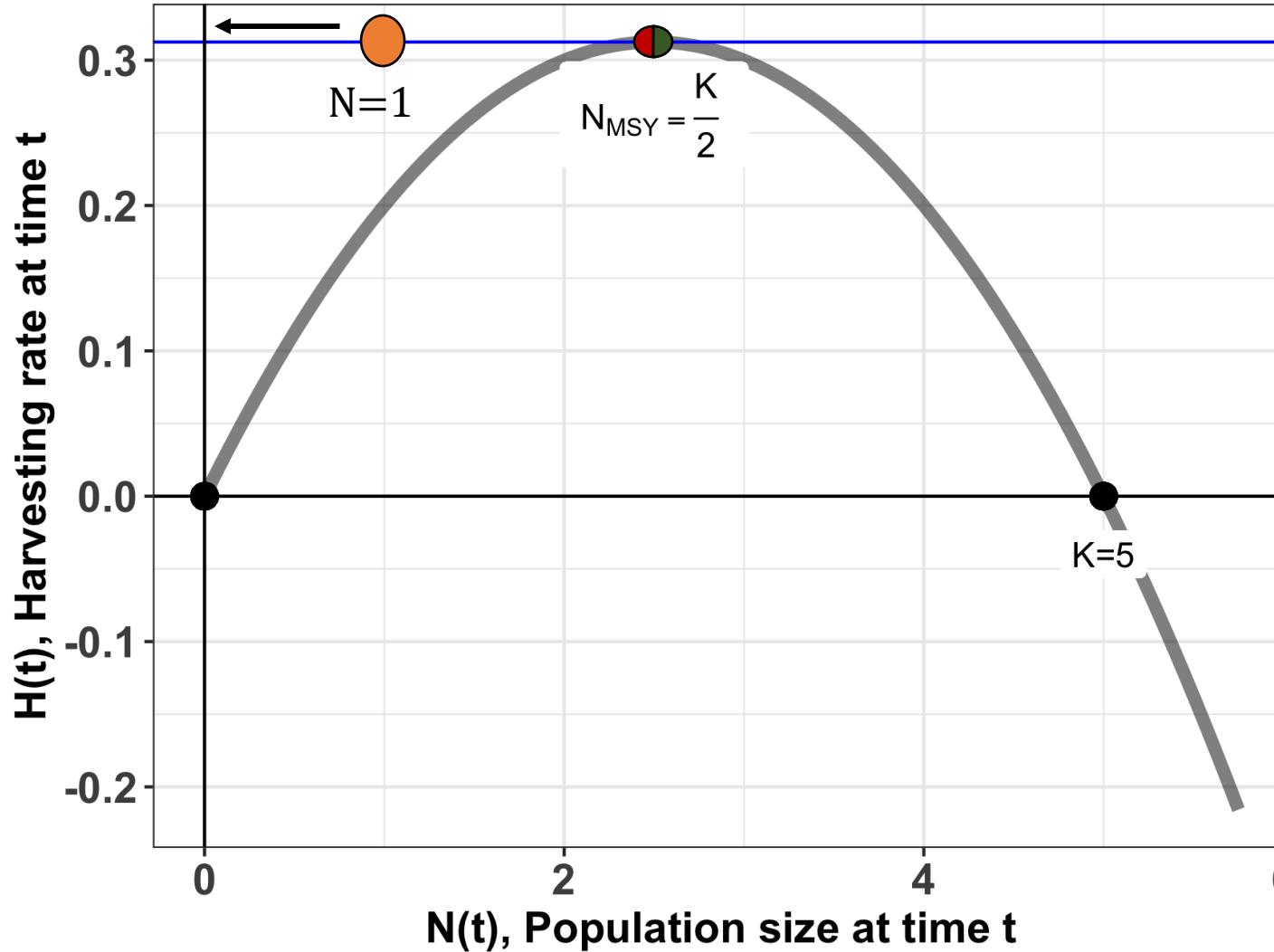
More



Clear responses

Remember MSY, the semi-stable equilibrium:

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



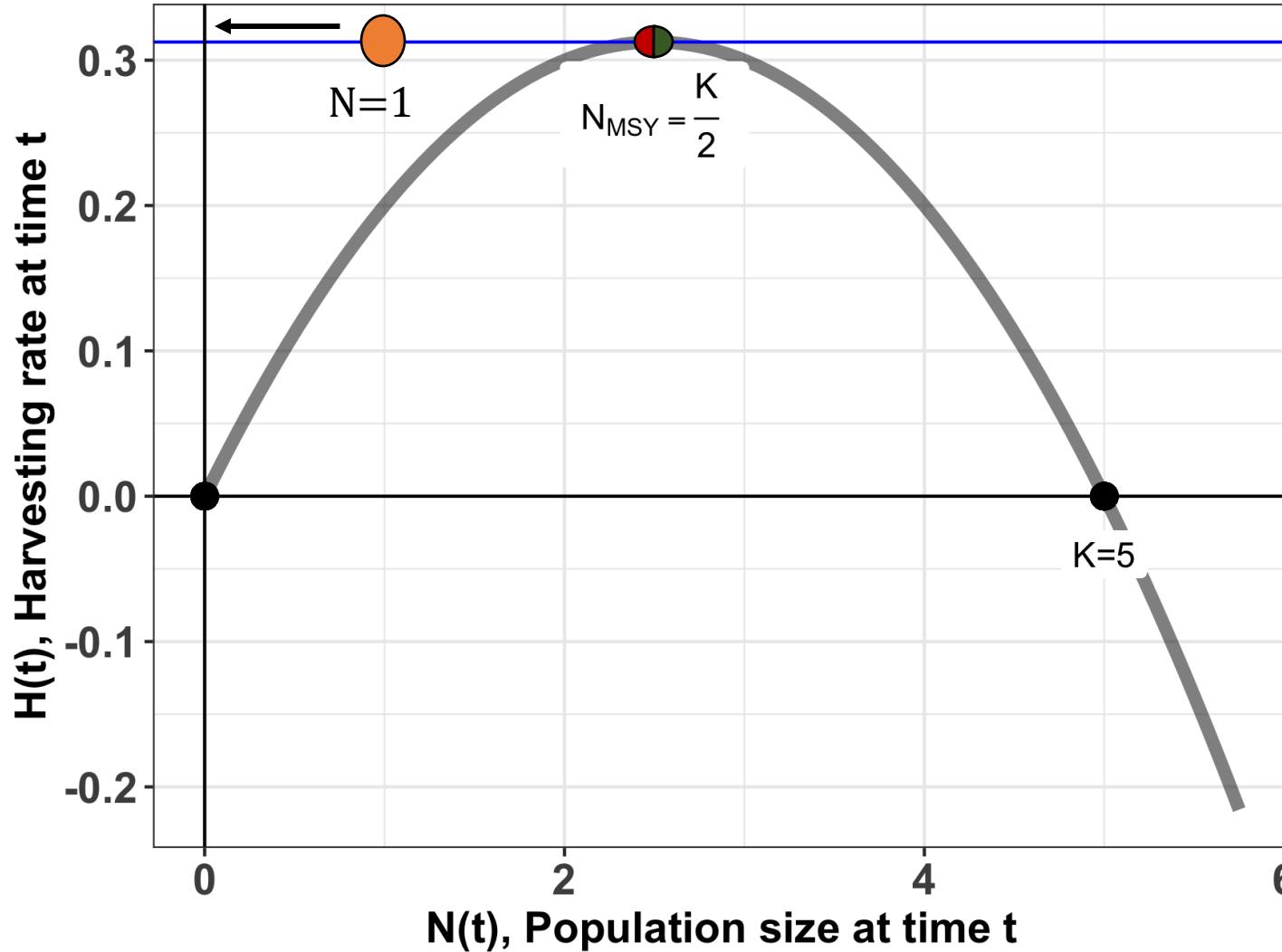
$$K=5$$
$$r=0.25$$
$$H=.3125$$

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

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

Remember MSY, the semi-stable equilibrium:

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



$$K=5$$

$$r=0.25$$

$$H=.3125$$

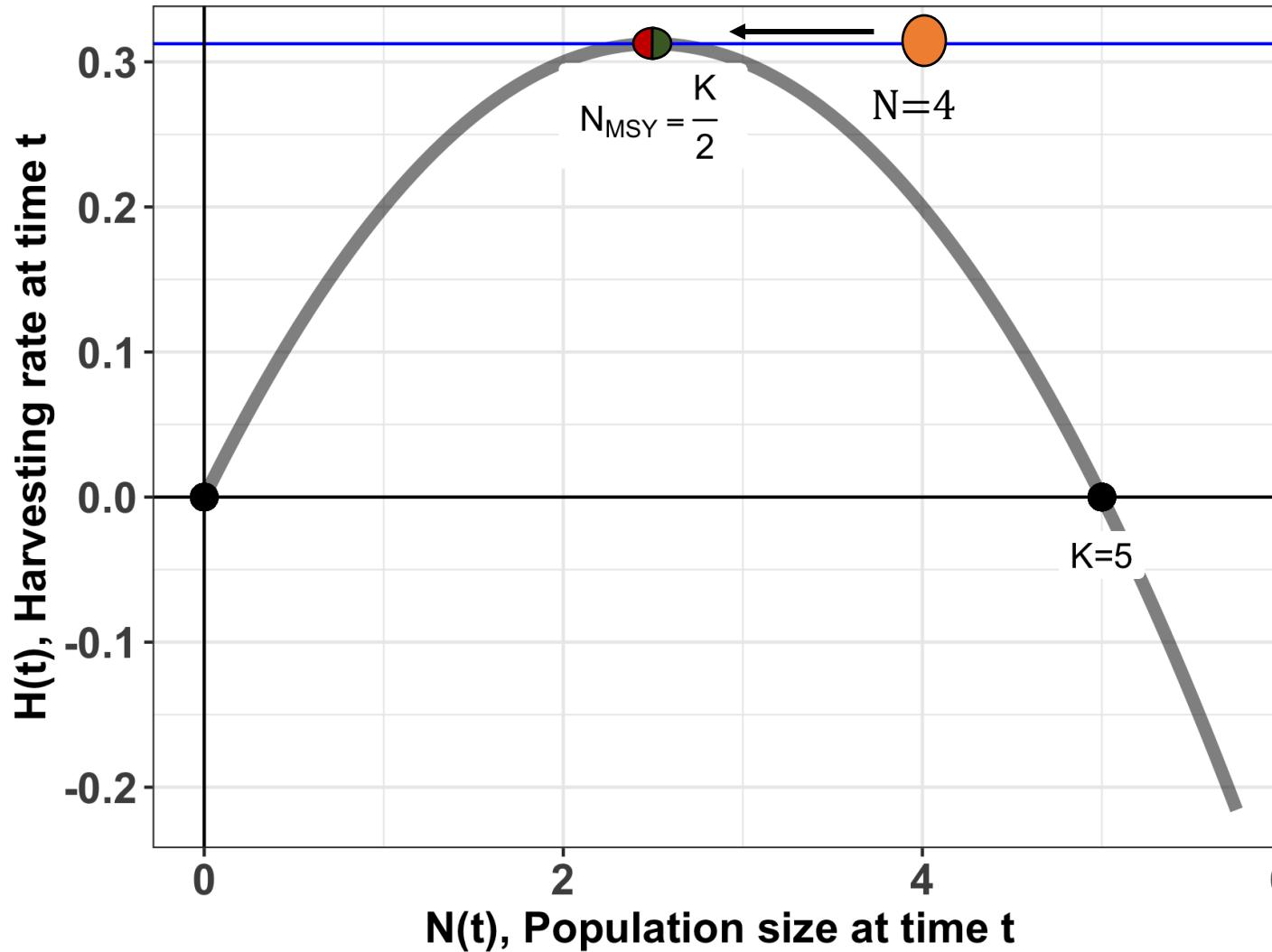
$$\frac{dN}{dt} = 0.25 * 1 \left(1 - \frac{1}{5}\right) - .3125$$

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

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

Remember MSY, the semi-stable equilibrium:

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



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

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

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

# Four possible outcomes for competition

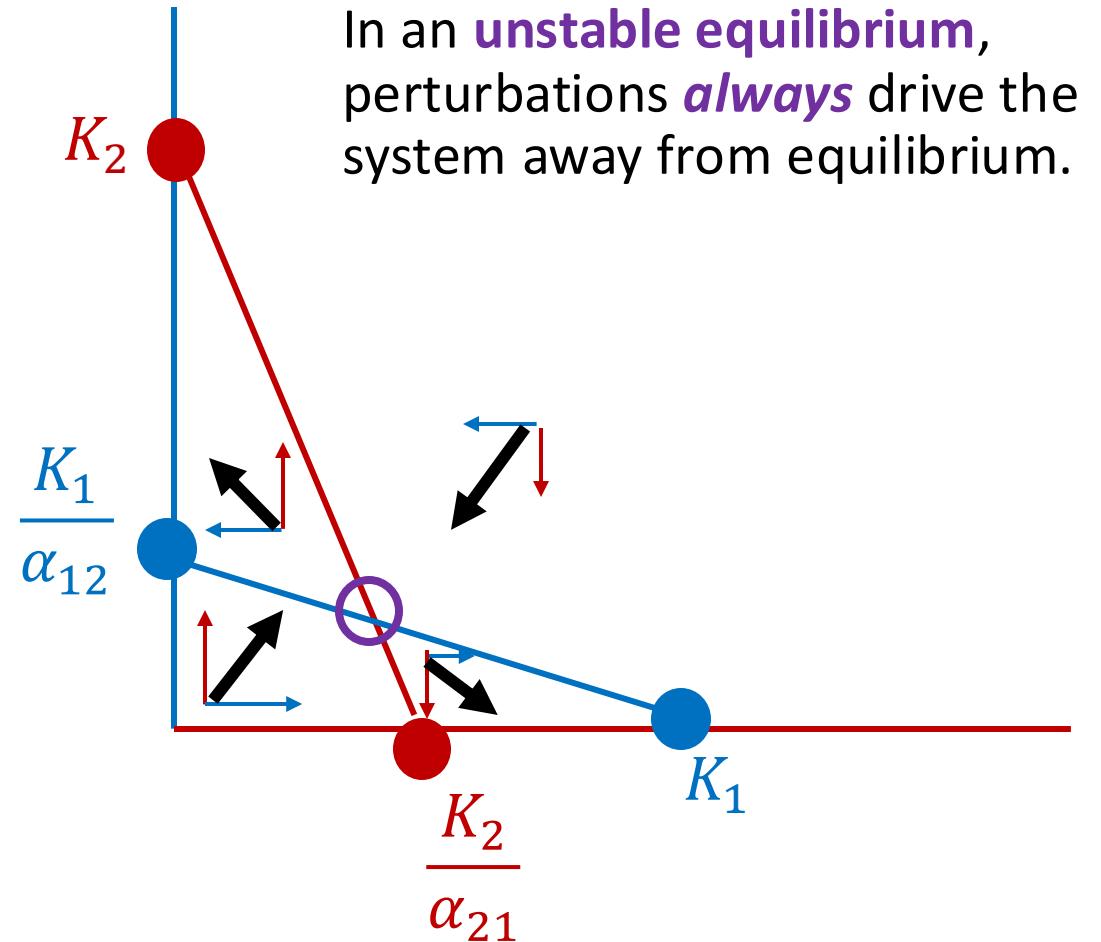
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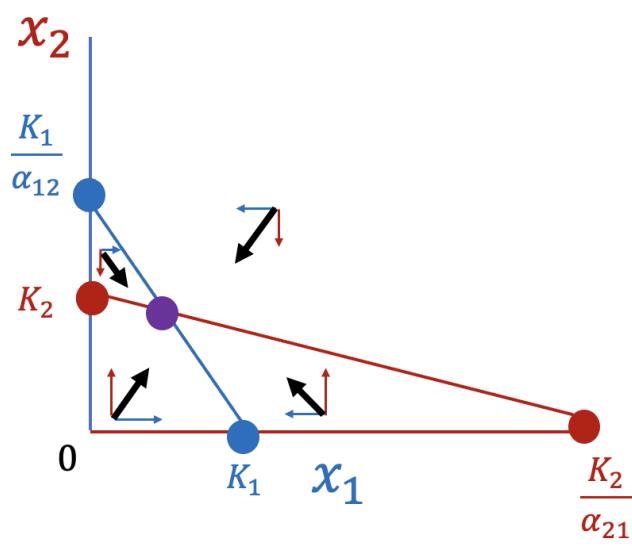
$$\frac{K_1}{\alpha_{12}} < K_2 \text{ & } \frac{K_2}{\alpha_{21}} < K_1$$

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

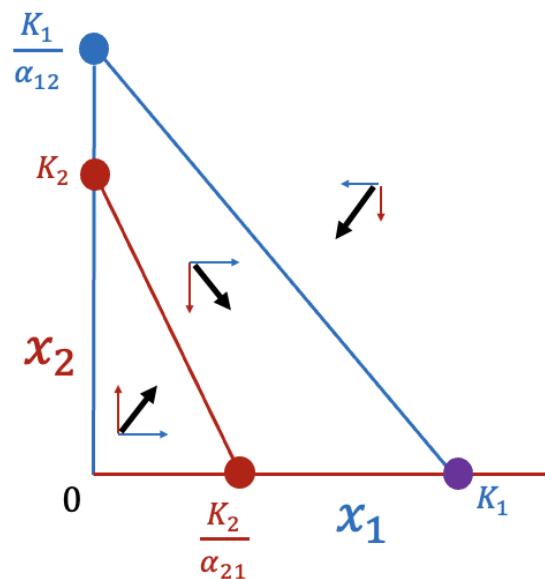


**Phase plane analysis:** graphical determination of the behavior of the state variables in a dynamical system (here, populations of animals)

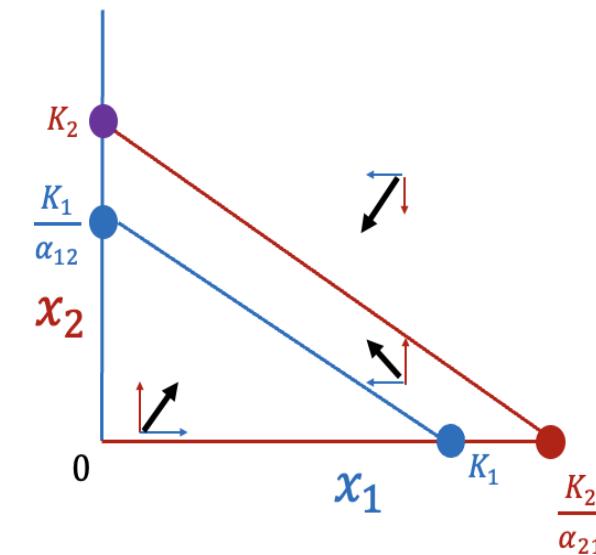
### Case 1: Stable coexistence



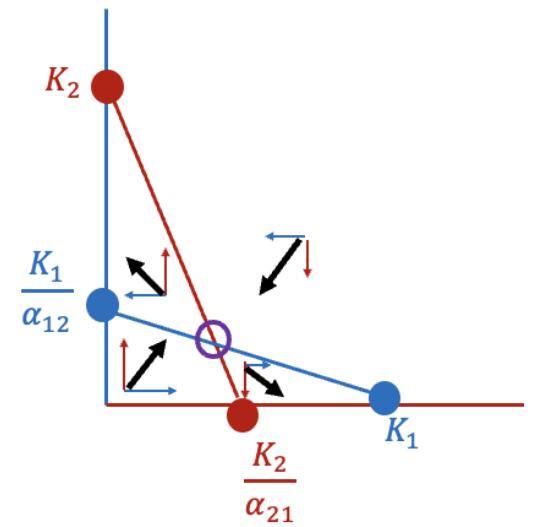
### Case 2: Spp. 1 wins



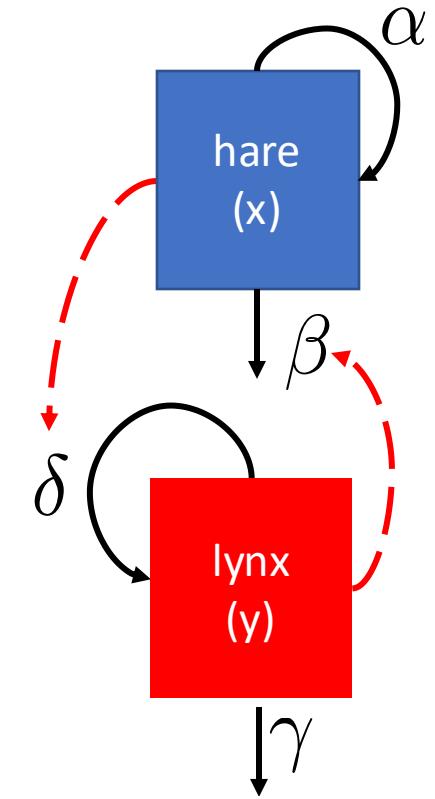
### Case 3: Spp. 2 wins



### Case 4: Precedence



Note the difference with a predator-prey model!

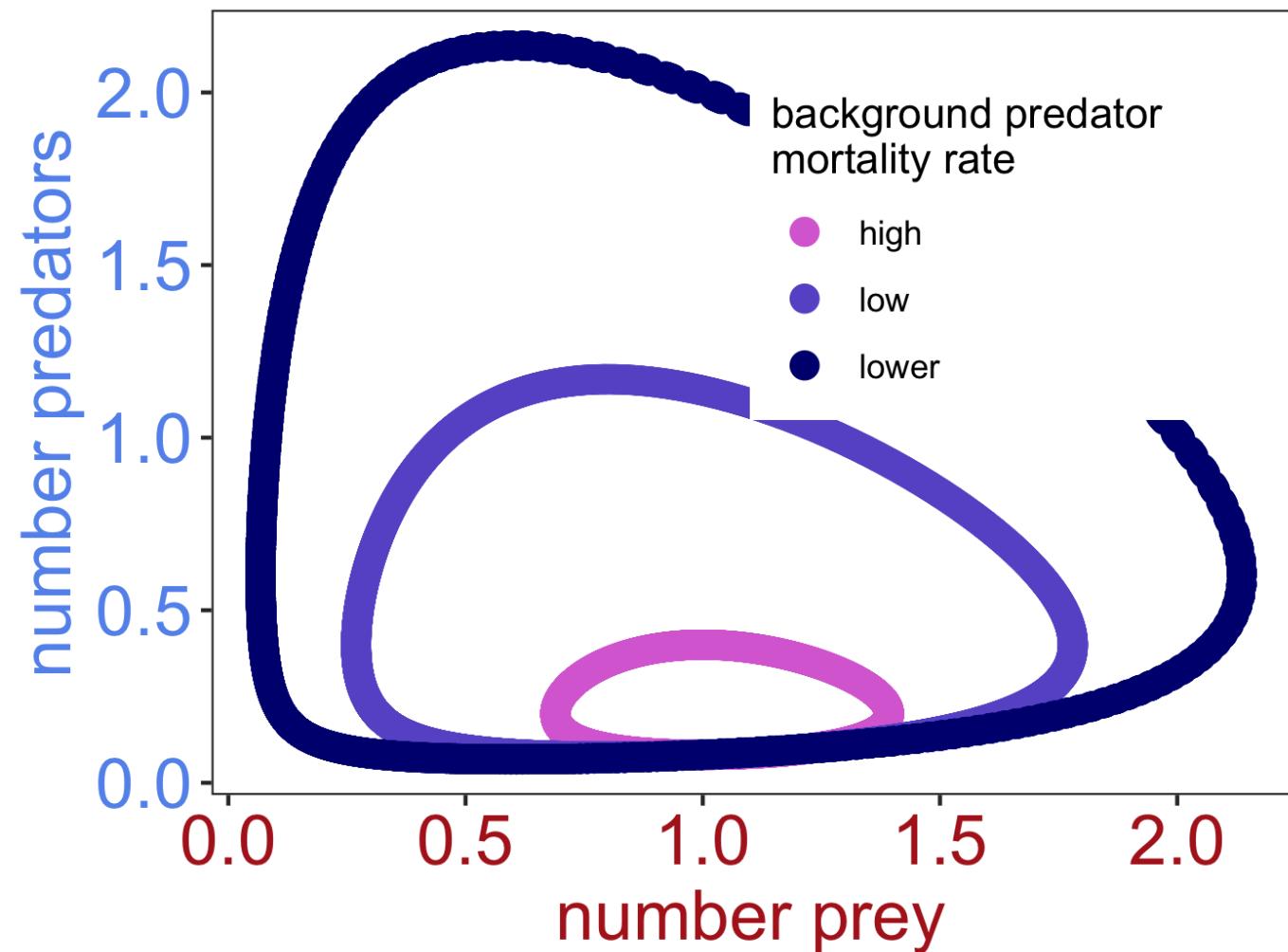


How does **hare** abundance **vary** with changes in **lynx** abundance?

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

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

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

# Principle of **competitive exclusion**



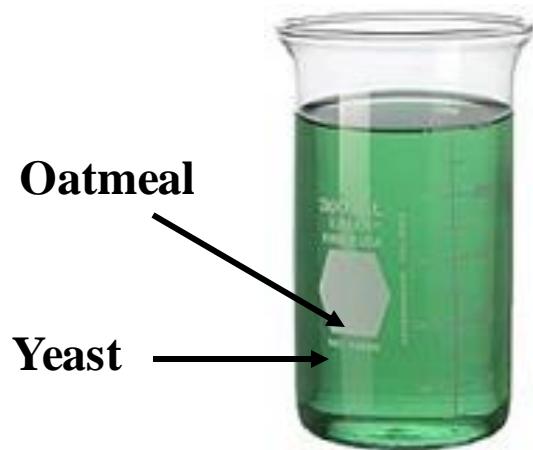
*Paramecium aurelia*



*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*



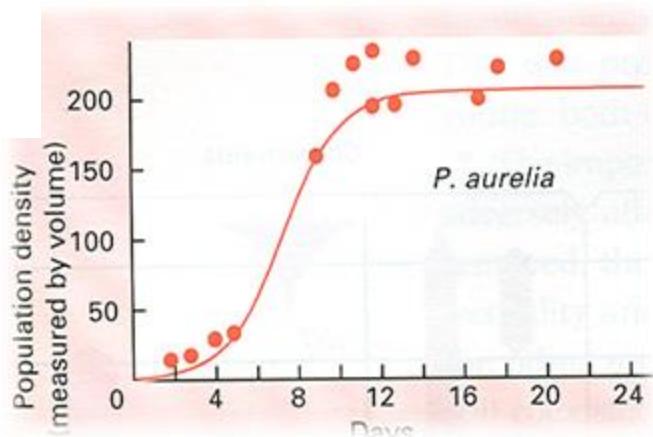
Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

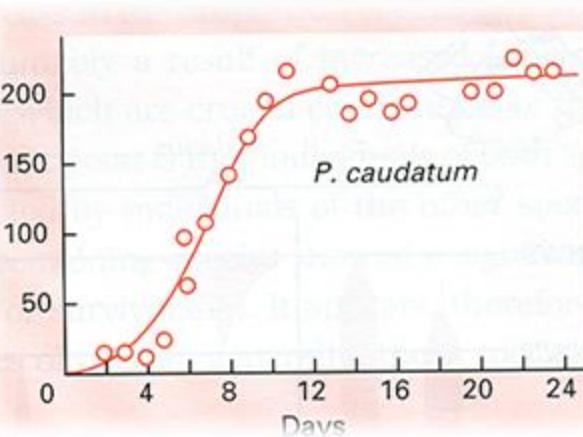
In isolation, each species grew logistically.



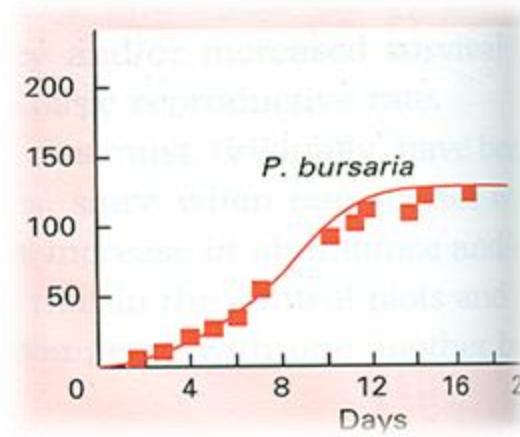
*Paramecium aurelia*



*Paramecium caudatum*



*Paramecium bursaria*



Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

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



*Paramecium aurelia*

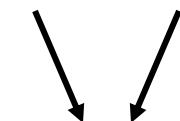
*Paramecium caudatum*



*Paramecium caudatum*



*Paramecium bursaria*



Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

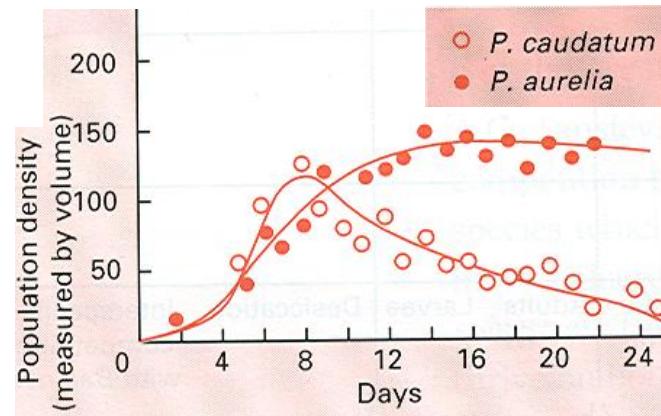
Competitive exclusion  
was observed:



*Paramecium aurelia*



*Paramecium caudatum*



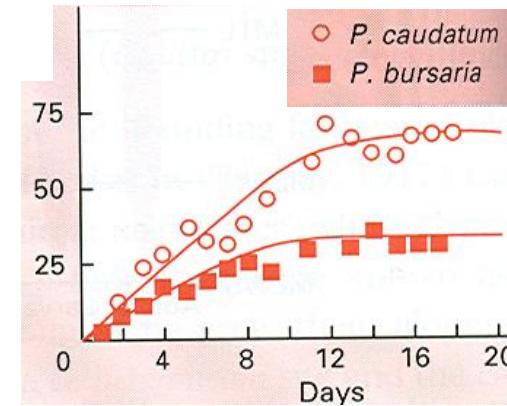
Coexistence was observed:



*Paramecium caudatum*



*Paramecium bursaria*



Gause 1934. *J Experimental Biology.*

Gause 1935. *Science.*

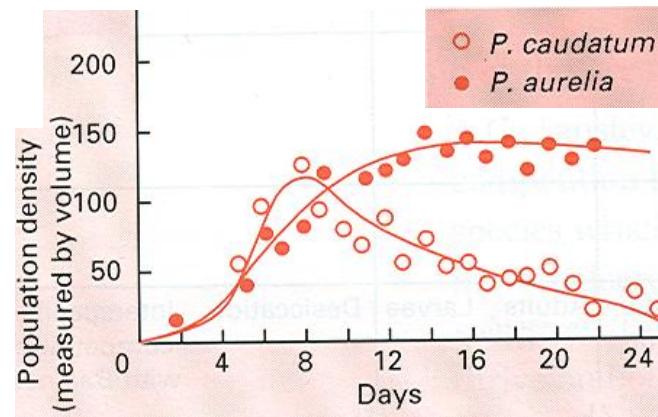
Competitive exclusion  
was observed:



*Paramecium aurelia*



*Paramecium caudatum*



Species coexisted below  
each species' respective  
individual carrying capacity.

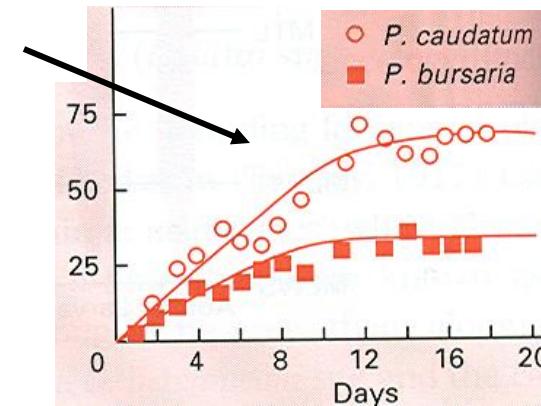
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*Paramecium caudatum*



*Paramecium bursaria*



Gause 1934. *J Experimental Biology.*

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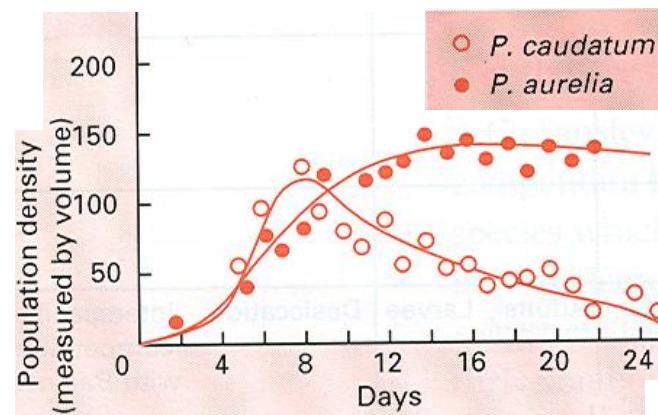
Competitive exclusion  
was observed:



*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:

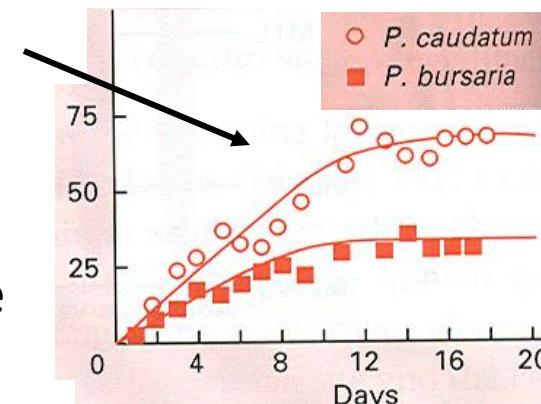


*Paramecium caudatum*



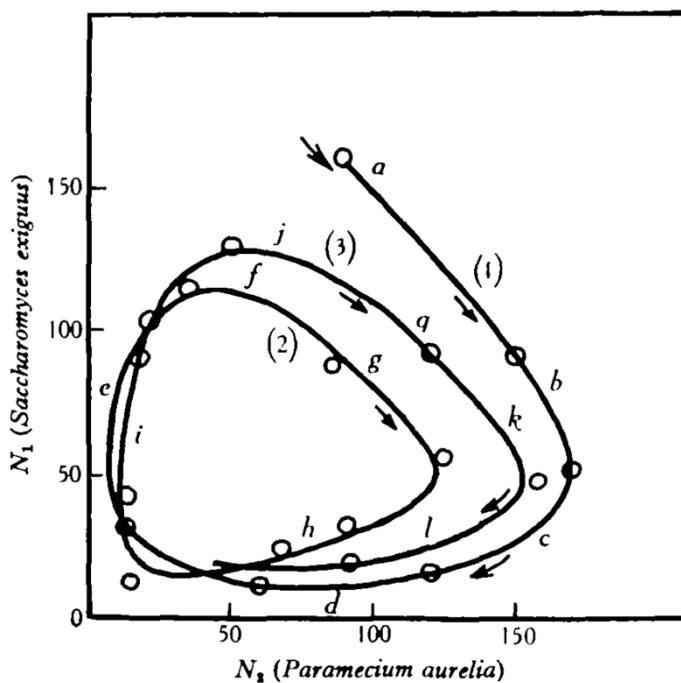
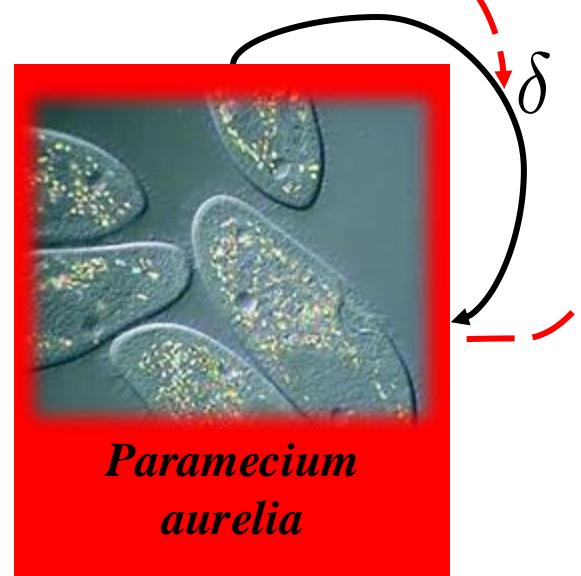
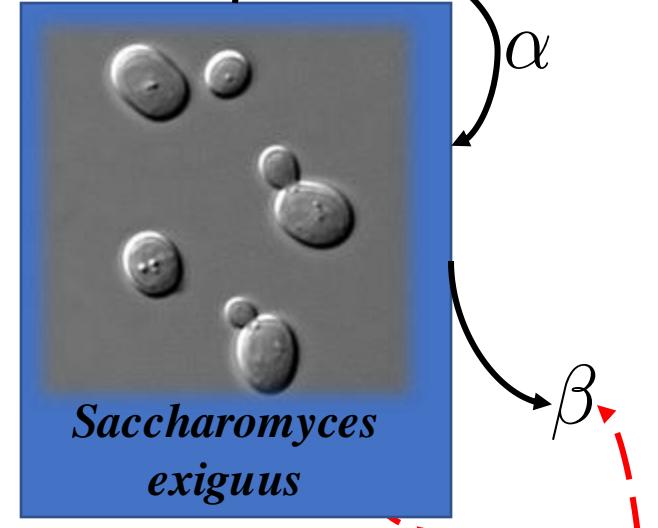
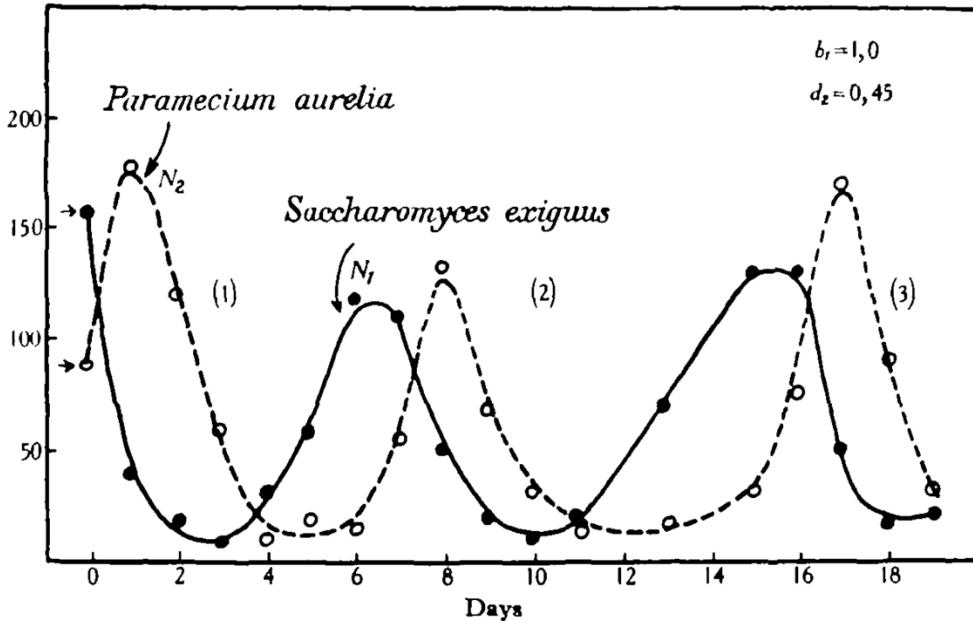
*Paramecium bursaria*

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:



$\gamma$

Gause 1935. *Science.*

$\alpha$

$\beta$

$\delta$

# Gause's experiments:

Competitive exclusion was observed:



*Paramecium aurelia*

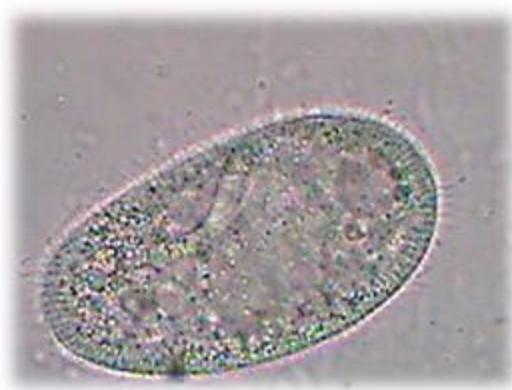


*Paramecium caudatum*

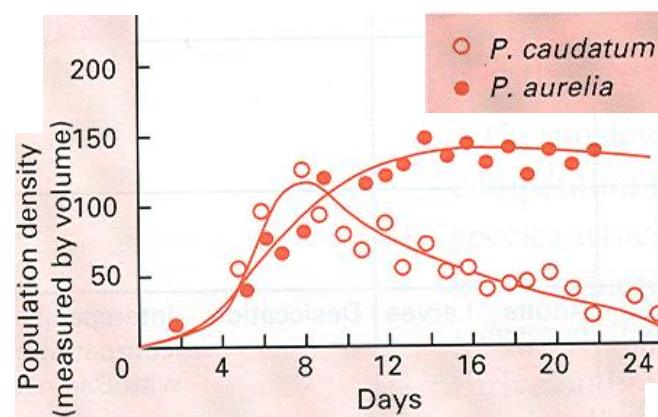
Coexistence was observed:



*Paramecium caudatum*

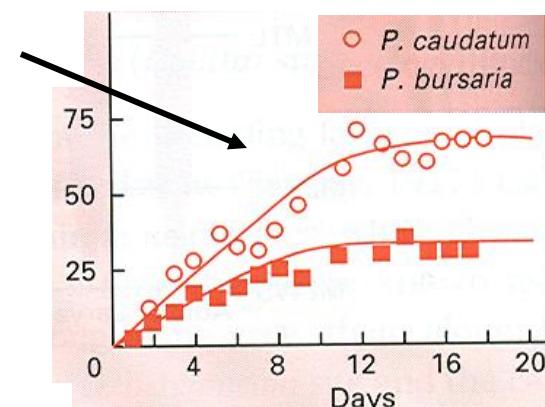


*Paramecium bursaria*



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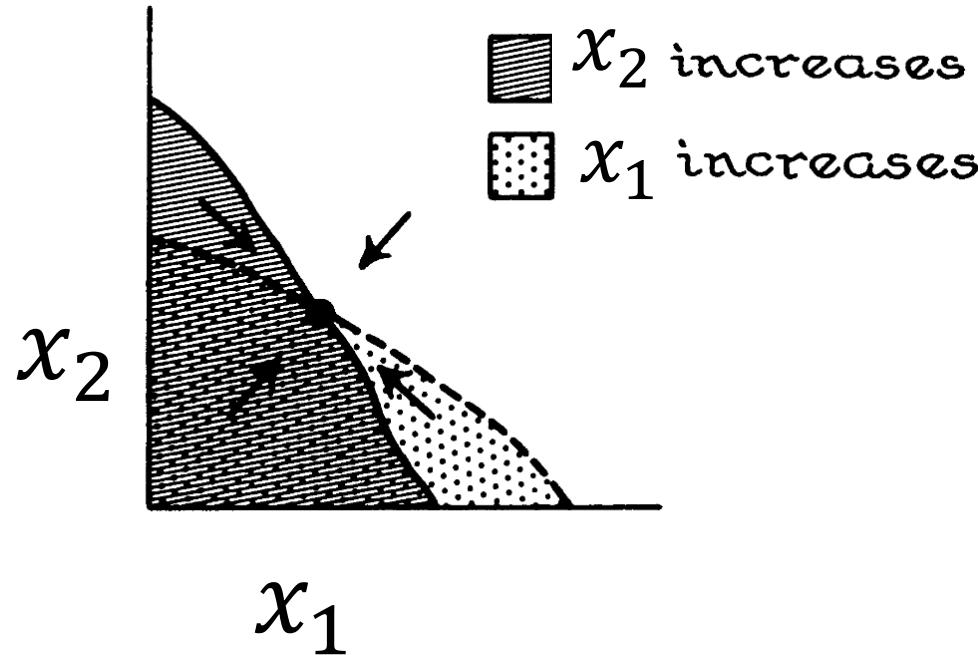


Gause 1934. *J Experimental Biology.*

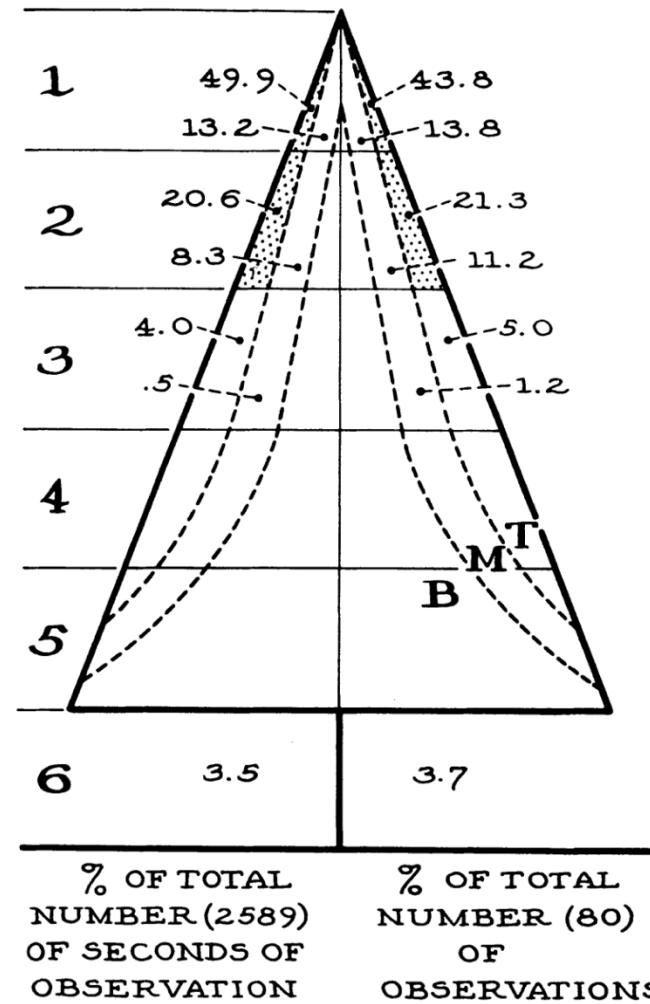
Gause 1935. *Science.*

# Niche partitioning enables organisms to avoid competitive exclusion

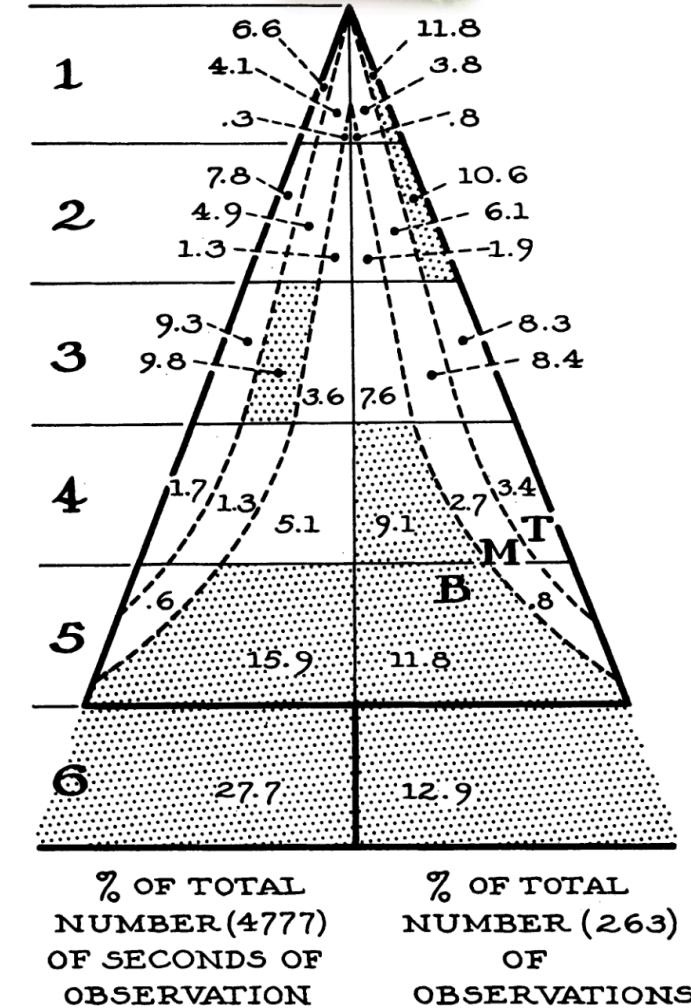
**Niche**: a match of a species to a specific environmental condition



Cape May  
Warbler

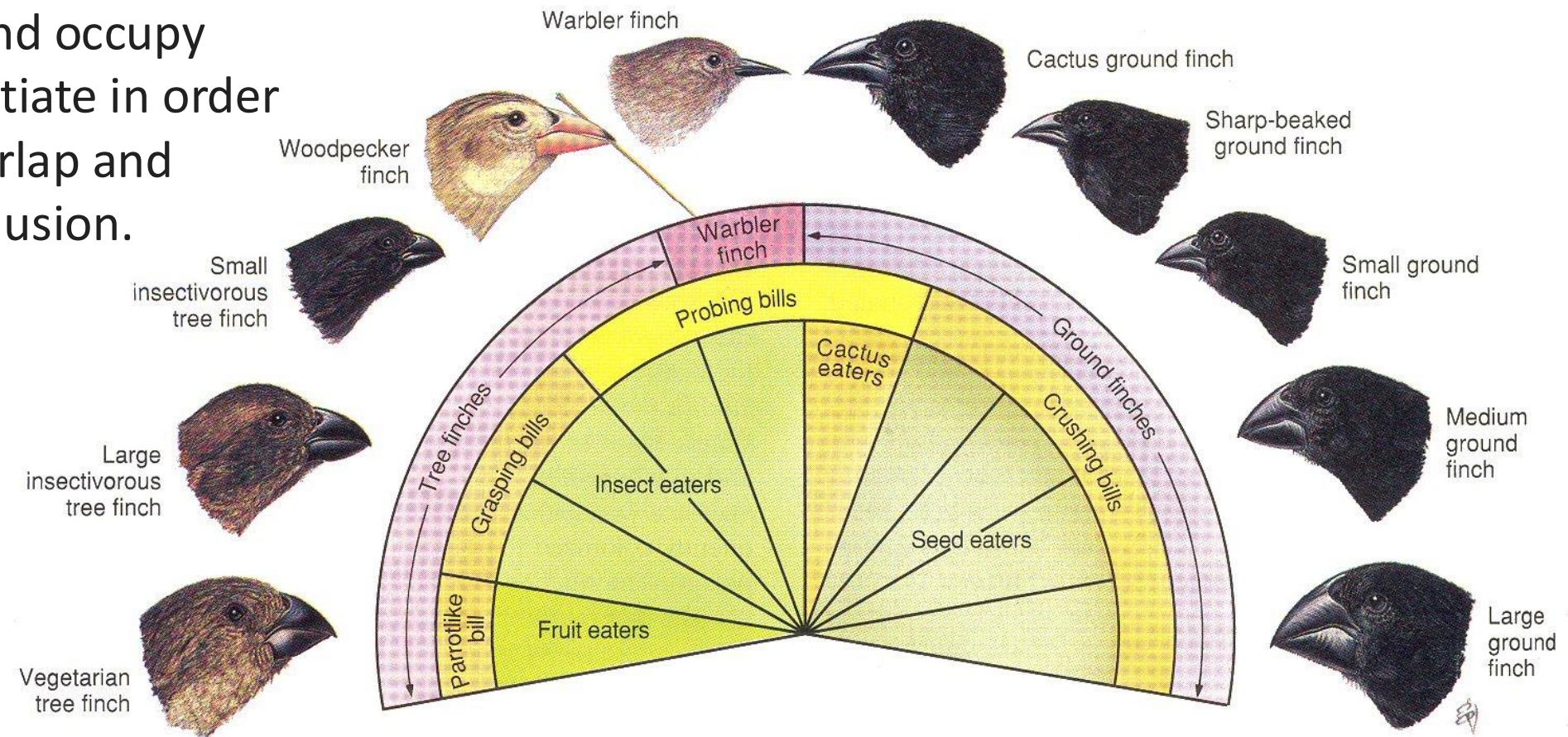


Myrtle  
Warbler



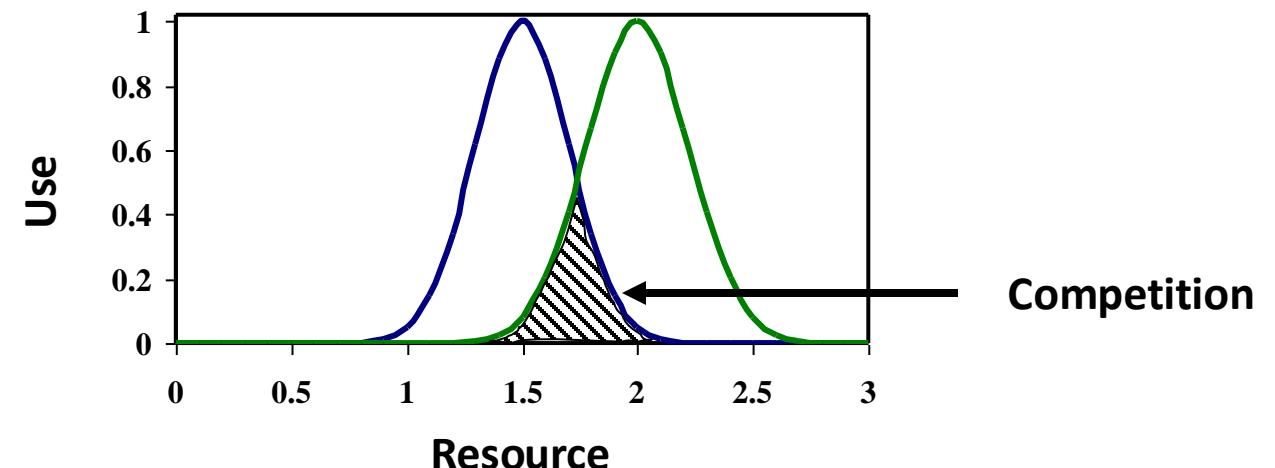
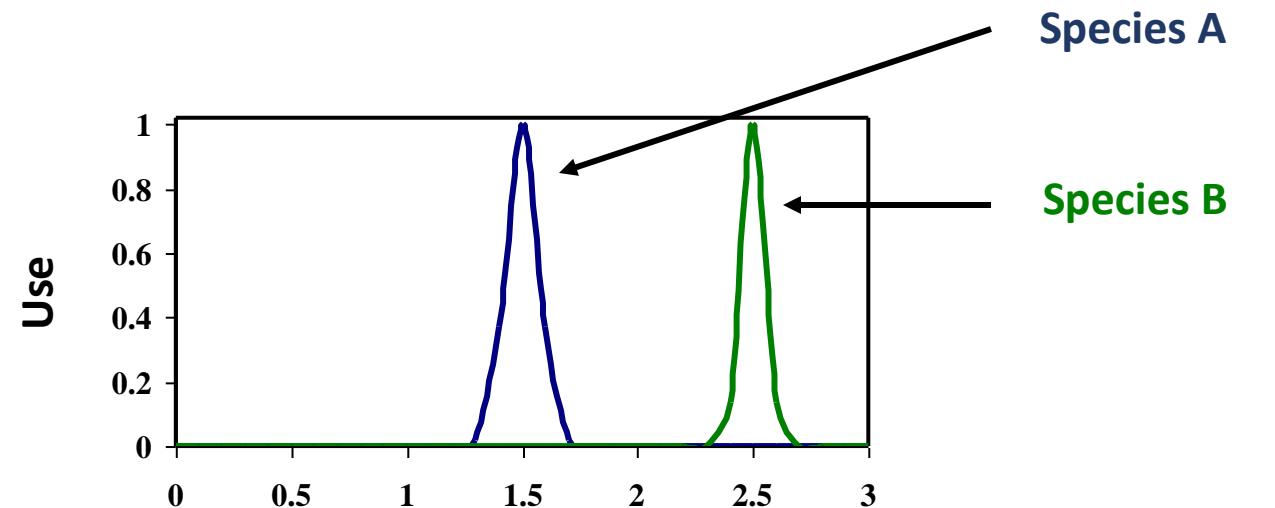
# Niche partitioning enables organisms to avoid competitive exclusion

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



# Niche partitioning enables organisms to avoid competitive exclusion

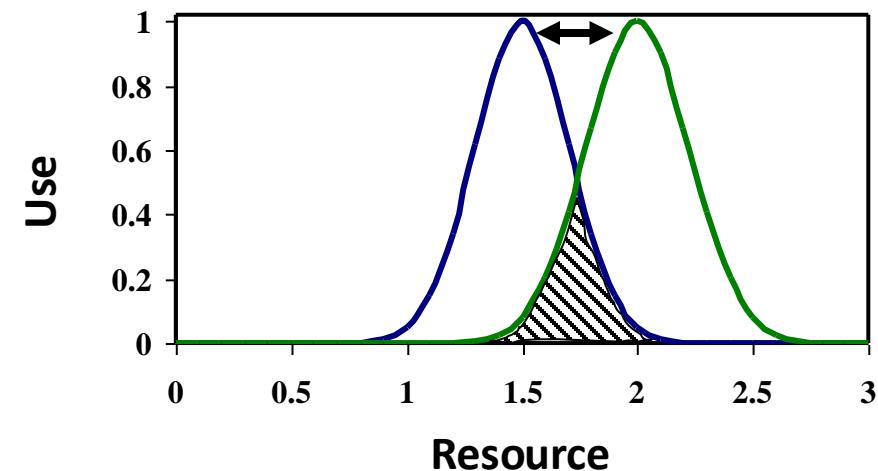
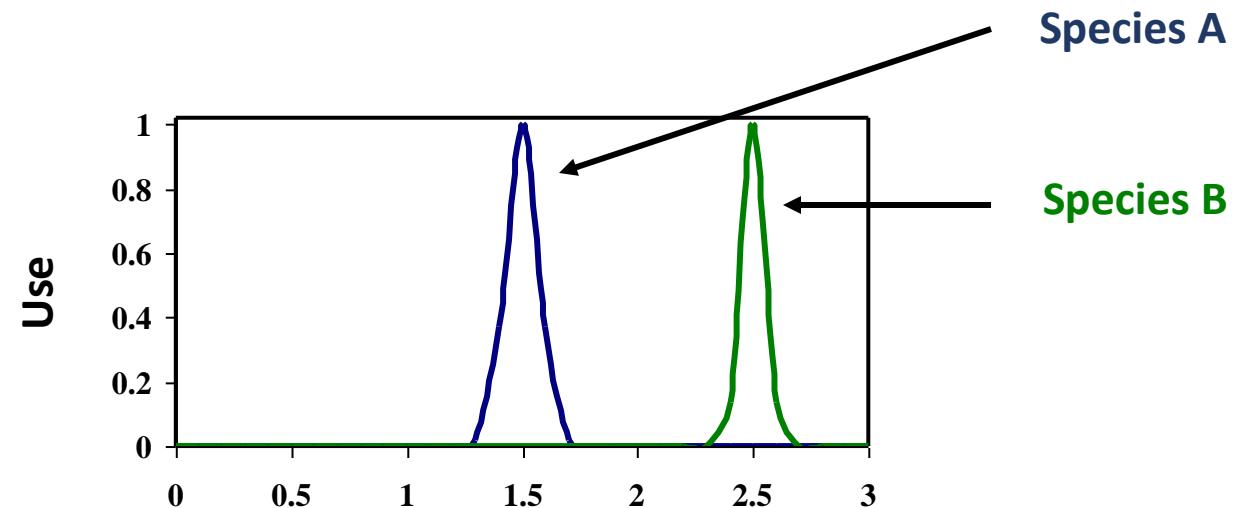
**Character displacement:** similar species that live in the same geographical region and occupy similar niches differentiate in order to minimize niche overlap and avoid competitive exclusion.



When niches overlap, competition results

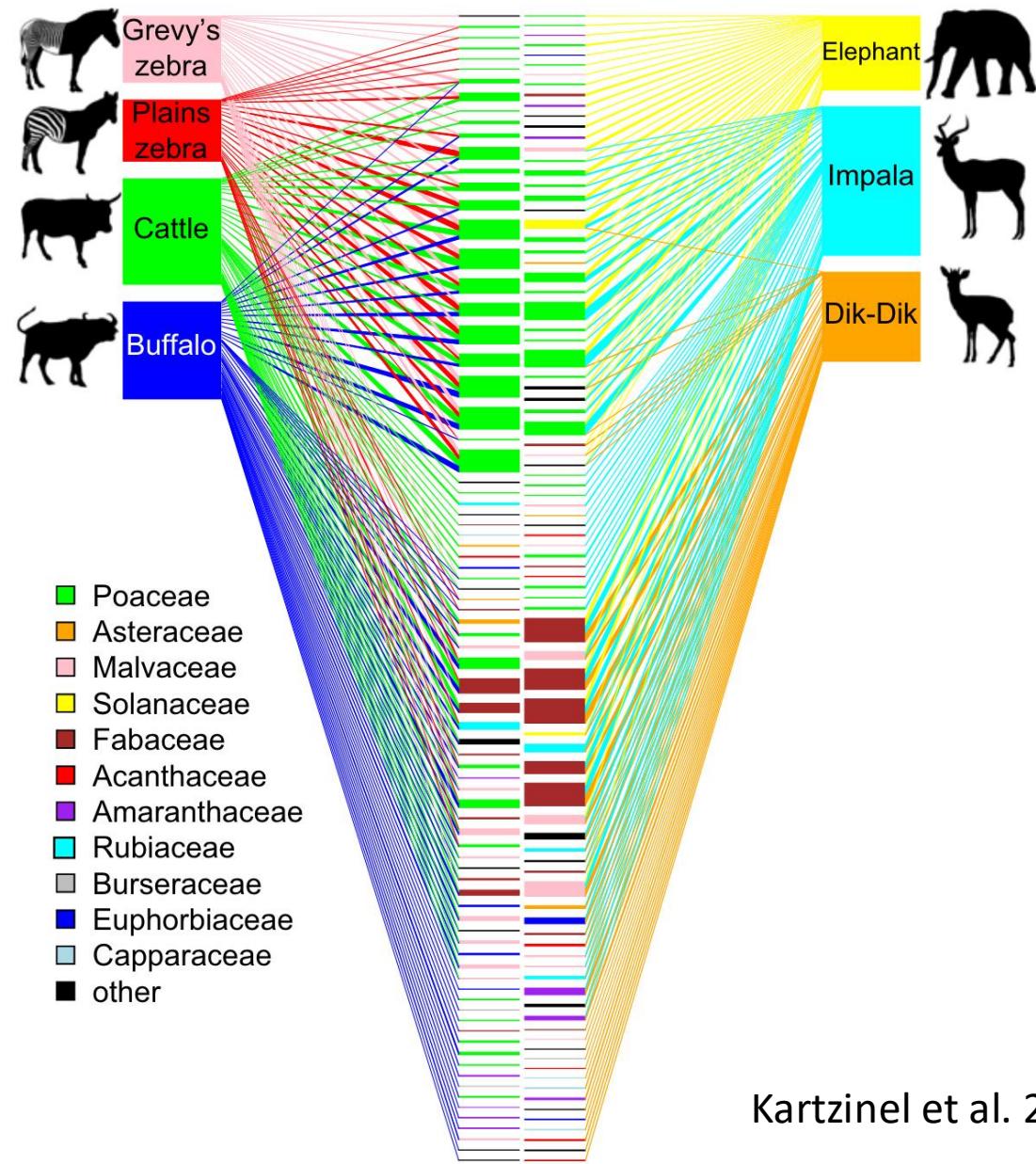
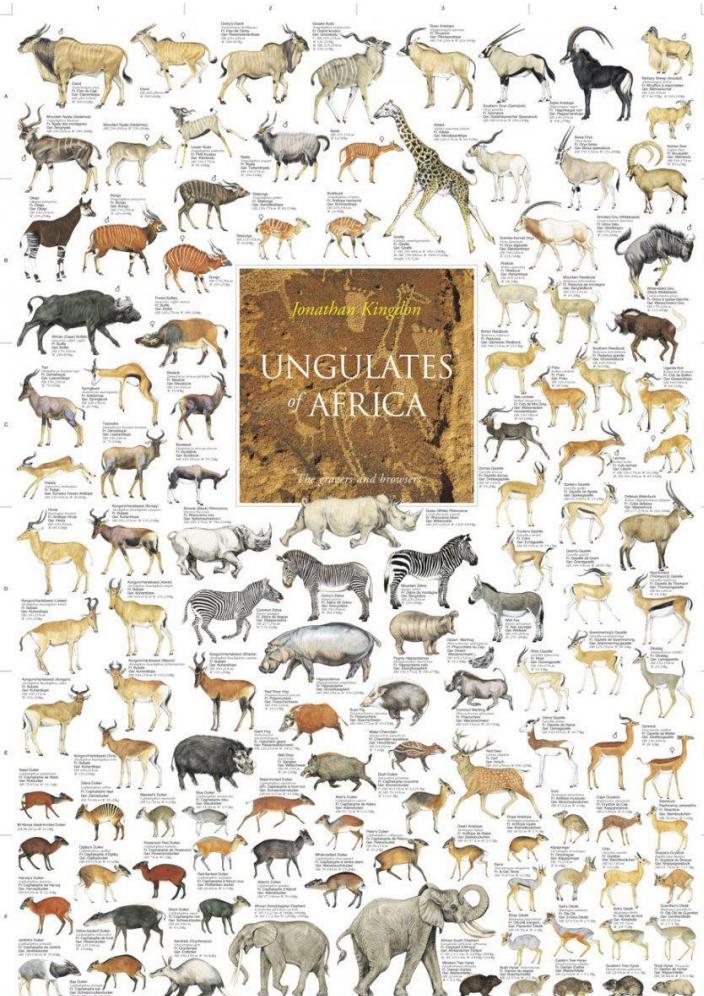
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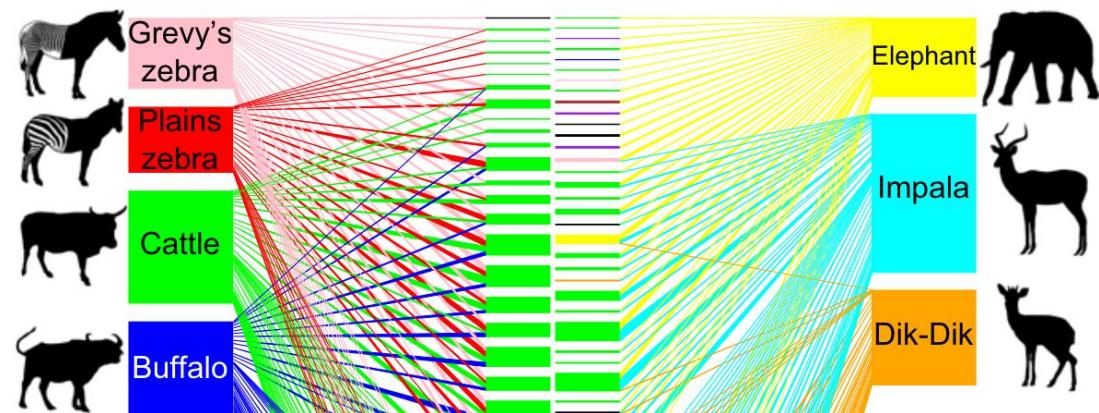
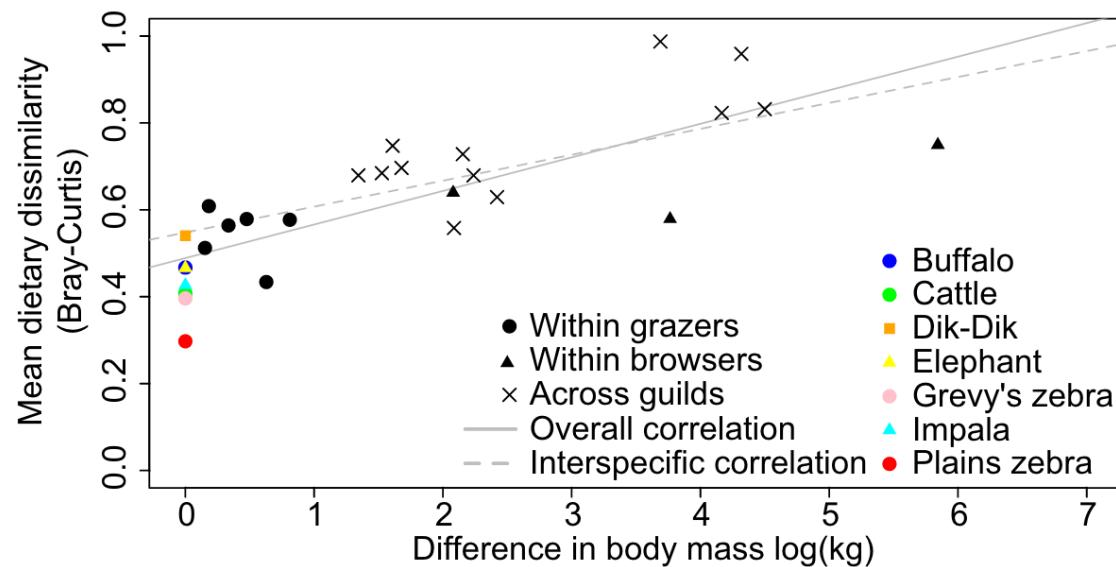
# Niche partitioning enables organisms to avoid competitive exclusion

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

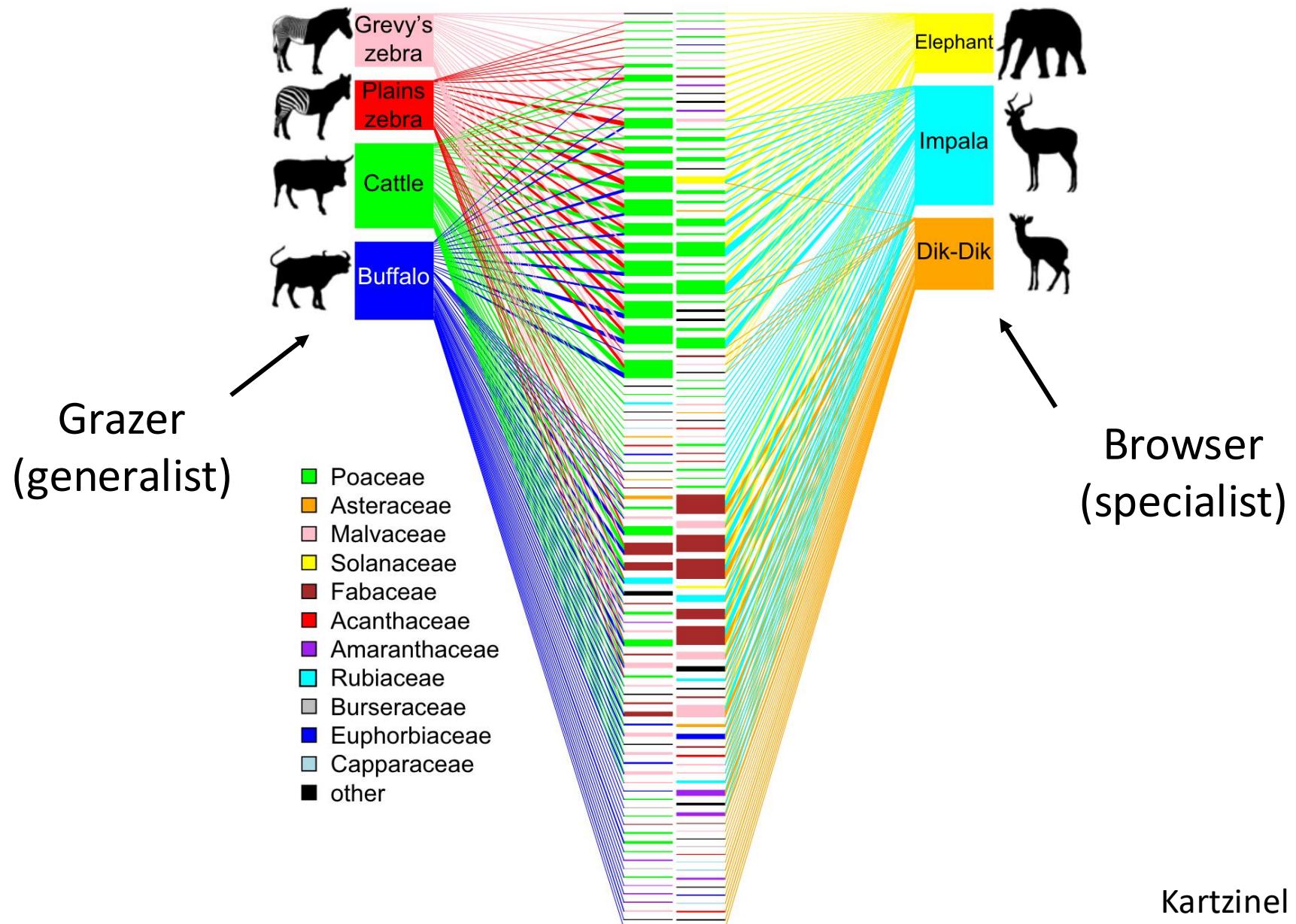


# Niche partitioning enables organisms to avoid competitive exclusion

Dietary overlap is higher in similar-sized mammals



# Consumer resource partitioning in the African savanna





**"Complete competitors cannot coexist" unless:**

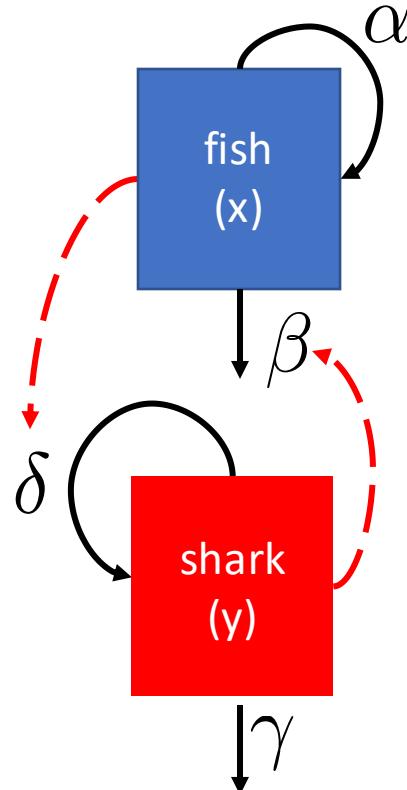
127

a. there is a precedence effect

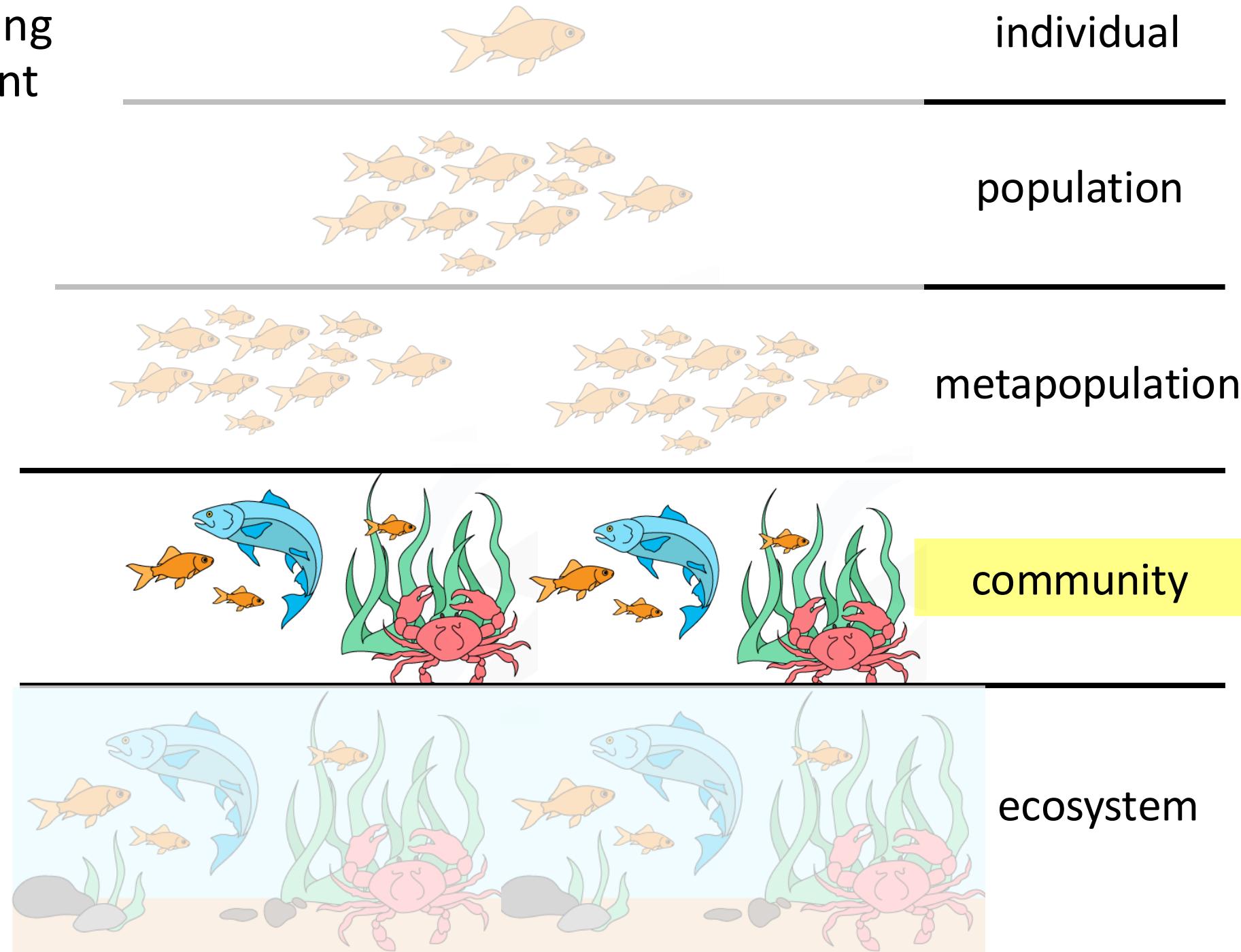
b. space, low dispersal, and stochasticit...

SEE MORE ▾

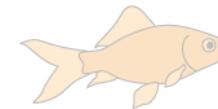
**Community** = interacting populations of different species



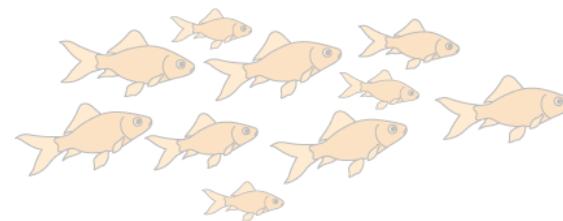
How does fish abundance **vary** with changes in shark abundance?



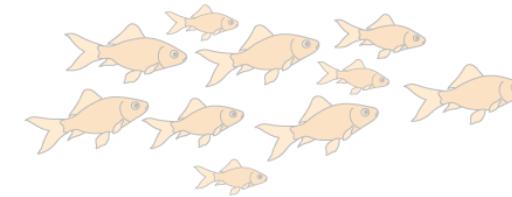
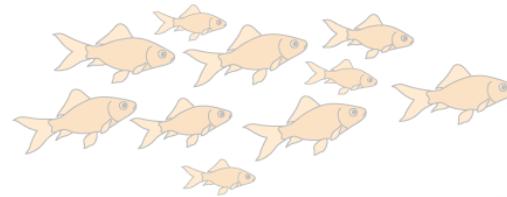
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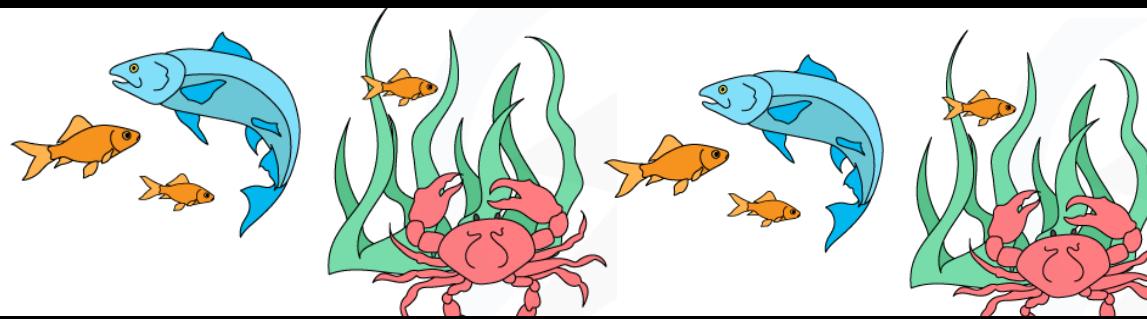
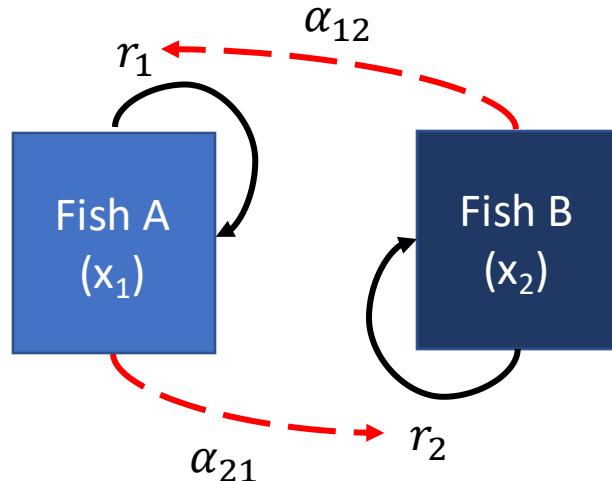
individual



population

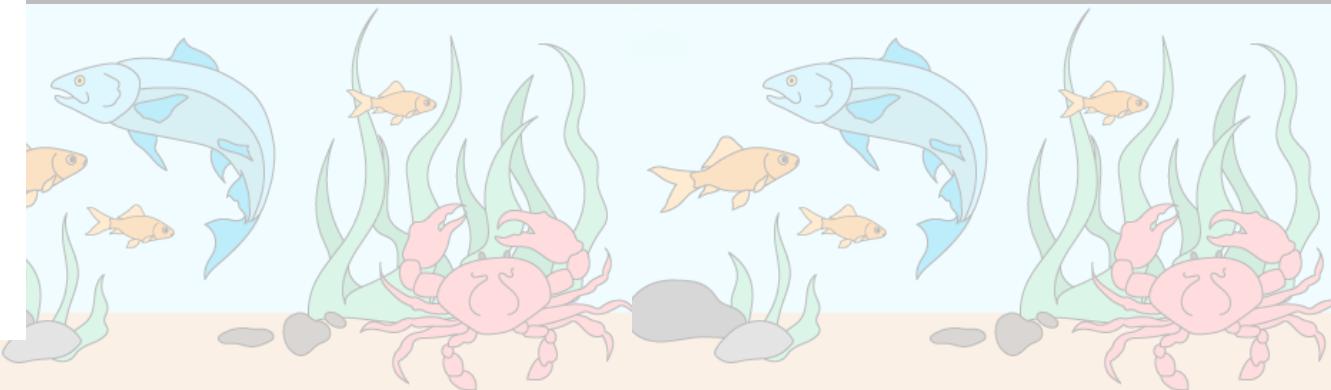


metapopulation



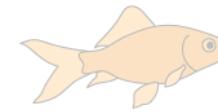
community

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

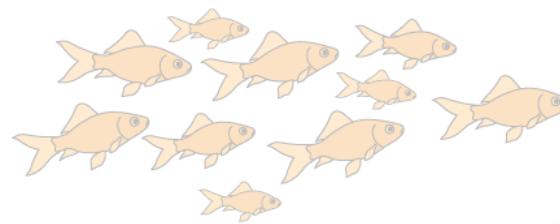


ecosystem

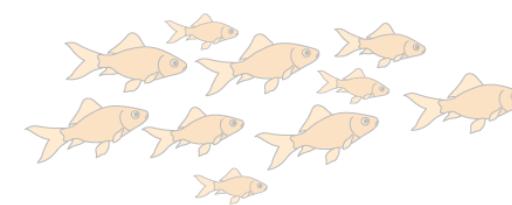
**Community** = interacting populations of different species



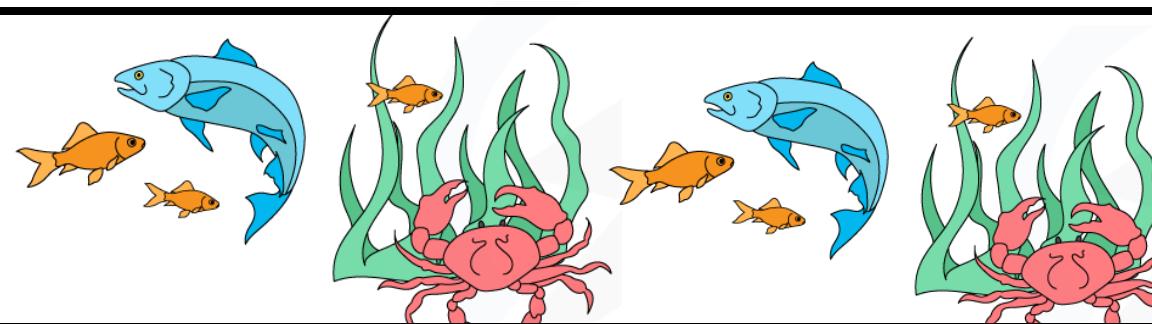
individual



population

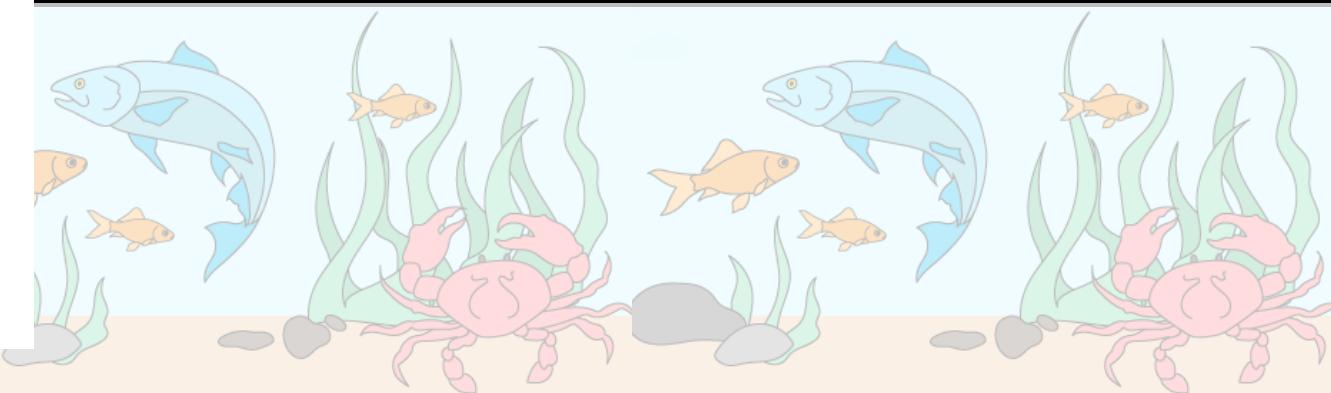


metapopulation



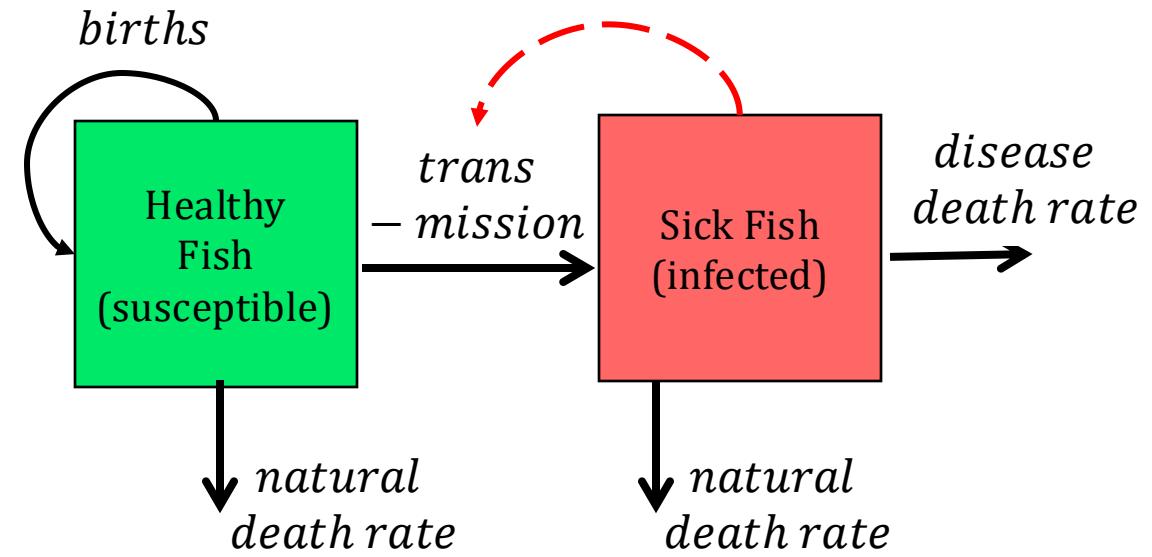
community

How does the abundance of **fish** change based on **infection with Mycobacterium marinum** (wasting disease)?



ecosystem

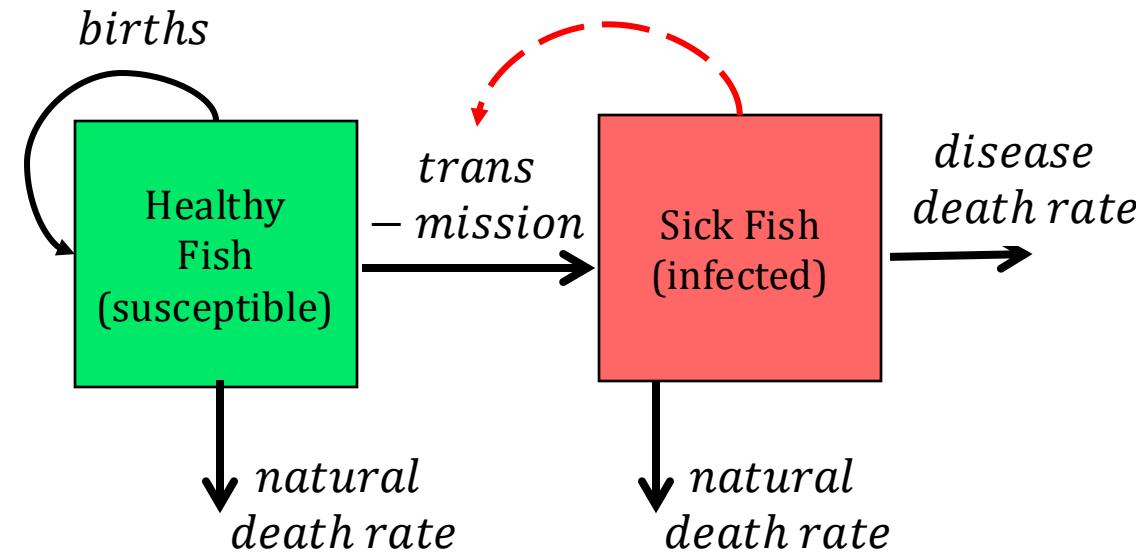
**Community** = interacting populations of different species



How does the abundance of **fish** change based on **infection with Mycobacterium marinum** (wasting disease)?

**Community** = interacting populations of different species

Species can interact in several distinct ways.

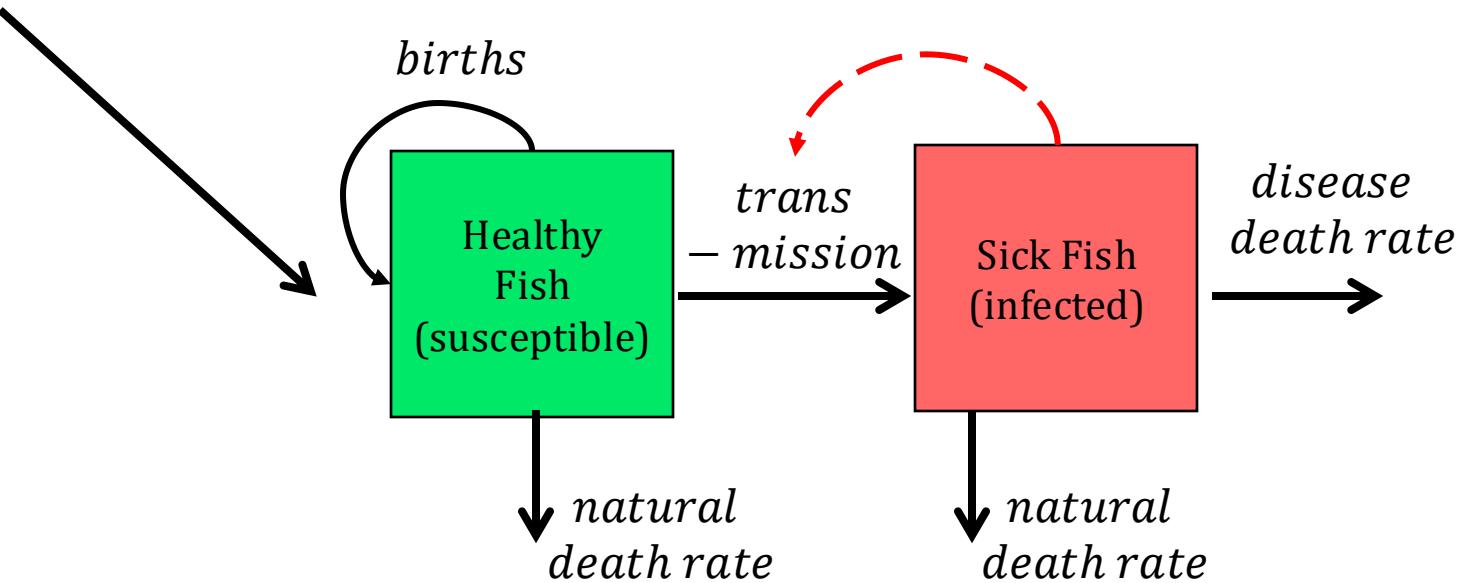


How does the abundance of **fish** change based on **infection with Mycobacterium marinum** (wasting disease)?

- **Mutualism** – both species benefit
- **Commensalism** – one species benefits, the other is unaffected
- **Predation** – one species benefits, the other is harmed (eaten!)
- **Competition** – two species compete for the same limiting resource, both harmed by the interaction
  - Direct = wolves and coyote at a moose carcass
  - Indirect = diurnal cheetah, nocturnal leopard at a giraffe carcass
- **Parasitism** – one species (the parasite) lives *in* or *on* the other species (the host)

# *Population Biology*

Each box is a distinct population!

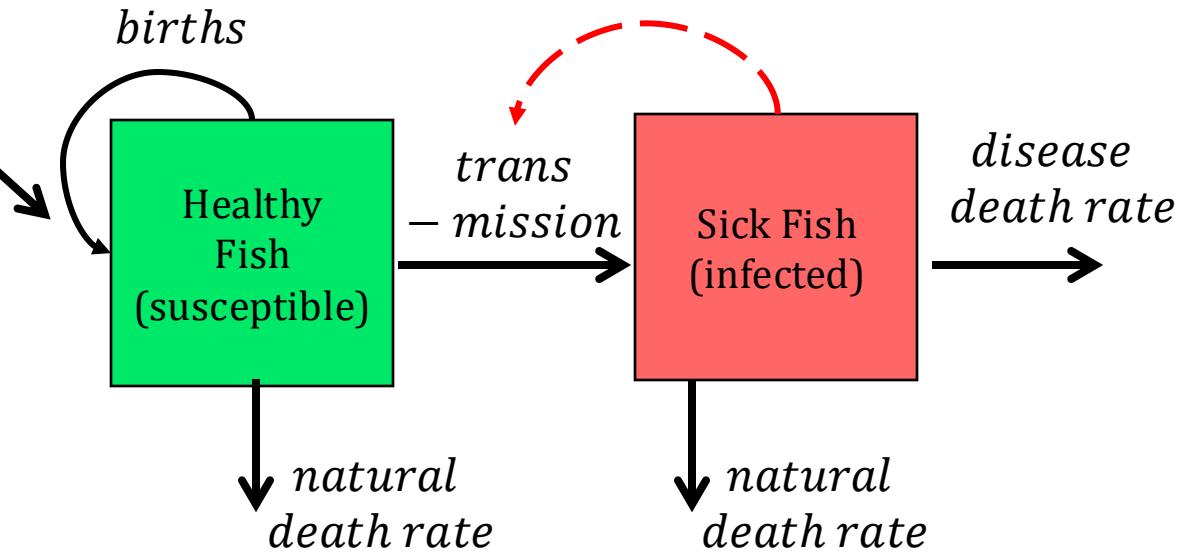


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Each box is a distinct population!

When we model these populations, everyone in the box is considered the same.



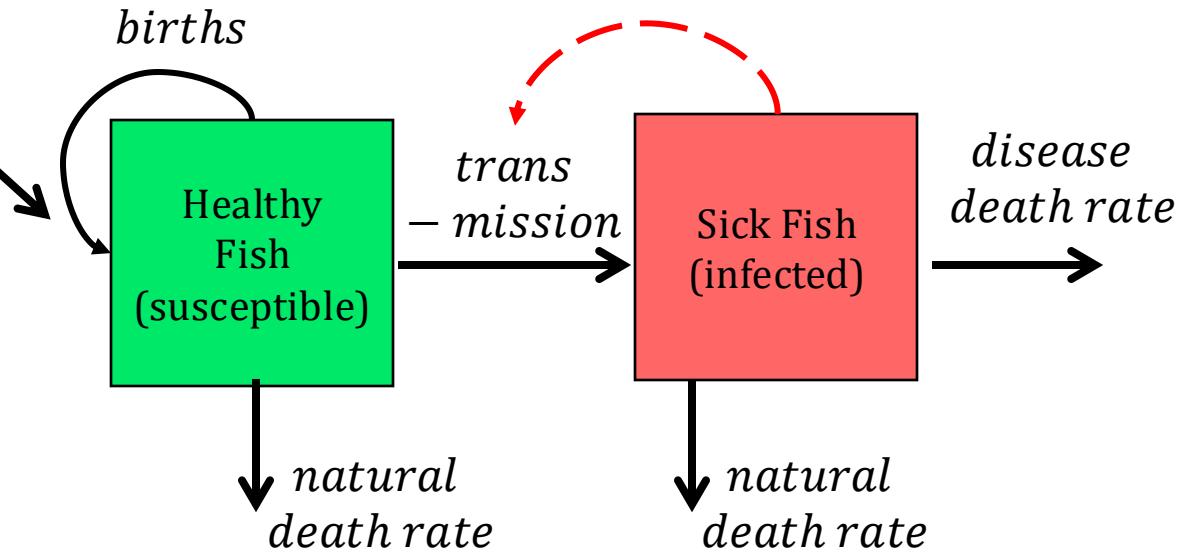
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In a continuous time model (ODE), each box would get its own differential equation!



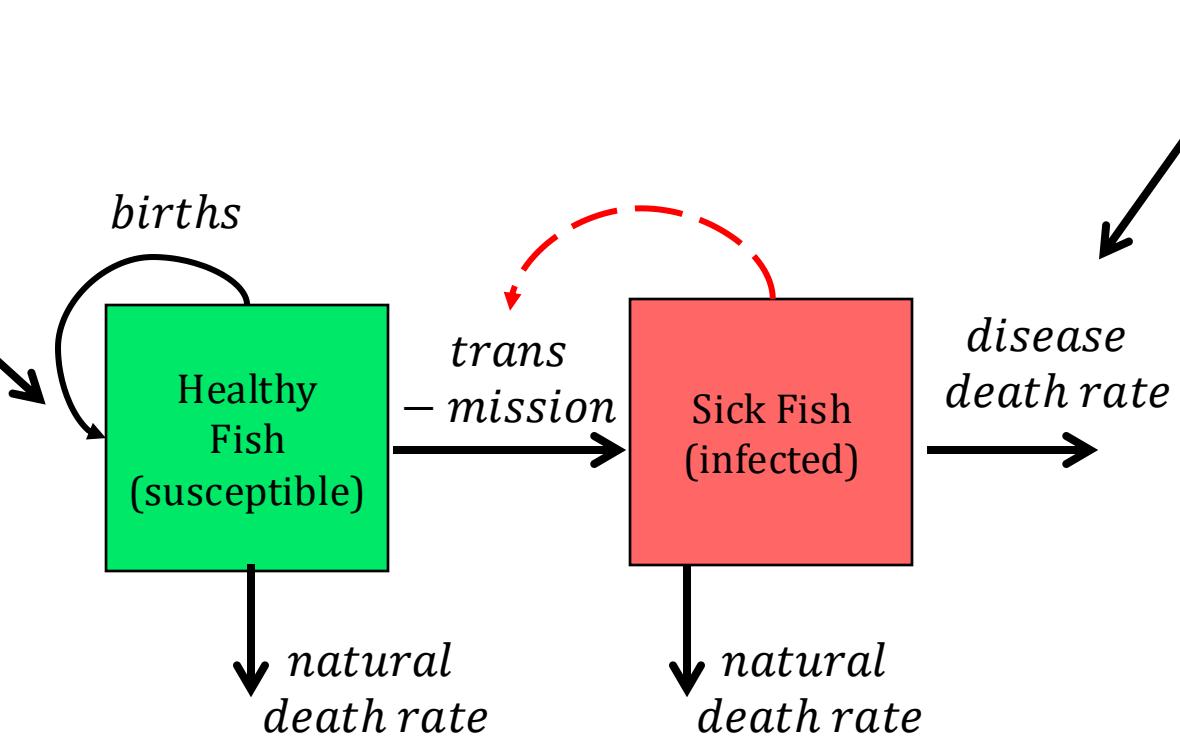
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Solid lines are processes by which individuals in each population move between boxes.

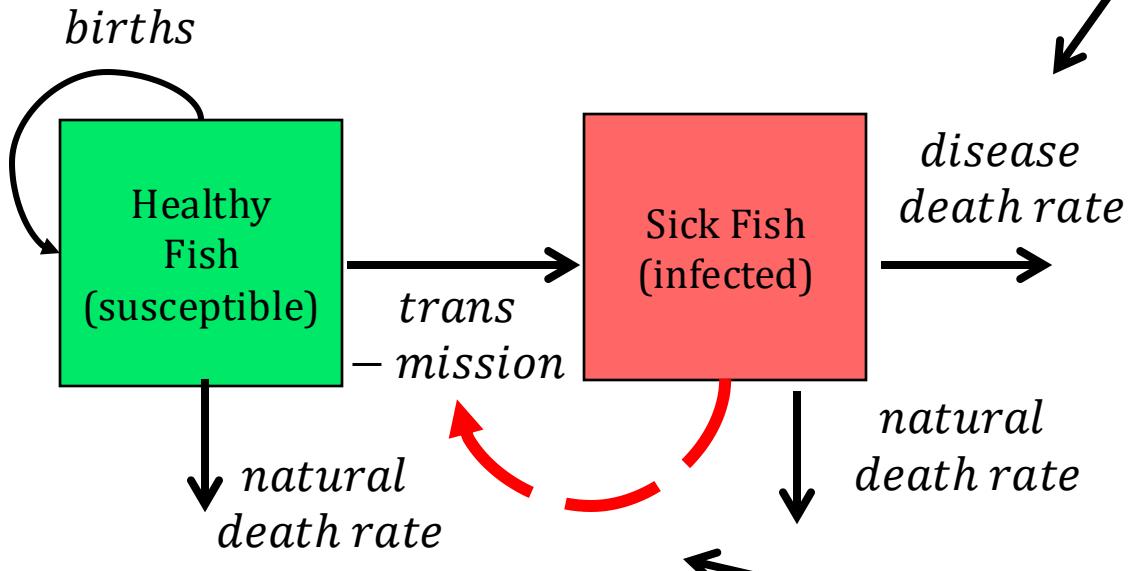
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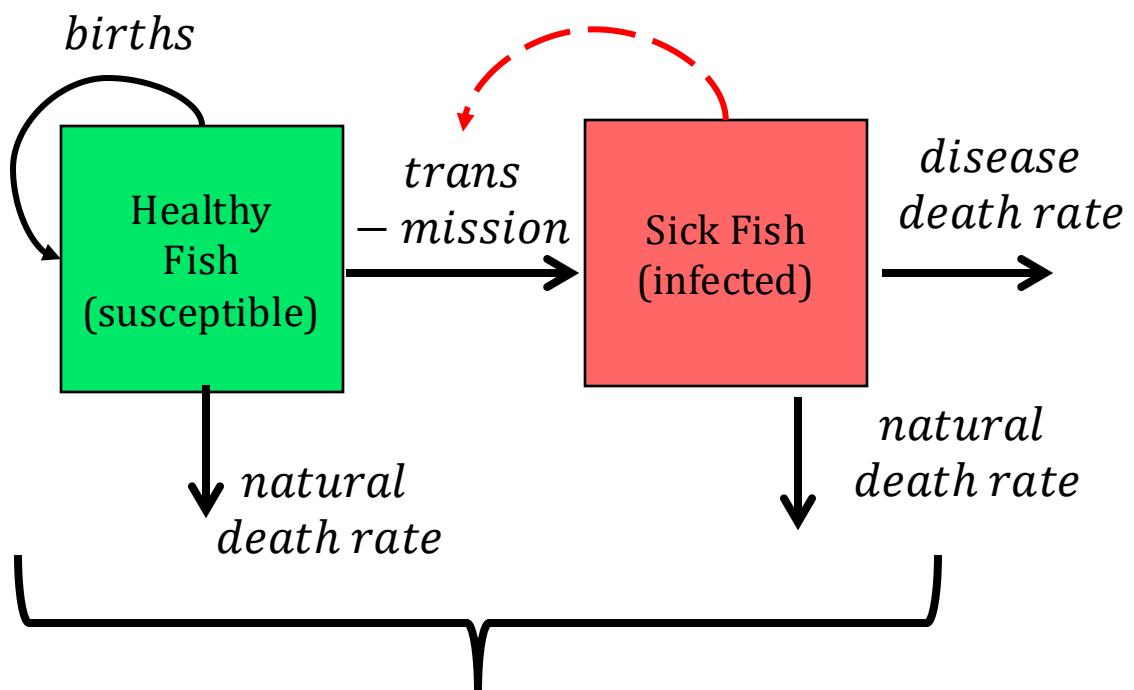


Solid lines are processes by which individuals in each population move between boxes.

Dashed lines are influences of populations on rates (transmission is higher when there are more sick fish)

*How does the abundance of **fish** change based on **infection with Mycobacterium marinum** (wasting disease)?*

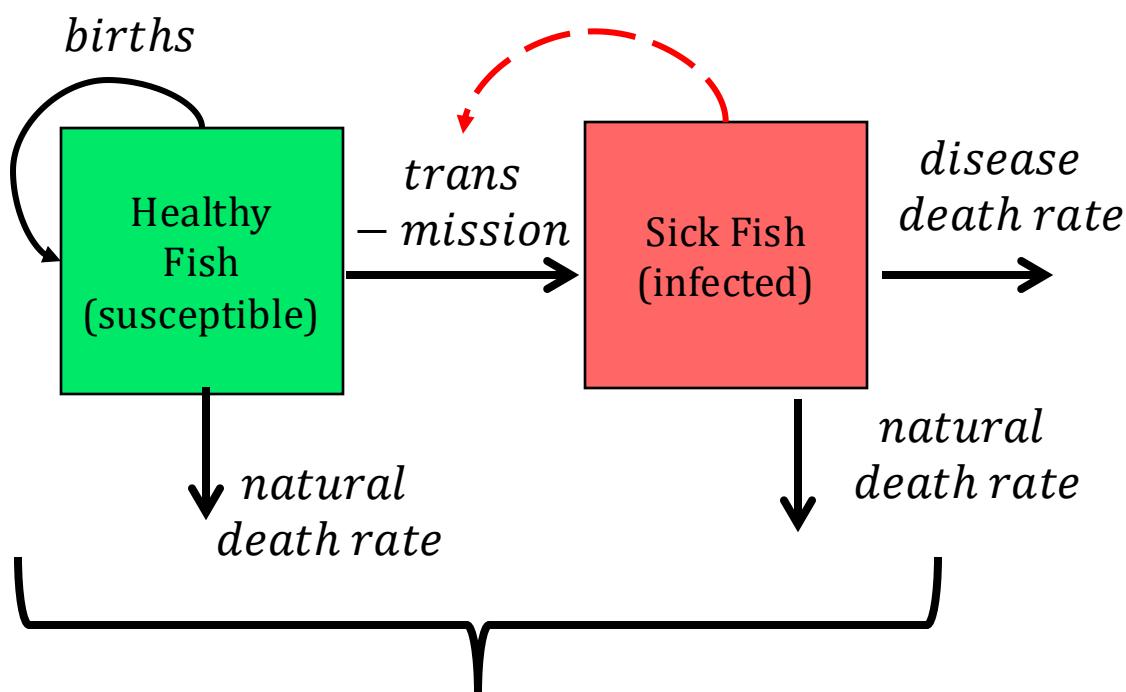
# *Population Biology*



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In disease ecology, we model populations based on their **infection status**.

# Population Biology



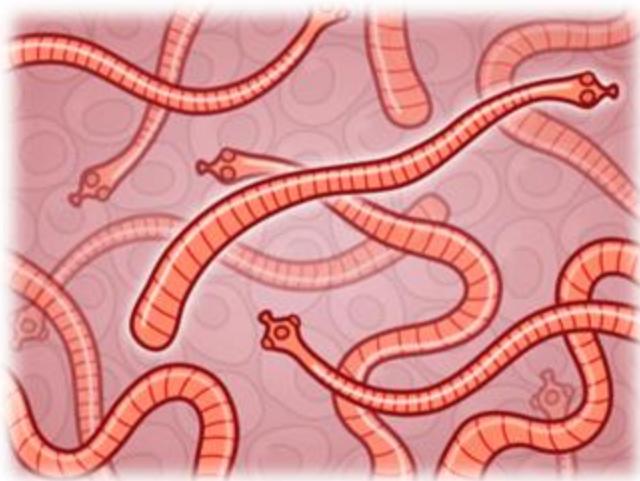
In disease ecology, we model populations based on their **infection status**.

*How does the abundance of fish change based on infection with **Mycobacterium marinum** (wasting disease)?*

Previously, we modeled populations of **different species**, or of **distinct life history classes within a species**.

# Parasites and Pathogens

- Parasite: an organism that lives in or on another organism and benefits at the expense of others.
  - Ex: helminths (parasitic worms: tapeworms, roundworms, hookworms), ectoparasites (ticks, fleas)



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Pathogen: *Yersinia pestis*

Disease: Plague

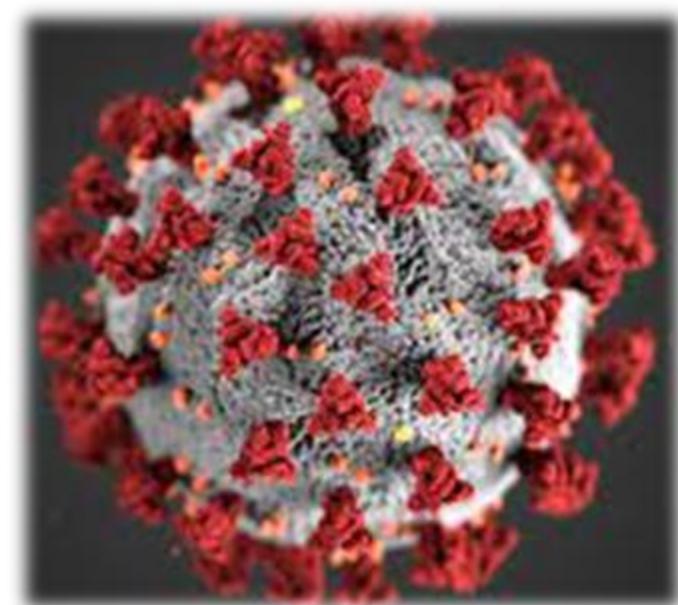


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↑  
Pathogen: SARS-CoV-2  
Disease: COVID-19



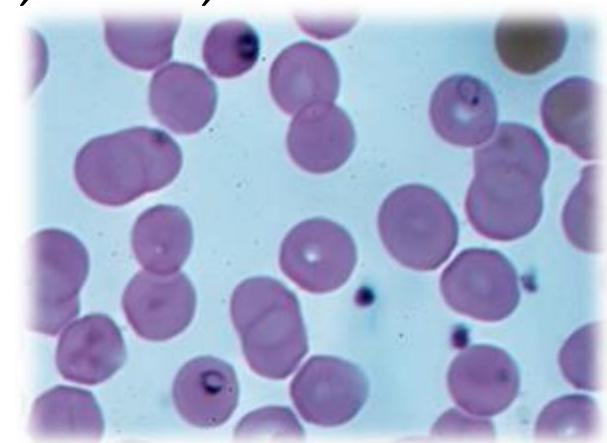
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Pathogen: SARS-CoV-2  
Disease: COVID-19

Pathogen: *Plasmodium falciparum, P. vivax, P. malariae, P. ovale, P. knowlesi*  
Disease: malaria



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  - Ex: Soay sheep, grapes

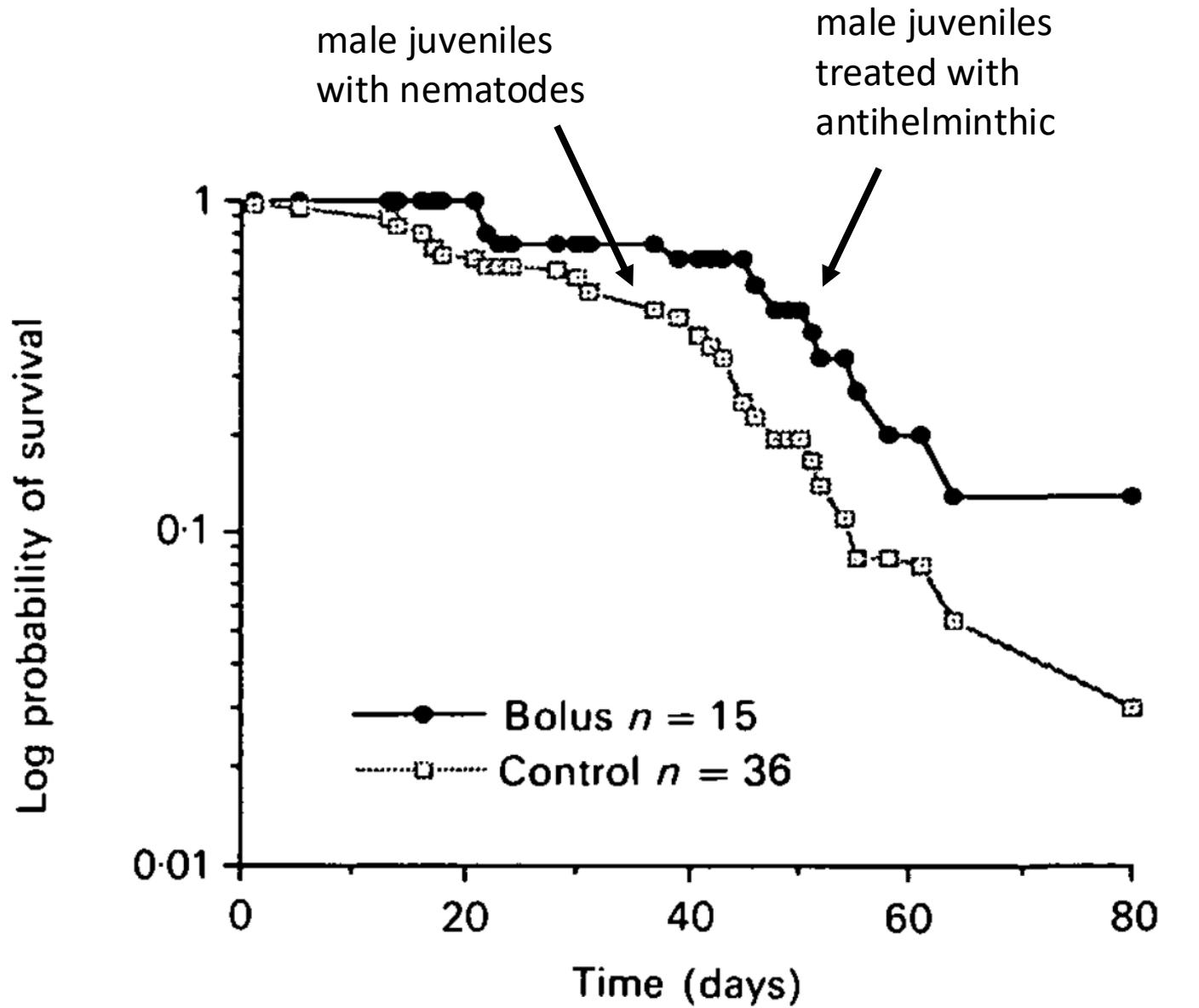
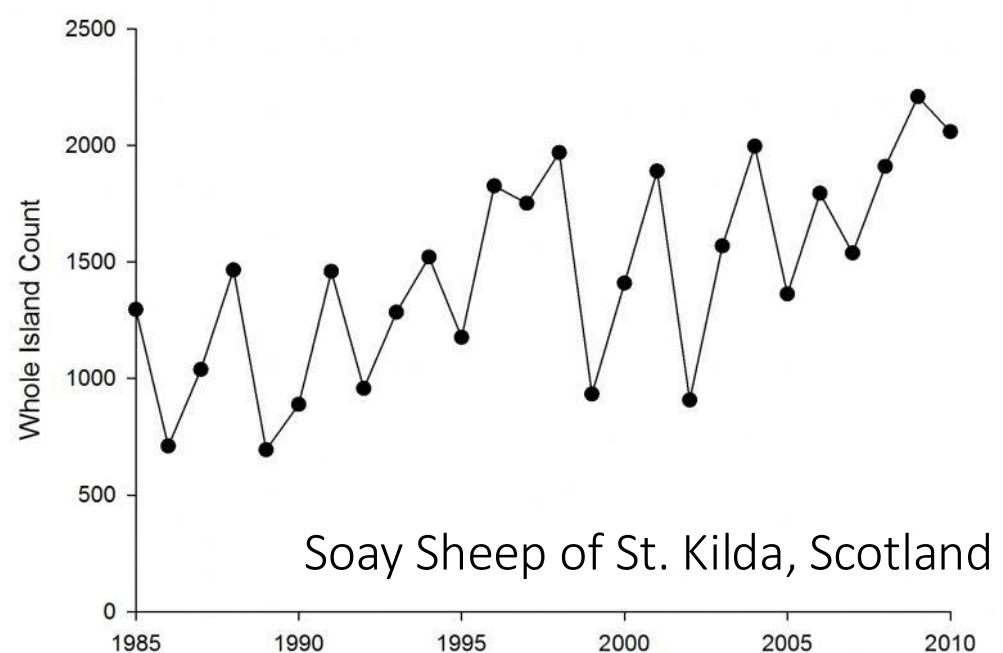


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  - Ex: Soay sheep, grapes
- Vector: an arthropod agent that carries and transmits a pathogen or parasite from host to host
  - Ex: mosquitoes, ticks, fleas



We already know that  
parasites can play a role in  
regulating populations!



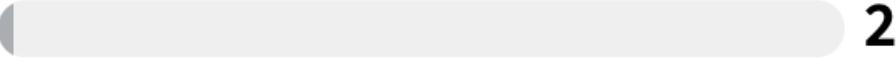
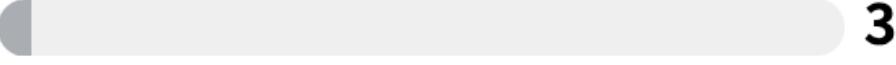
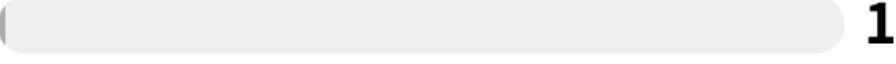
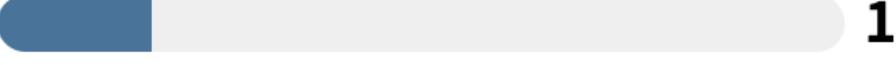
Early work in red grouse experimentally demonstrated the power of parasites to regulate populations.



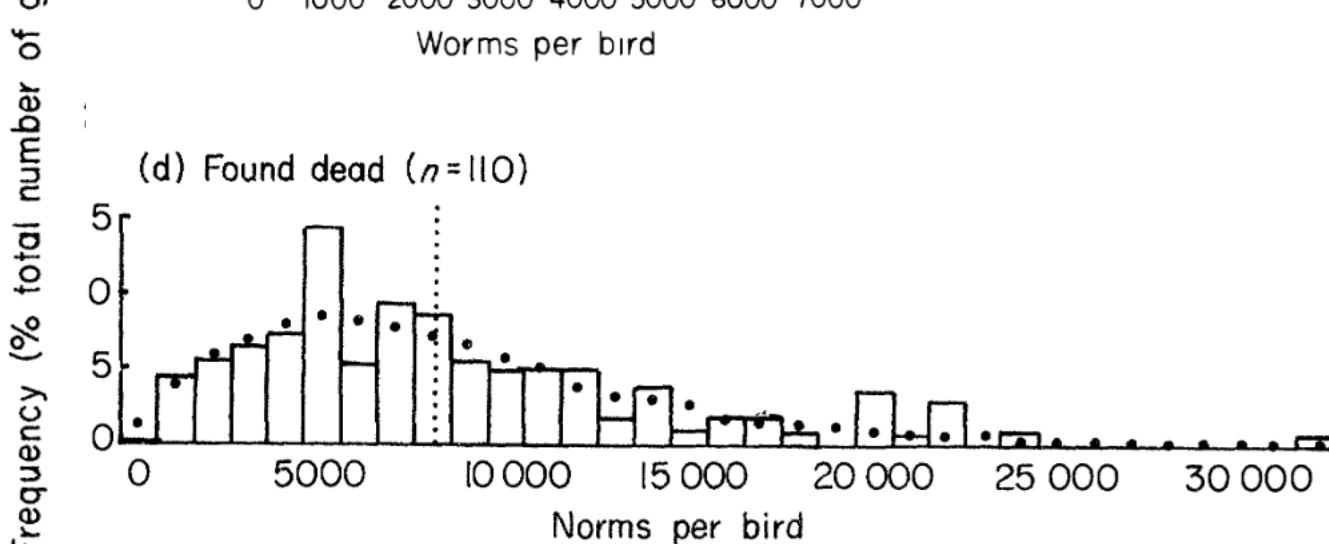
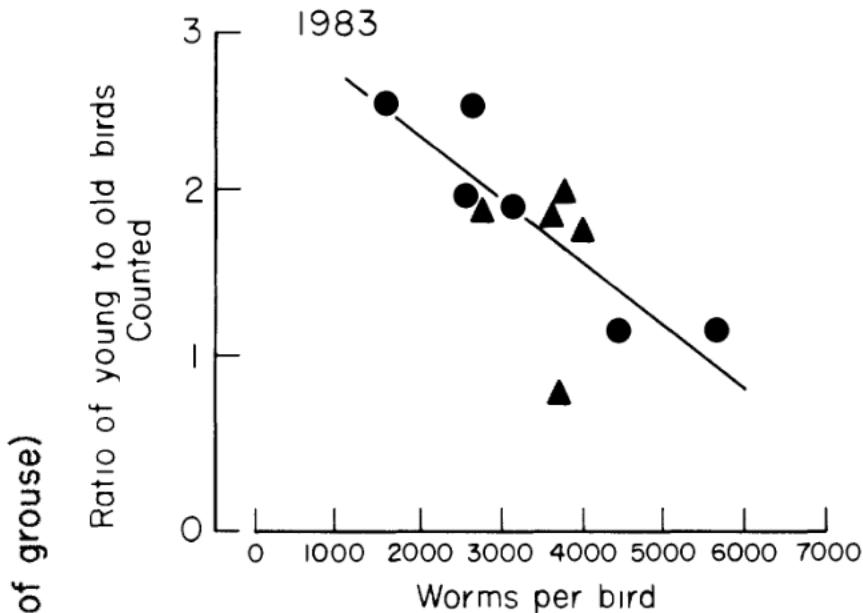
Hudson 1986. *J Animal Ecology*.  
Hudson et al 1992. *J Animal Ecology*.  
Hudson et al 1998. *Science*.



## What factors do we know contribute to annual fluctuations in the population density of the Soay sheep of St Kilda?

- A Density-dependent effects ...  1%
- B Higher mortality in b...  0%
- C Higher ewe mortality at hi...  2%
- D Lowered survival in...  3%
- E Geometric growth  1%
- F. A, B   14%
- G. A, B, C, D, E  79%

Early work in red grouse experimentally demonstrated the power of parasites to regulate populations.

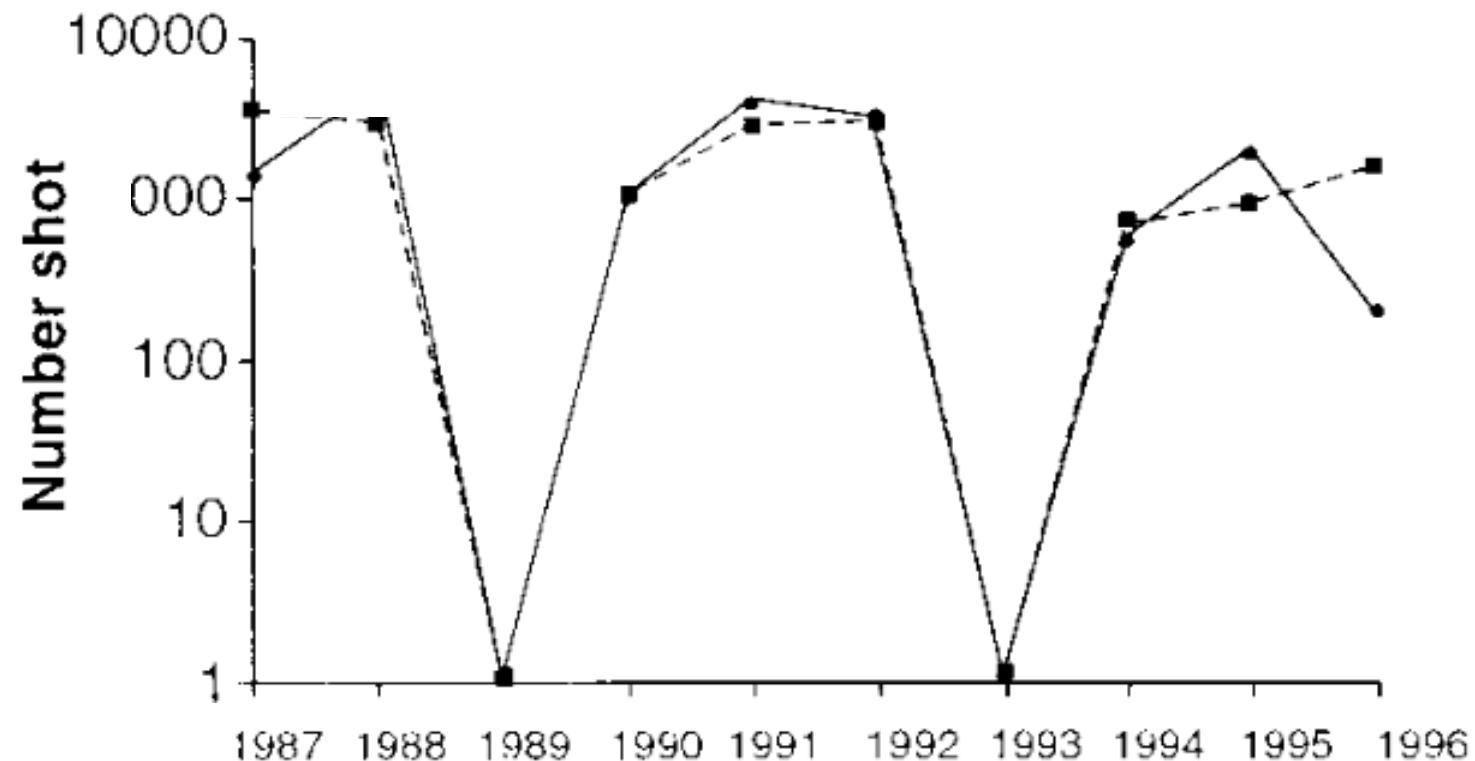


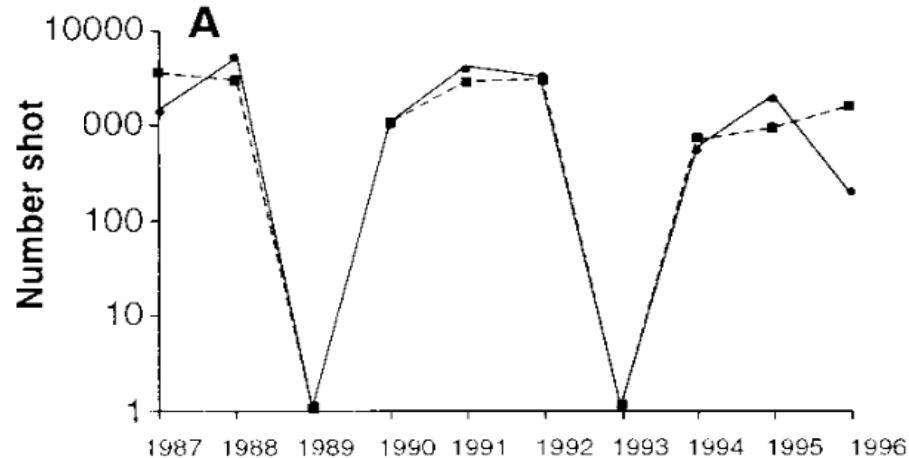
Higher burden of the intestinal strongyle worm, *Trichostrongylus tenuis*, both reduces breeding success and increases mortality in red grouse.

Hudson 1986. *J Animal Ecology*.

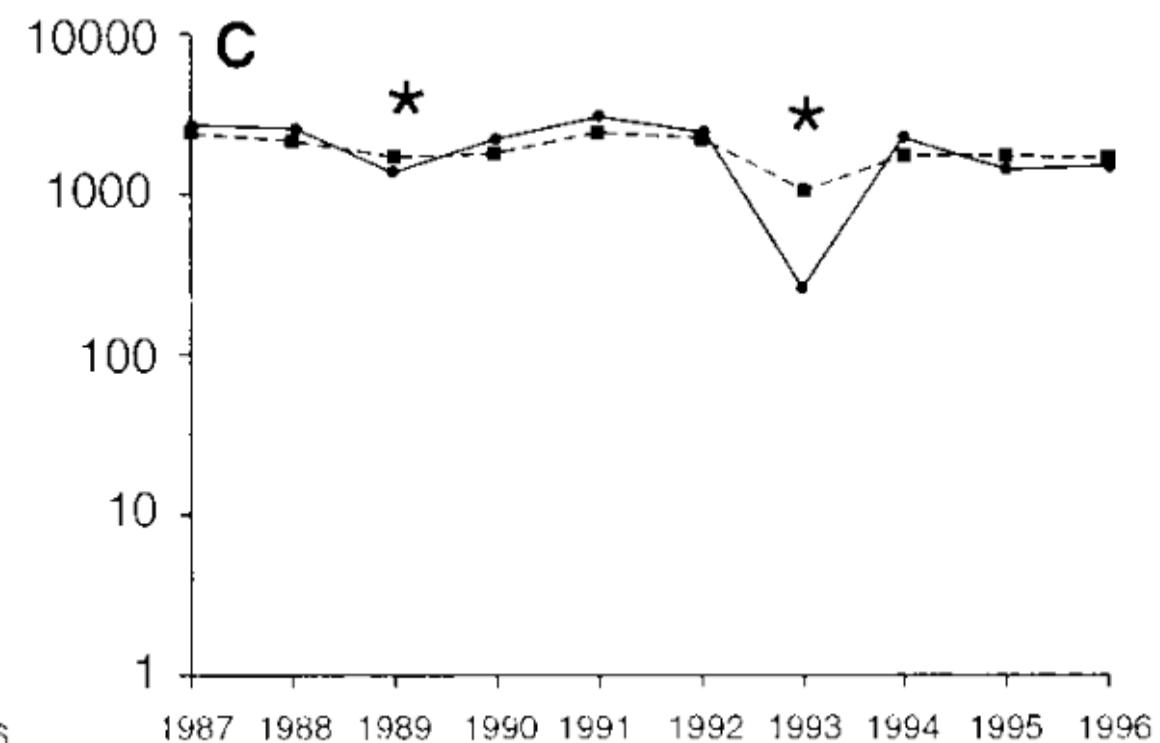
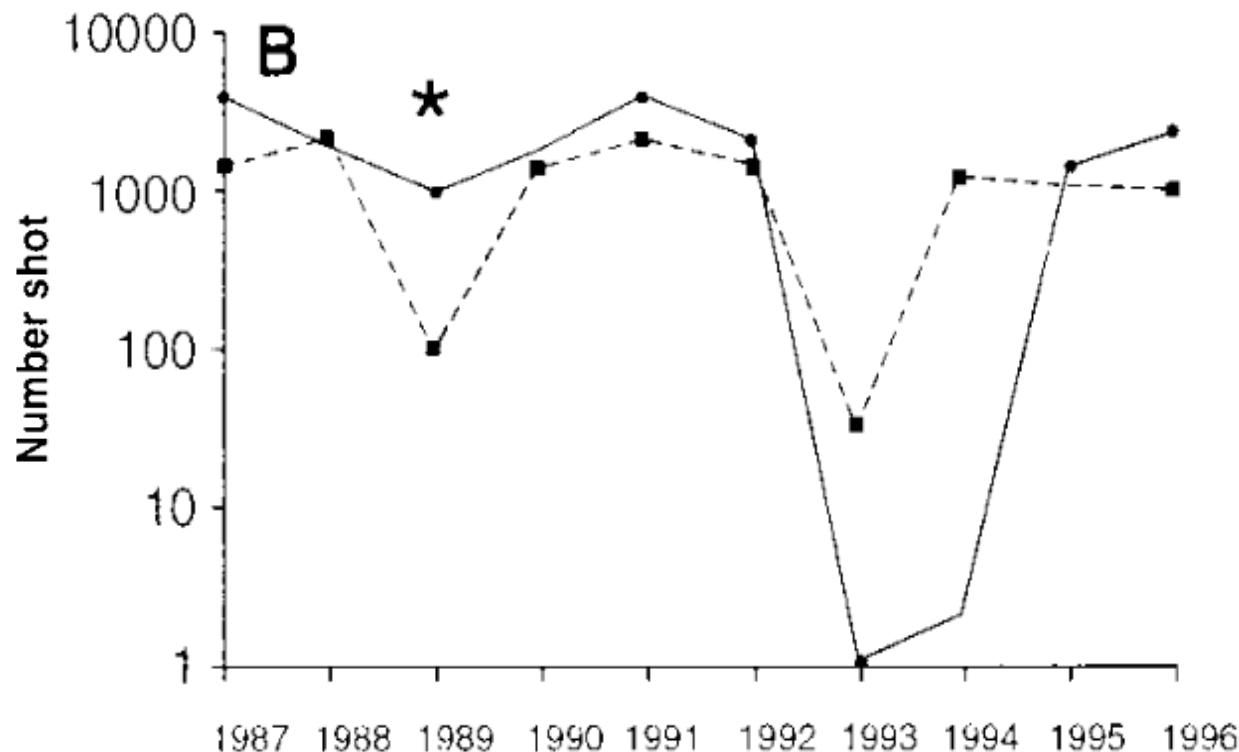
Hudson et al 1992. *J Animal Ecology*.

Worms were hypothesized to be responsible for the observed population cycles in ‘bag data’ from northern England.





Deworming eliminated population cycles to prove this effect!



Parasites and pathogens have also shaped human history.

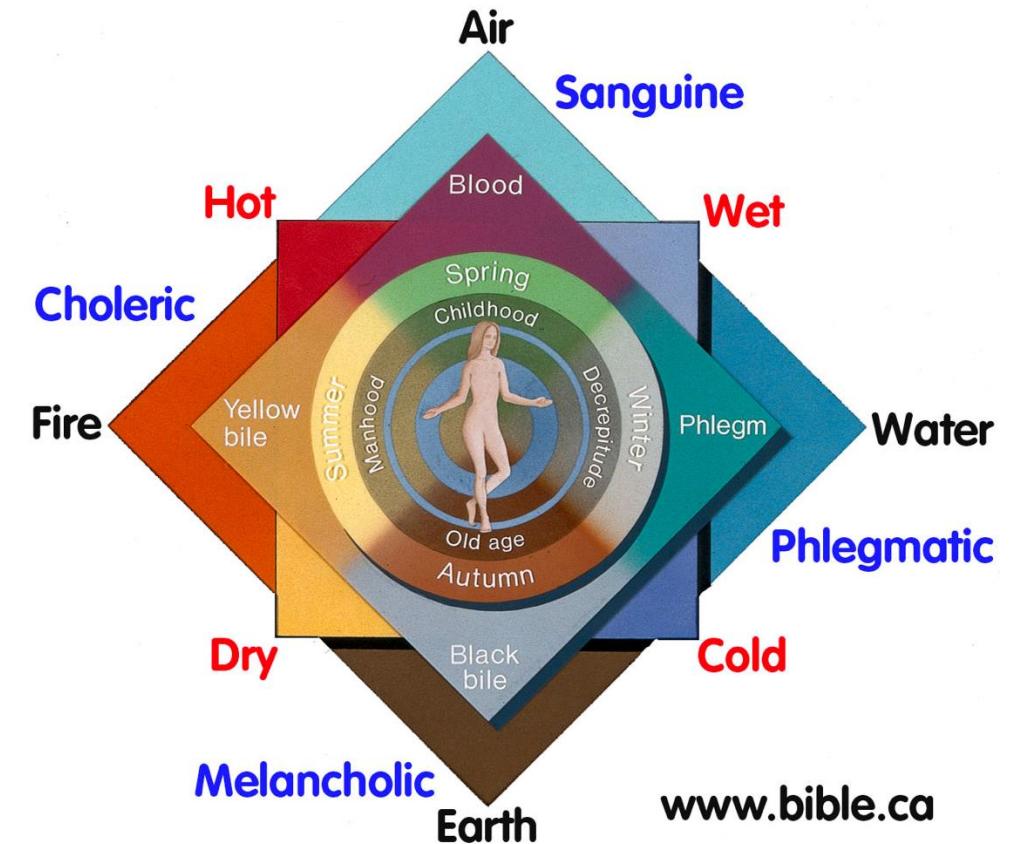
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1. **Four Humors:** Hippocrates (c. 400 BC) wrote that disease results from an imbalance of the four humors

The Four Humors of Hippocratic Medicine  
450 BC - 1858 AD  
Melancholy Blood (depression)



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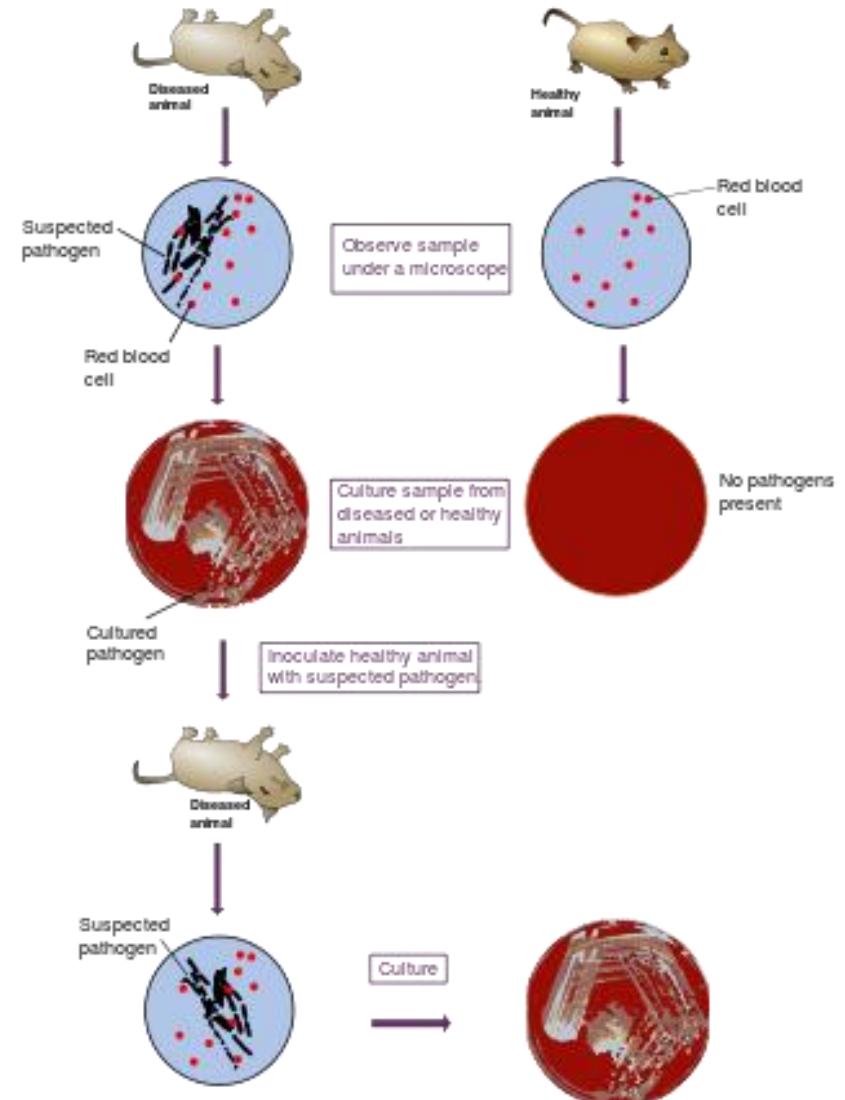
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3. **Germ Theory of Disease:** Idea that disease results from germs
  - Leuwenhoek's microscope (1675)
  - Koch's postulates (1890)



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4. **Classic epidemiology**

- Risk factors for disease = John Snow (1854)



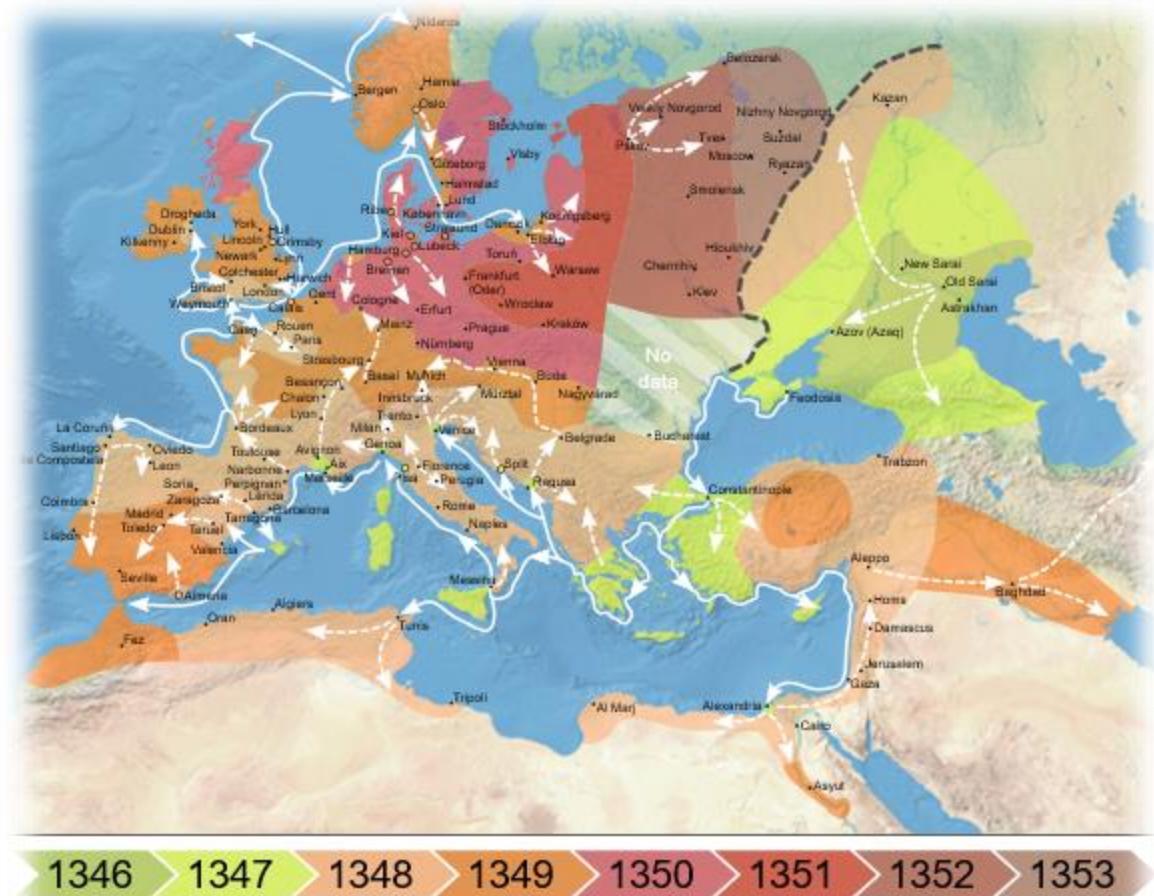
# Parasites and pathogens have also shaped human history.

- Plague of Justinian (541-549 AD)
  - First historically recorded pandemic of *Yersinia pestis*
  - Launched the ‘first plague pandemic’ resulting in the deaths of 15-100 million people, 25-60% of Europe’s population at the time



# Parasites and pathogens have also shaped human history.

- Plague of Justinian (541-549 AD)
- Black Death (1346-1353 AD)
  - Most fatal pandemic in human history, resulting in deaths of 75-200 million people
  - Killed 30-60% of Europe's population at the time; 17-54% of global population



1346 > 1347 > 1348 > 1349 > 1350 > 1351 > 1352 > 1353

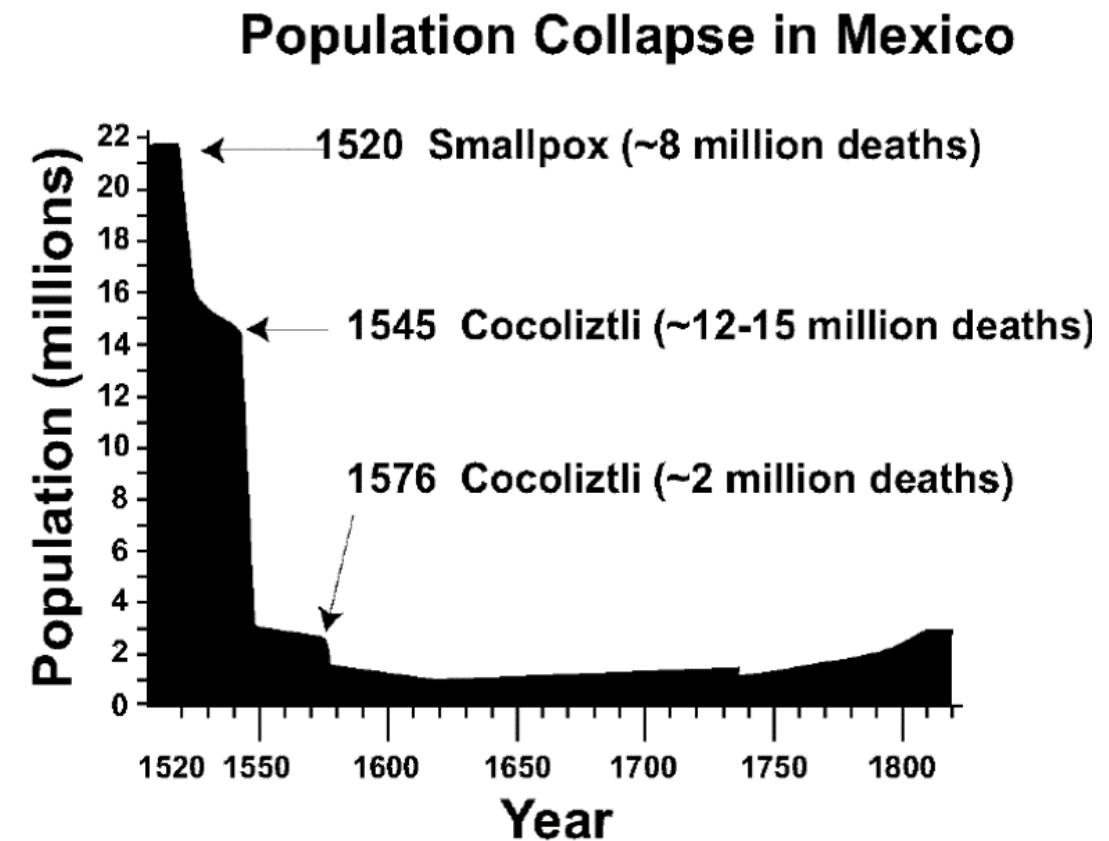
Approximate border between the Principality of Kiev and the Golden Horde - passage prohibited for Christians.

Land trade routes

Maritime trade routes

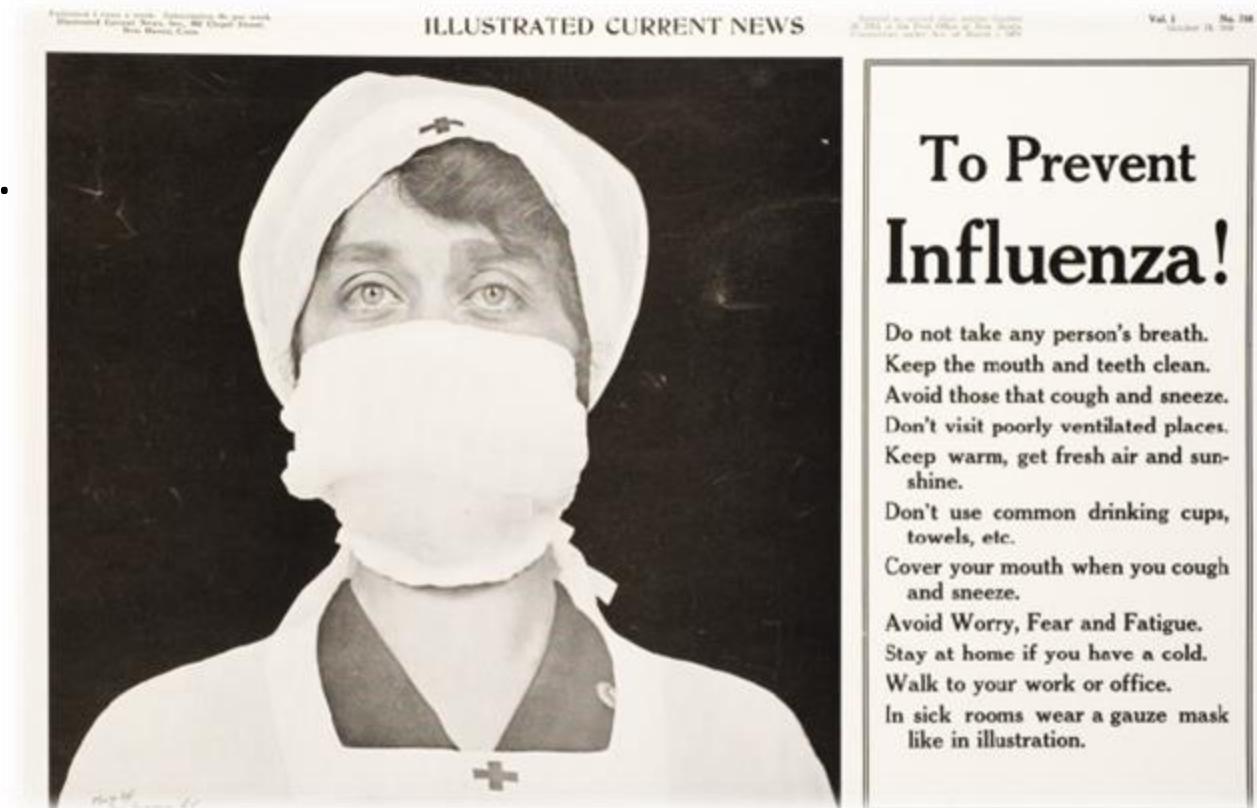
# Parasites and pathogens have also shaped human history.

- Plague of Justinian (541-549 AD)
- Black Death (1346-1353 AD)
- Cocoliztli (1545-1548)
  - Pathogen still unknown! Maybe viral hemorrhagic fever, maybe bacterium
  - Killed 80% of the population of Mexico



# Parasites and pathogens have also shaped human history.

- Plague of Justinian (541-549 AD)
- Black Death (1346-1353 AD)
- Cocoliztli (1545-1548)
- Spanish Influenza (1918-1920)
  - 17-100 million deaths worldwide.
  - 1-5% of global population
  - 2<sup>nd</sup>-most devastating pandemic in history (after Black Death)



Do not take any person's breath.  
Keep the mouth and teeth clean.  
Avoid those that cough and sneeze.  
Don't visit poorly ventilated places.  
Keep warm, get fresh air and sun-  
shine.

Don't use common drinking cups,  
towels, etc.

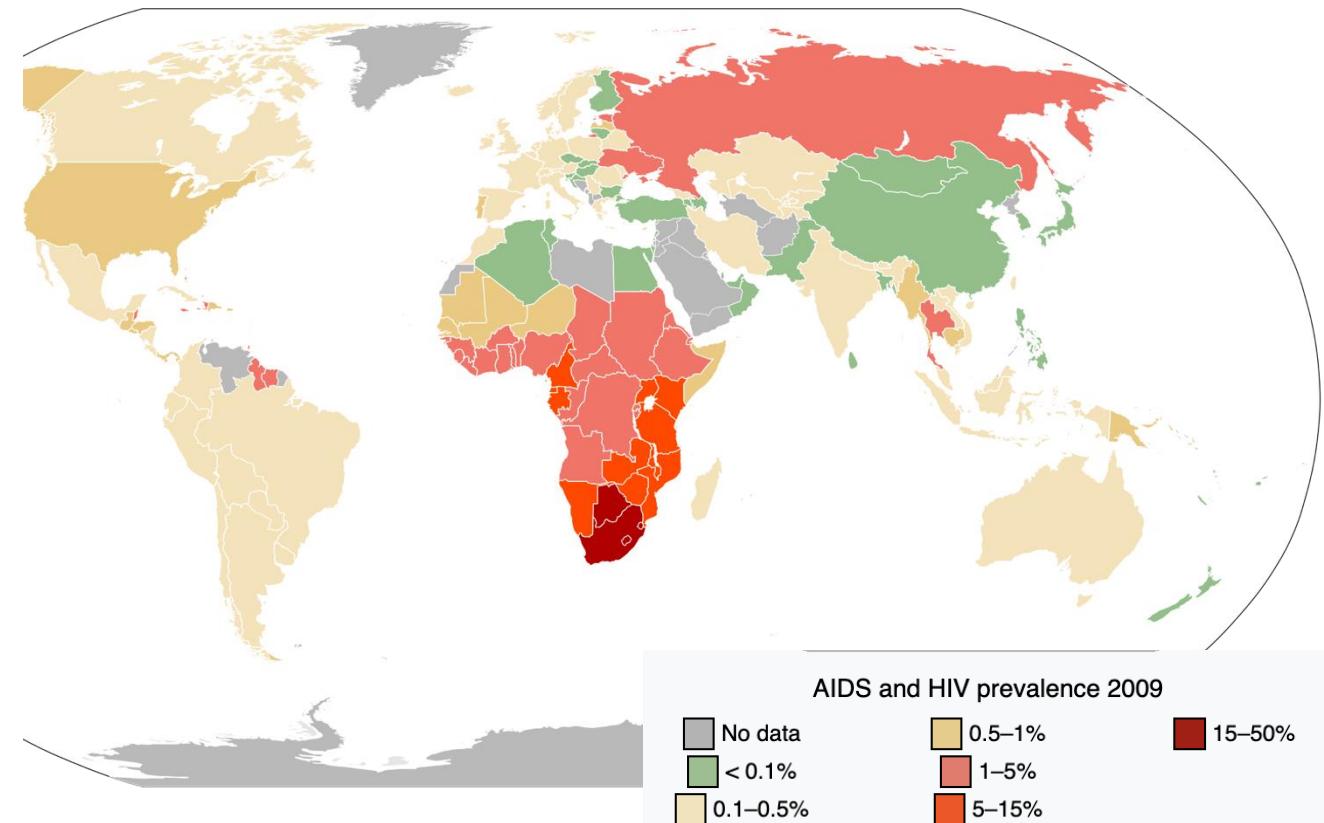
Cover your mouth when you cough  
and sneeze.

Avoid Worry, Fear and Fatigue.  
Stay at home if you have a cold.  
Walk to your work or office.

In sick rooms wear a gauze mask  
like in illustration.

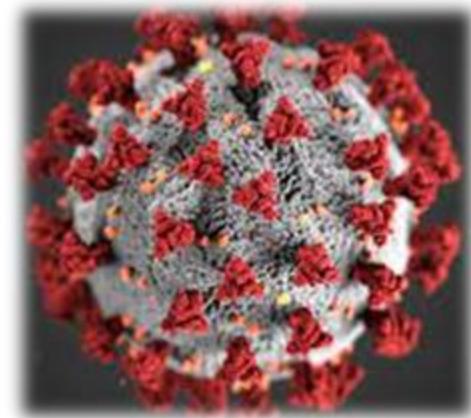
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- Spanish Influenza (1918-1920)
- HIV (~1960-now)
  - >40 million deaths and counting
  - Prevalence still >20% in some countries in southern Africa



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- Black Death (1346-1353 AD)
- Cocoliztli (1545-1548)
- Spanish Influenza (1918-1920)
- HIV (~1960-now)
- COVID-19 (2019-now)
  - ~7-29 million deaths worldwide
  - ~0.1-0.4% of population

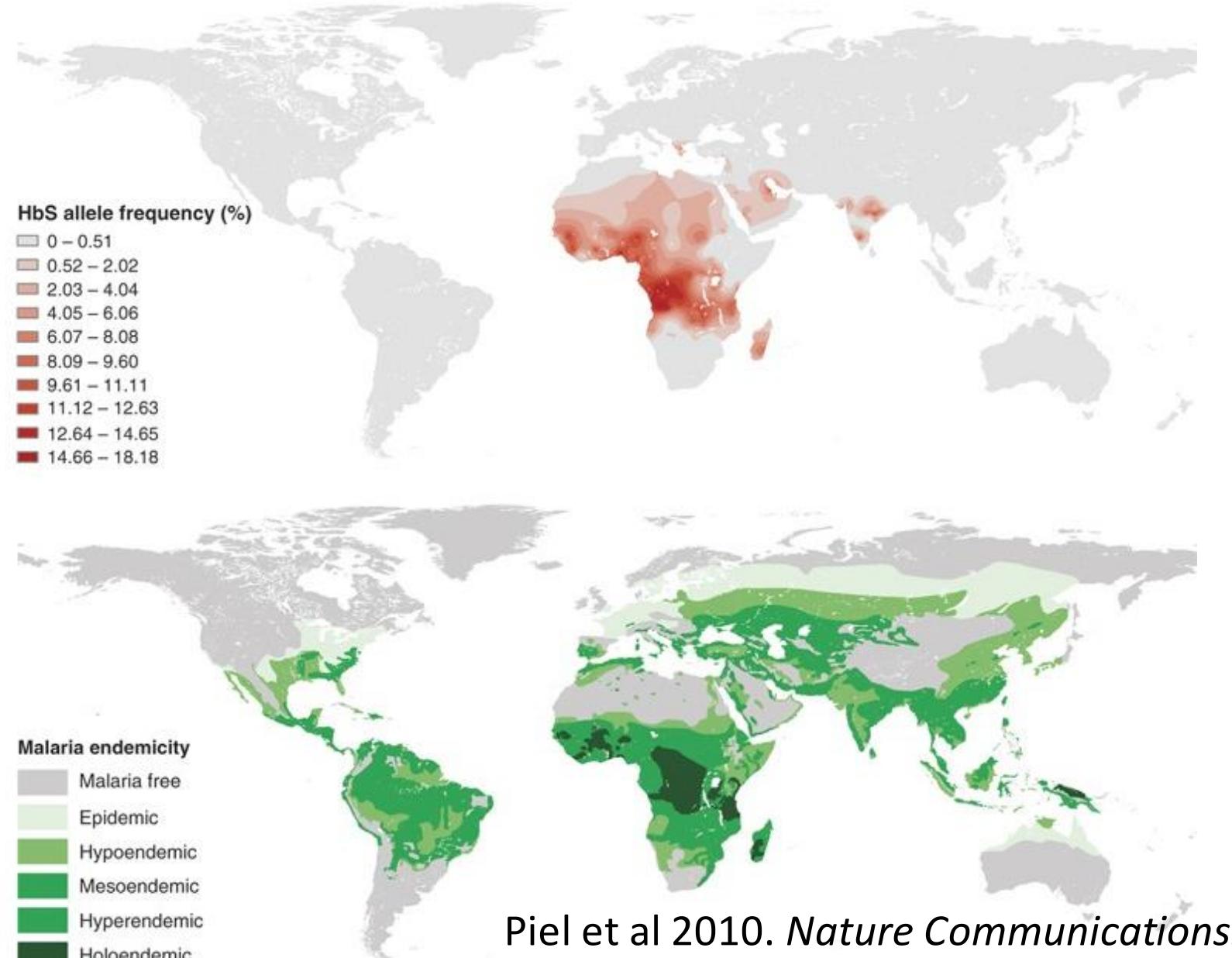


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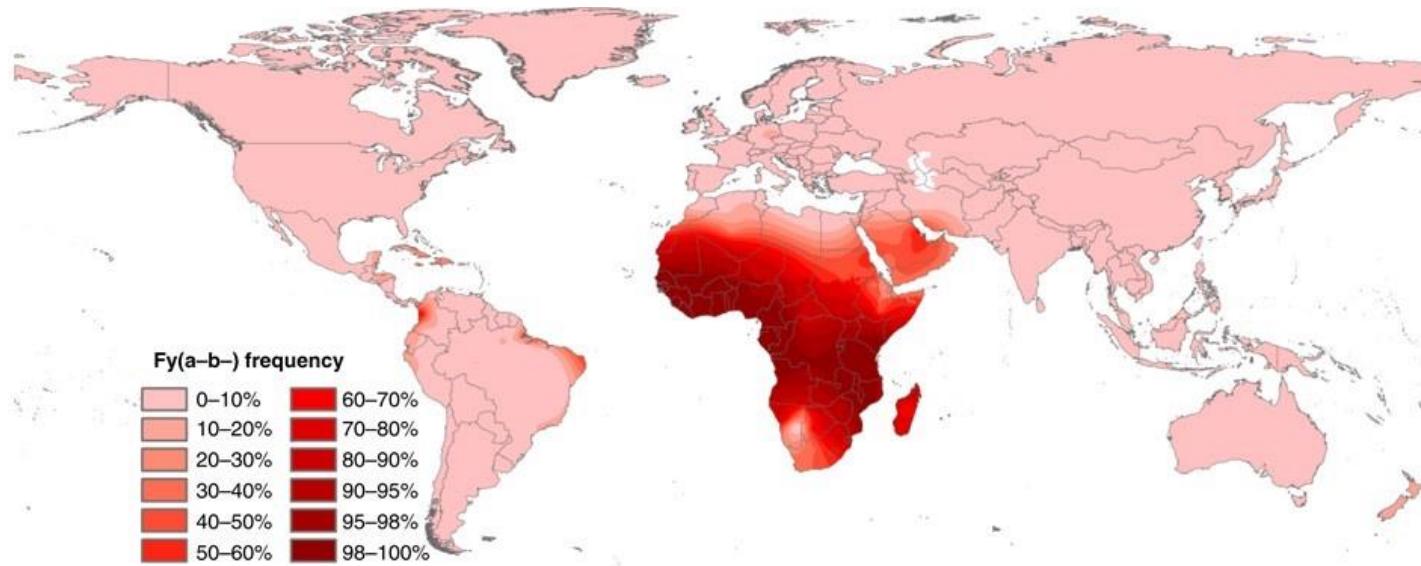
## Sickle cell anemia

- The HbS allele confers resistance to malaria but also results in sickle cell anemia when homozygous.
- Natural selection has favored this trait in malaria-endemic regions of the planet.
- As of 2021, WHO estimates 247 million malaria cases worldwide and >600,000 deaths, 95% in Africa.
- Children <5 account for 80% of malaria deaths.



# Parasites and pathogens have also shaped human DNA.

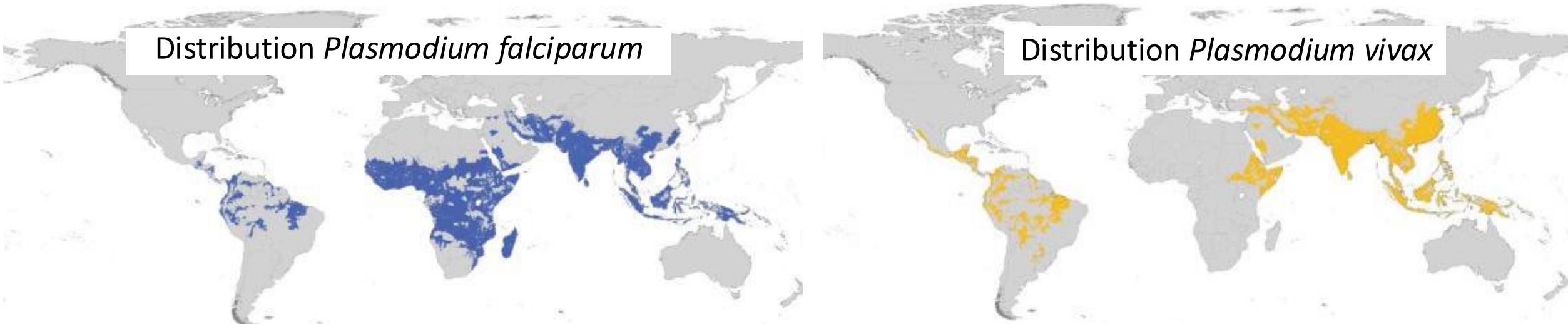
## Duffy antigen



- Modeled distribution of Duffy-negative human population

Distribution *Plasmodium falciparum*

Distribution *Plasmodium vivax*



Guerra et al. 2006. *Trends in Parasitology*  
Howes et al 2011. *Nature Communications*.

# Epidemiology vs. Disease Ecology

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- Epidemiology = “the study of **what** is on the people”
  - Coined by Spanish physician Villalba in 1802
- Disease Ecology = the study of **how** a disease spreads
  - Emphasis on the **interactions** of organisms with each other and the environment...when interactions result in disease

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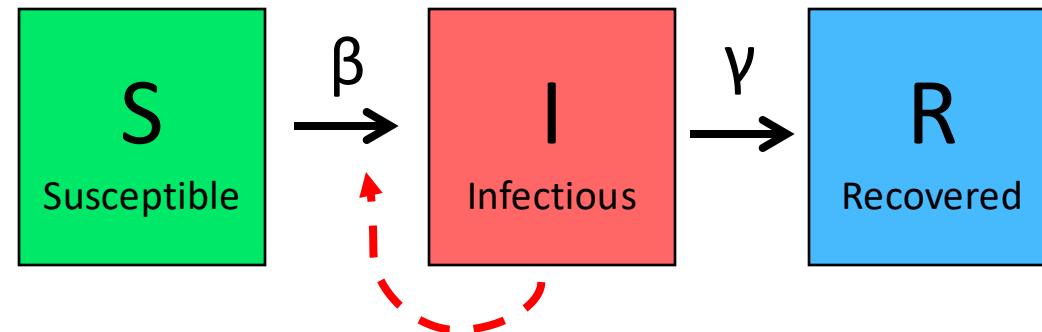
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  - Including chronic diseases!
- Often uses **cross-sectional** data to demonstrate associations of variables with outcome (disease)
- More statistical ( $y=mx+b$ )
  - **Pattern**

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- More mathematical ( $dN/dt$ )
  - **Process**

# The SIR Model

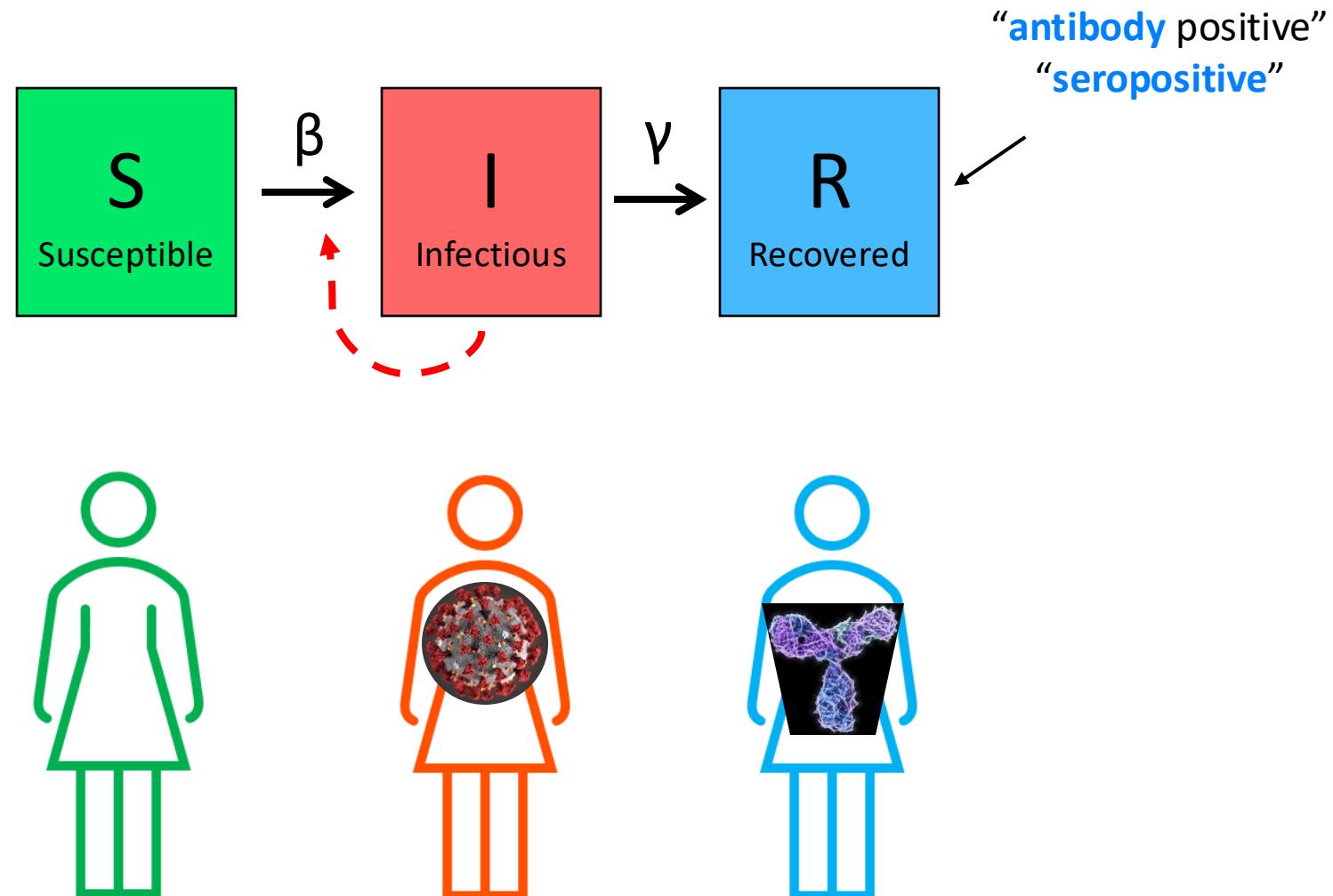


$\beta$  = transmission rate

$\gamma$  = recovery rate

Kermack and McKendrick 1927 *Proc Roy Soc A*

We class hosts into categories of **susceptible**, **infectious**, and **recovered** to model **pathogen dynamics**.



$\beta$  = transmission rate

$\gamma$  = recovery rate

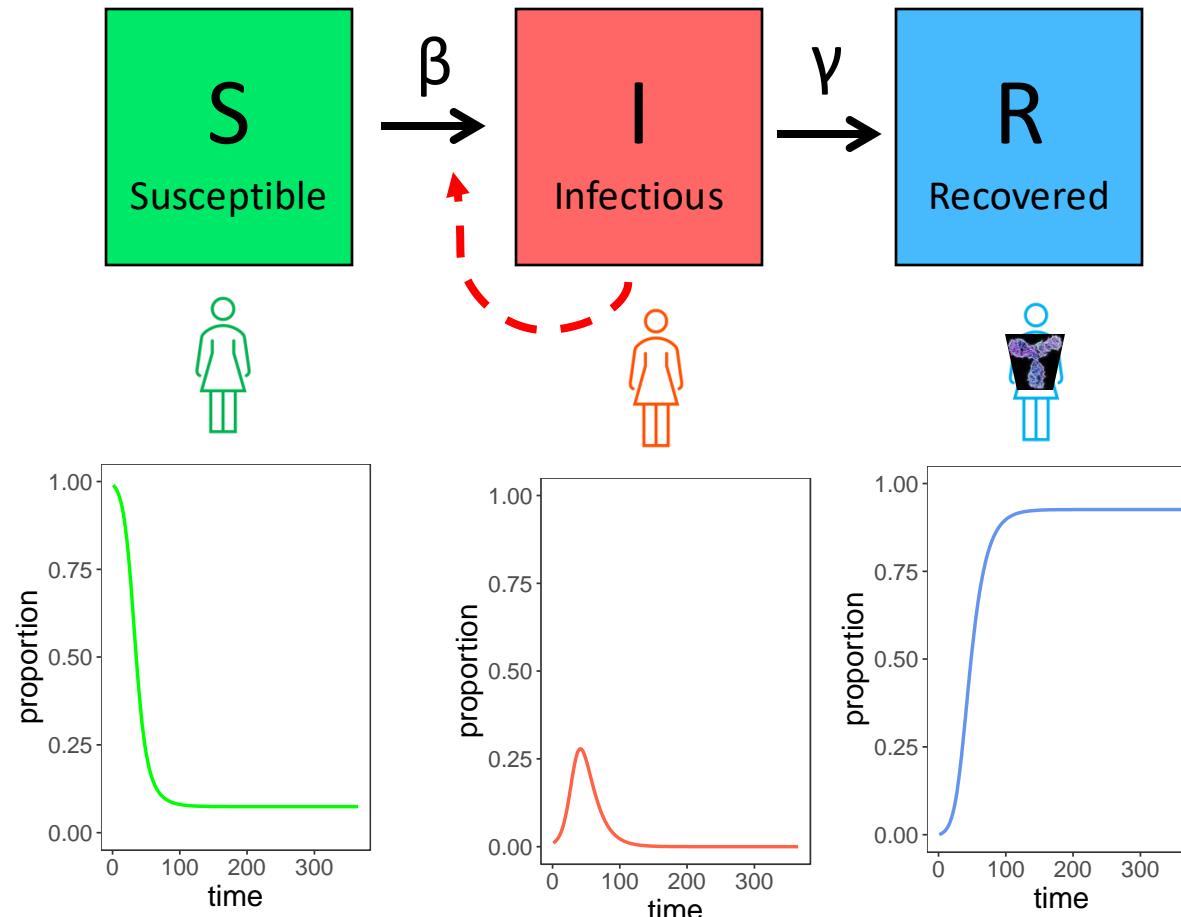
Kermack and McKendrick 1927 *Proc Roy Soc A*

We use computers to simulate systems of equations in the SIR framework.

$$\frac{dS}{dt} = -\beta SI$$

$$\frac{dI}{dt} = \beta SI - \gamma I$$

$$\frac{dR}{dt} = \gamma I$$



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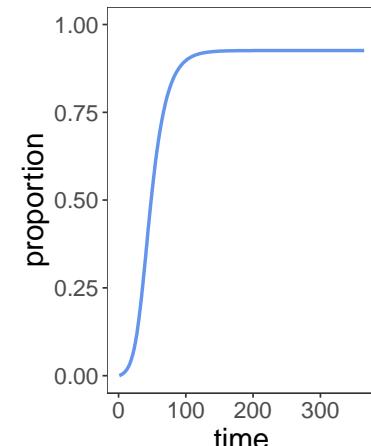
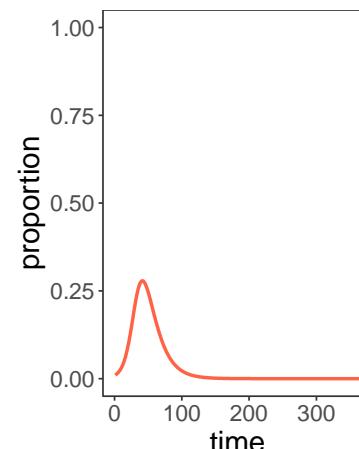
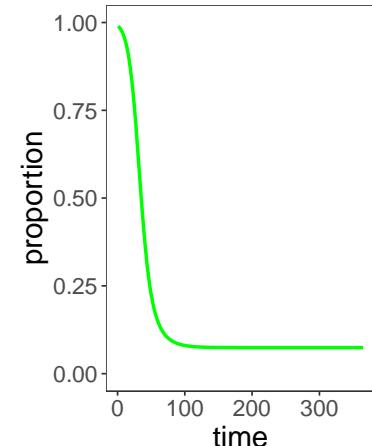
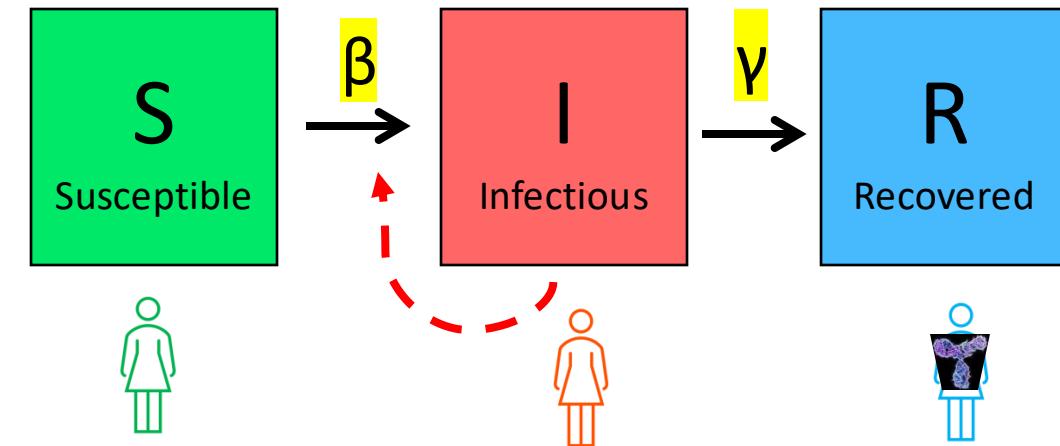
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$R_0$  is the pathogen **basic reproduction number**.

$$\frac{dS}{dt} = -\beta SI$$

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$$\frac{dR}{dt} = \gamma I$$



$$R_0 = \frac{\beta}{\gamma}$$

$\beta$  = transmission rate

$\gamma$  = recovery rate

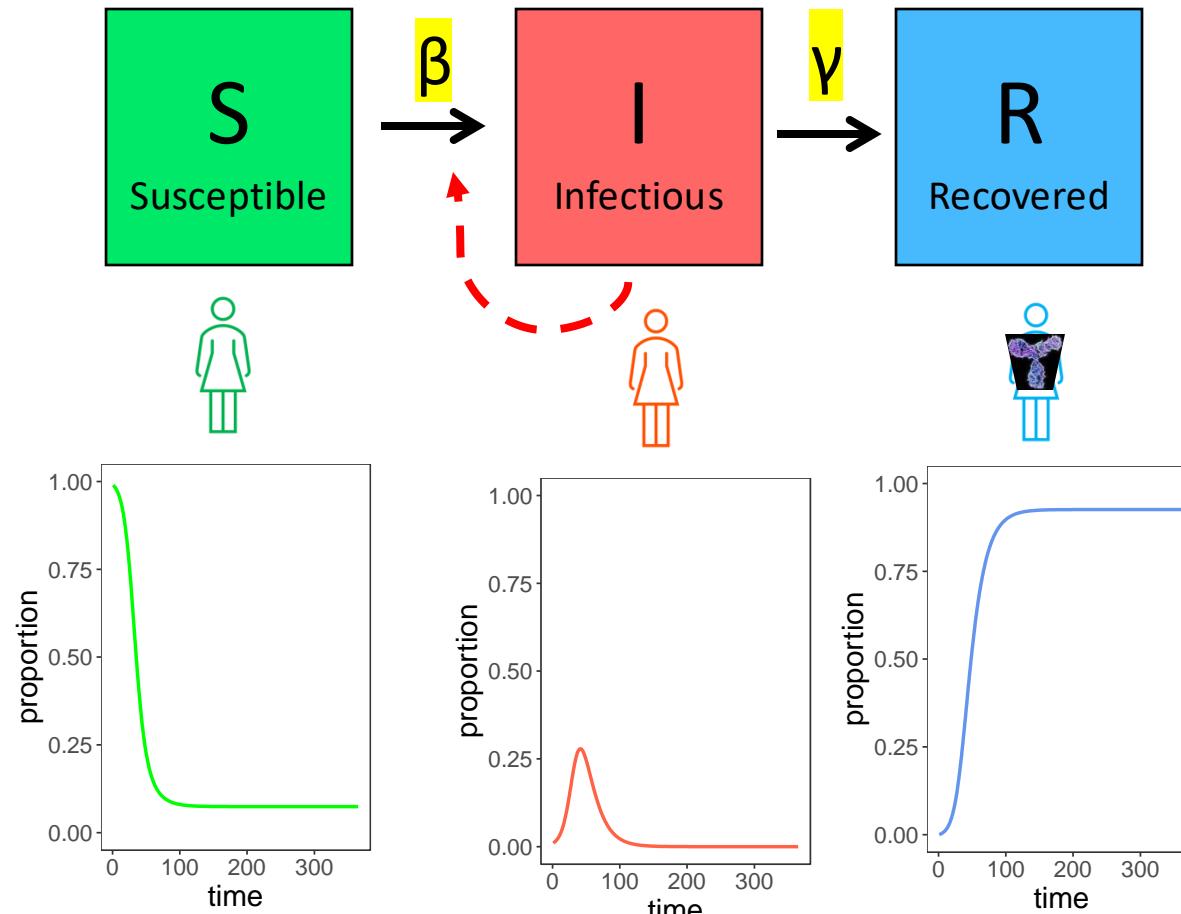
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$$\frac{dI}{dt} = \beta SI - \gamma I$$

$$\frac{dR}{dt} = \gamma I$$



$$R_0 = \frac{\beta}{\gamma}$$

infections  
created  
infections  
lost

$R_0$  must be  $>1$  for  
a disease to start  
spreading!

$\beta$  = transmission rate

$\gamma$  = recovery rate

# $R_o$

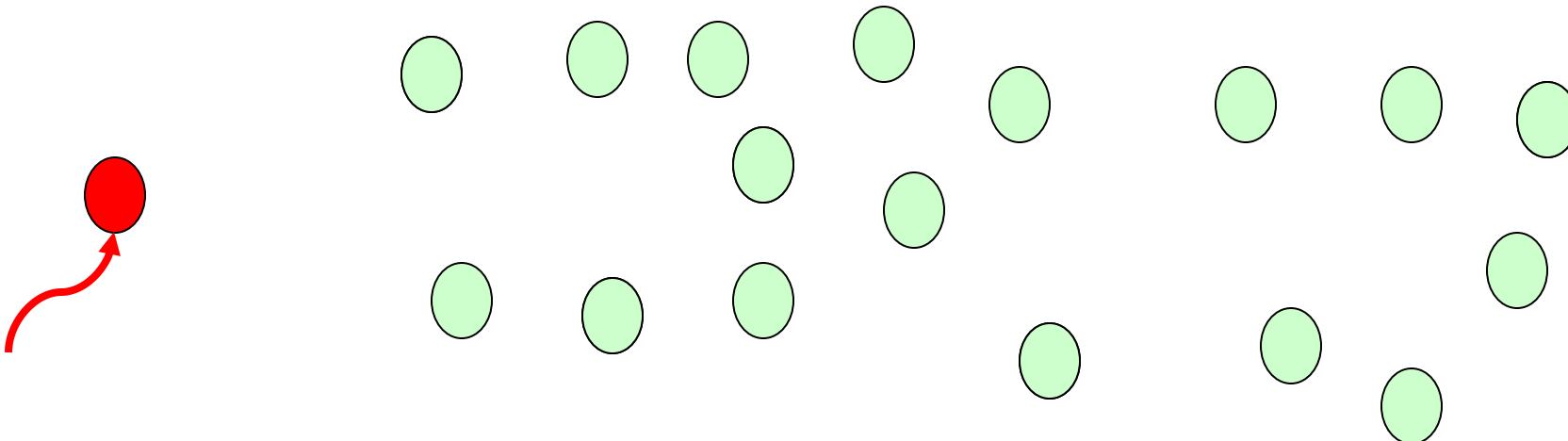
- The **basic reproduction number** for a pathogen

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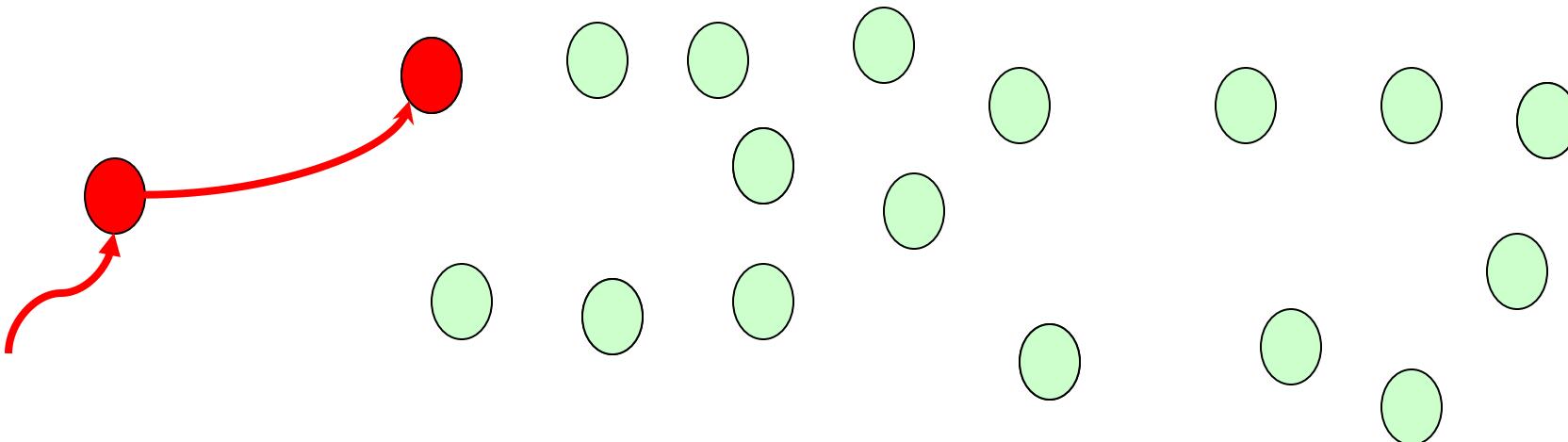
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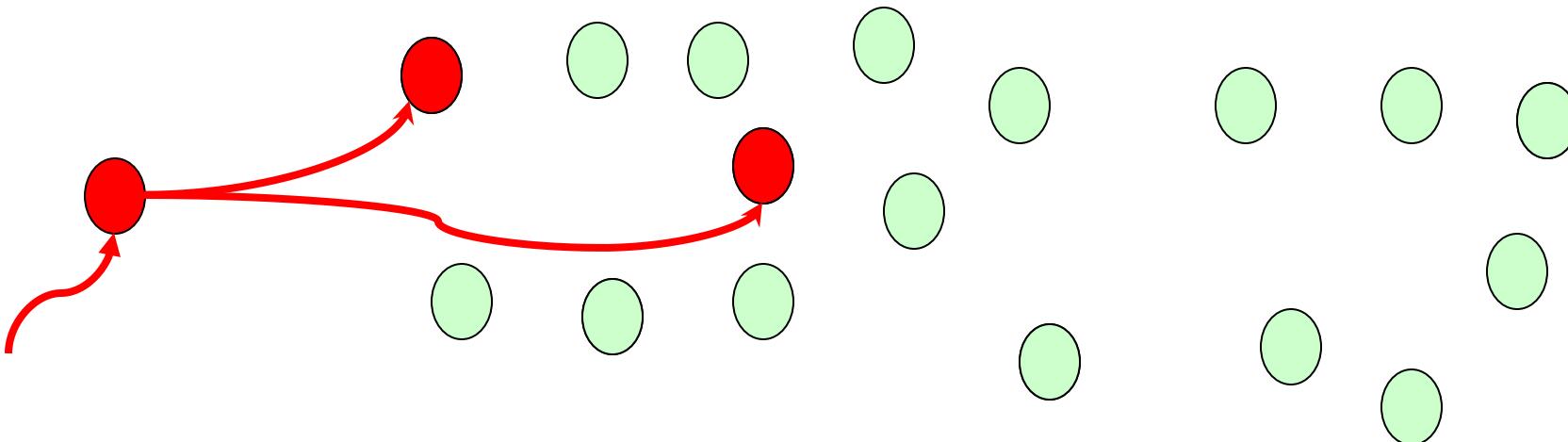
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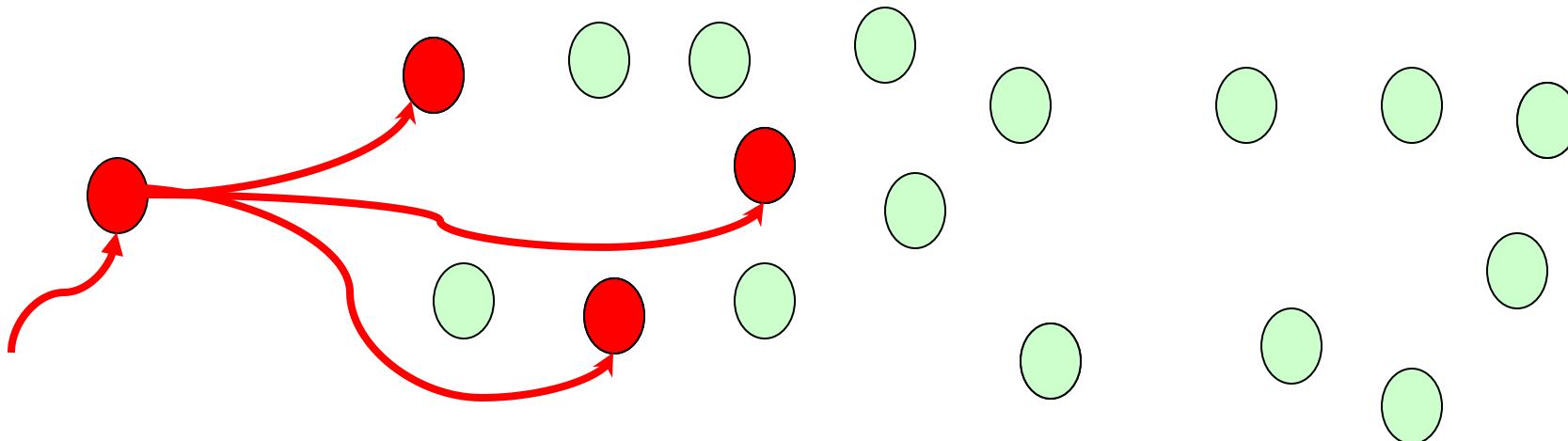
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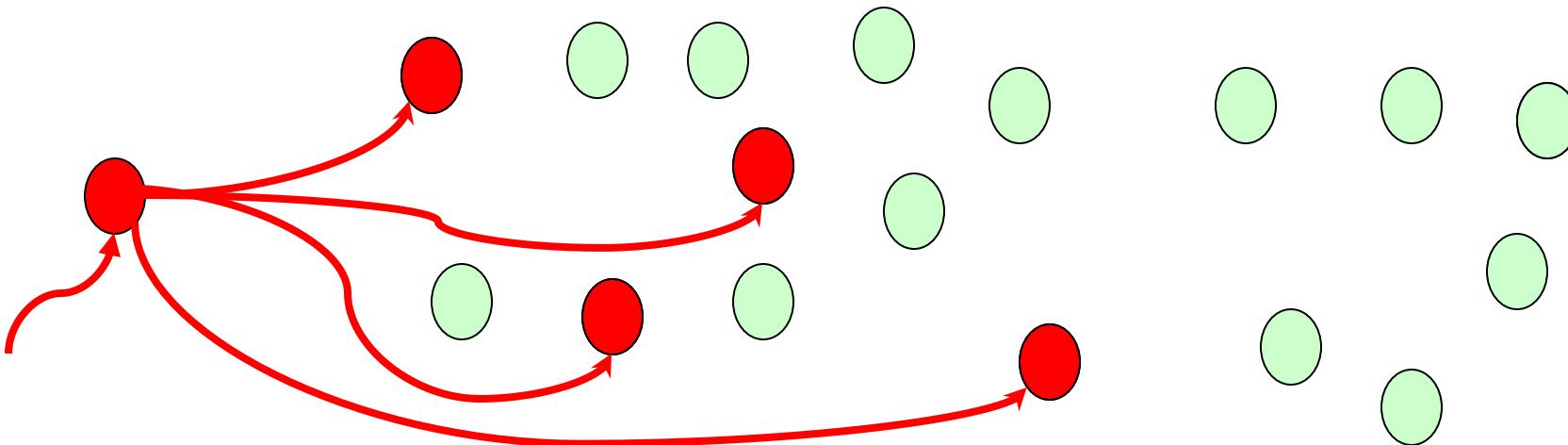
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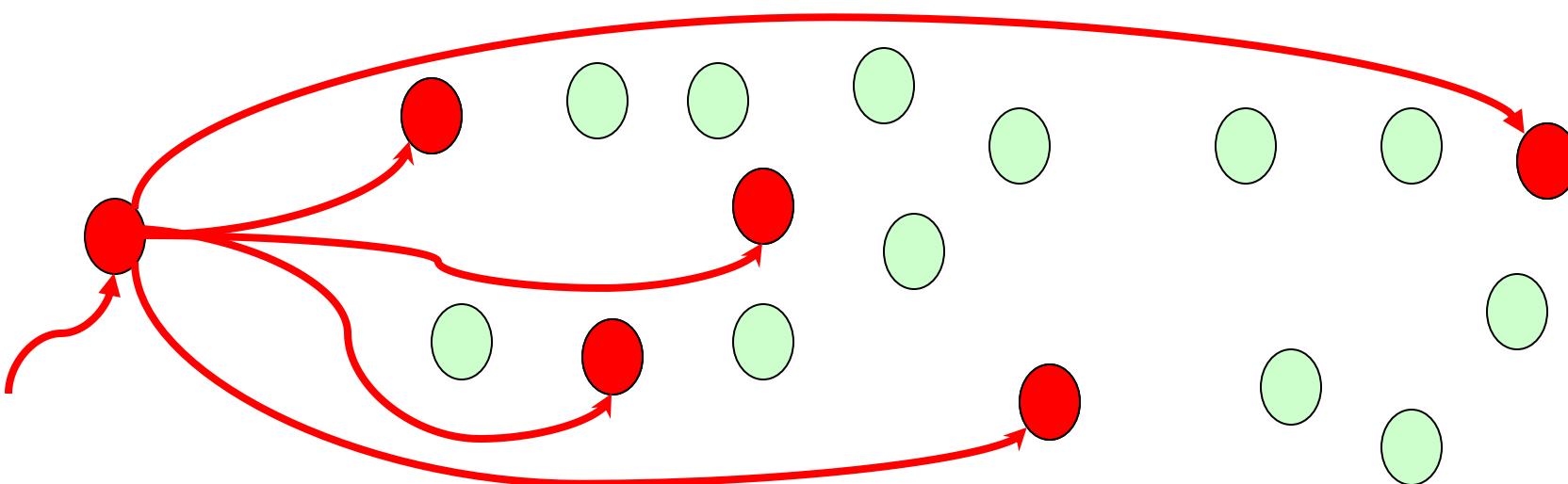
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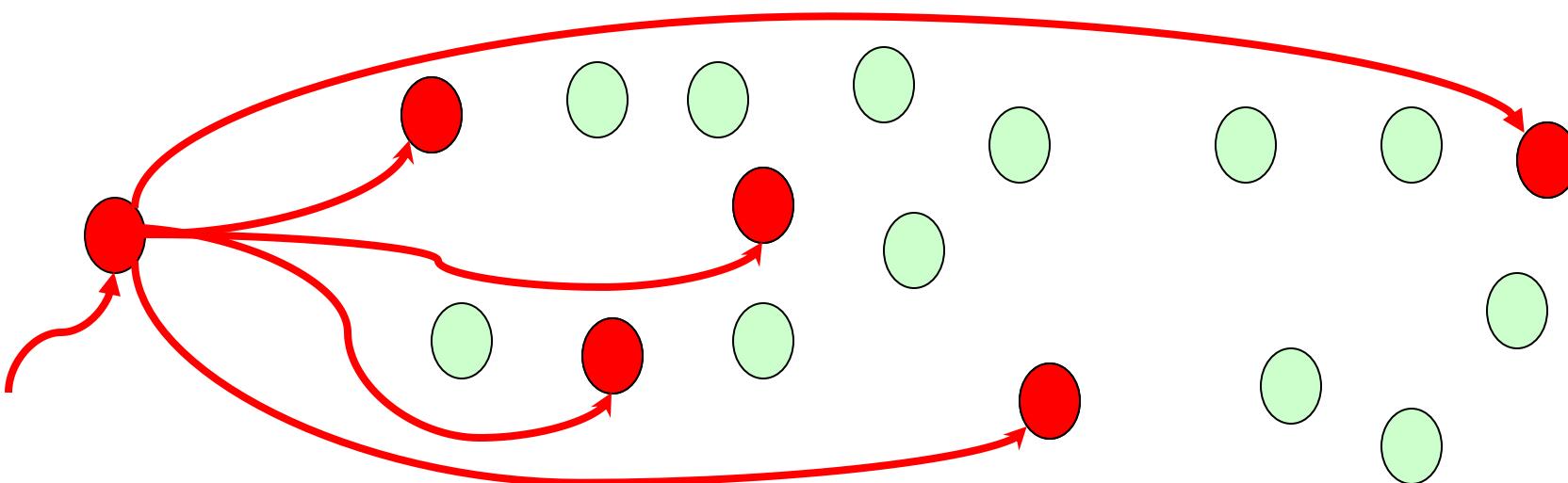
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What is  $R_o$ ?

# $R_o$

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- Defined as: the number of new cases caused by one infectious case in a **completely susceptible** population



What is  $R_o$ ?

$R_o = 5$

We can add realism to our models with births and deaths to **maintain** endemic pathogens.

$$\frac{dS}{dt} = b(S + I + R) - \beta SI - \mu S$$

$$\frac{dI}{dt} = \beta SI - \gamma I - \mu I$$

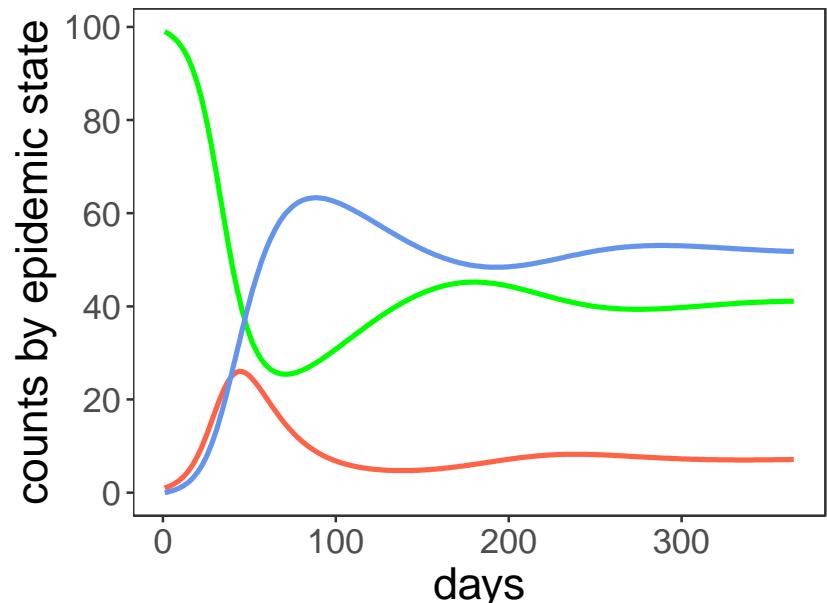
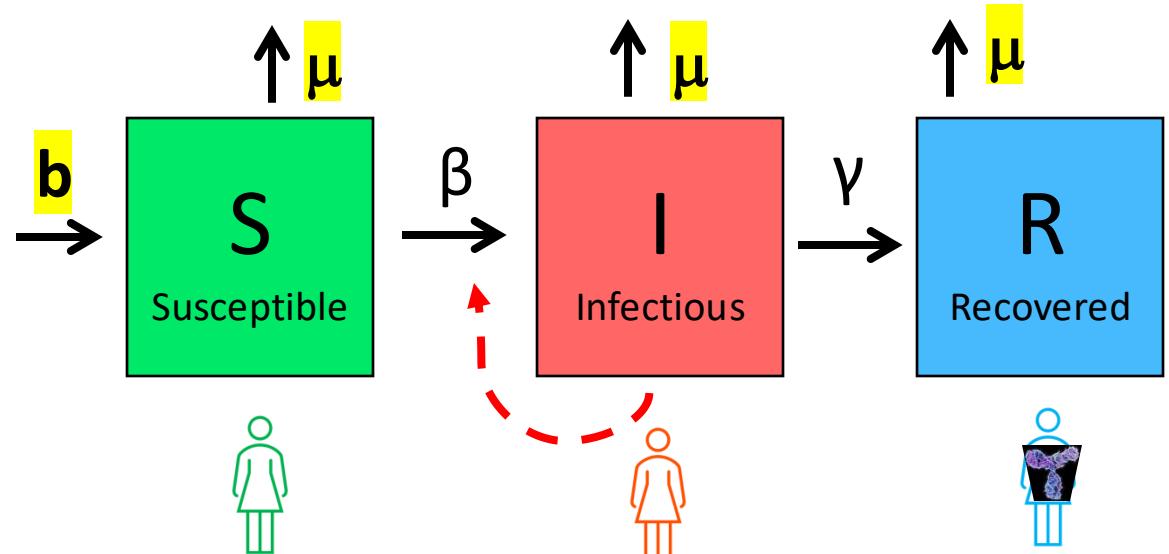
$$\frac{dR}{dt} = \gamma I - \mu R$$

**b** = birth rate

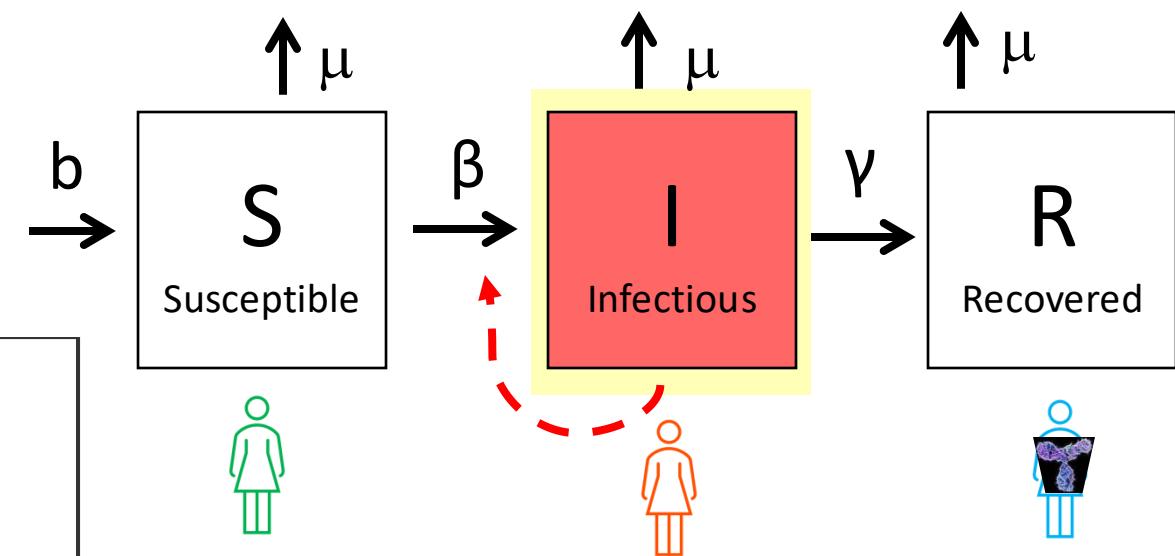
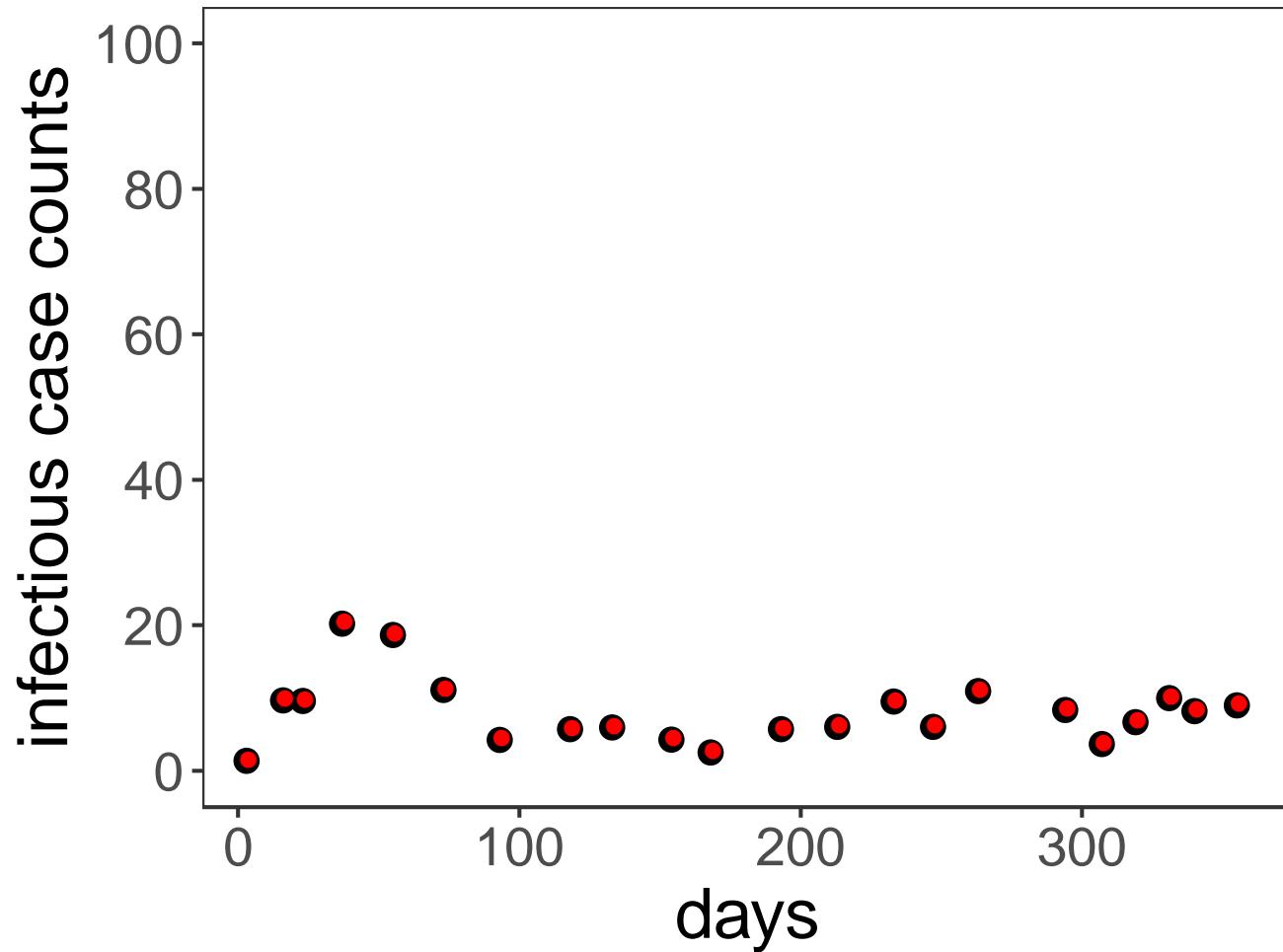
**$\mu$**  = death rate

$\beta$  = transmission rate

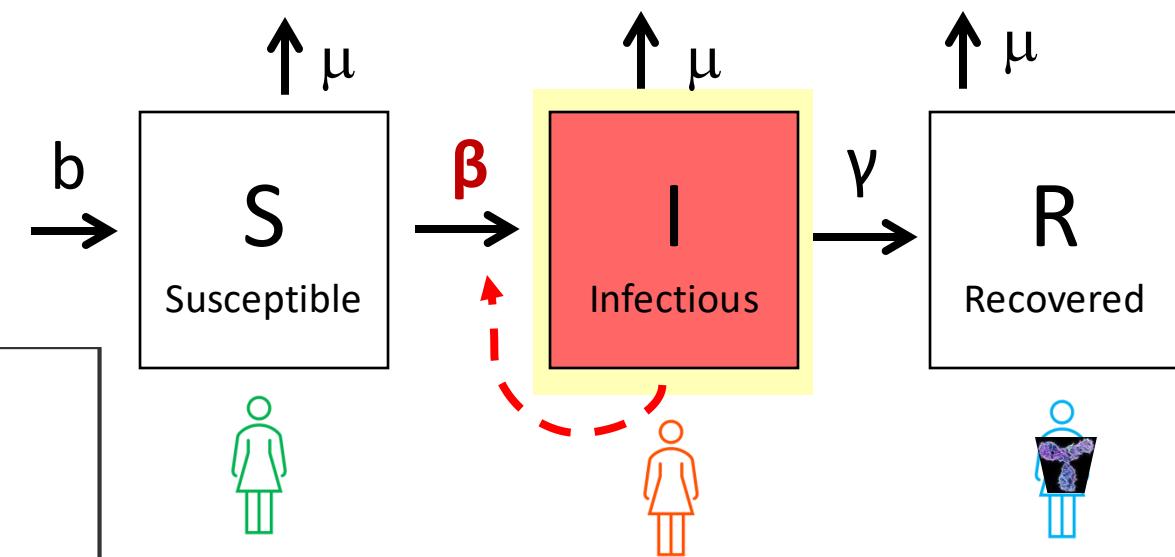
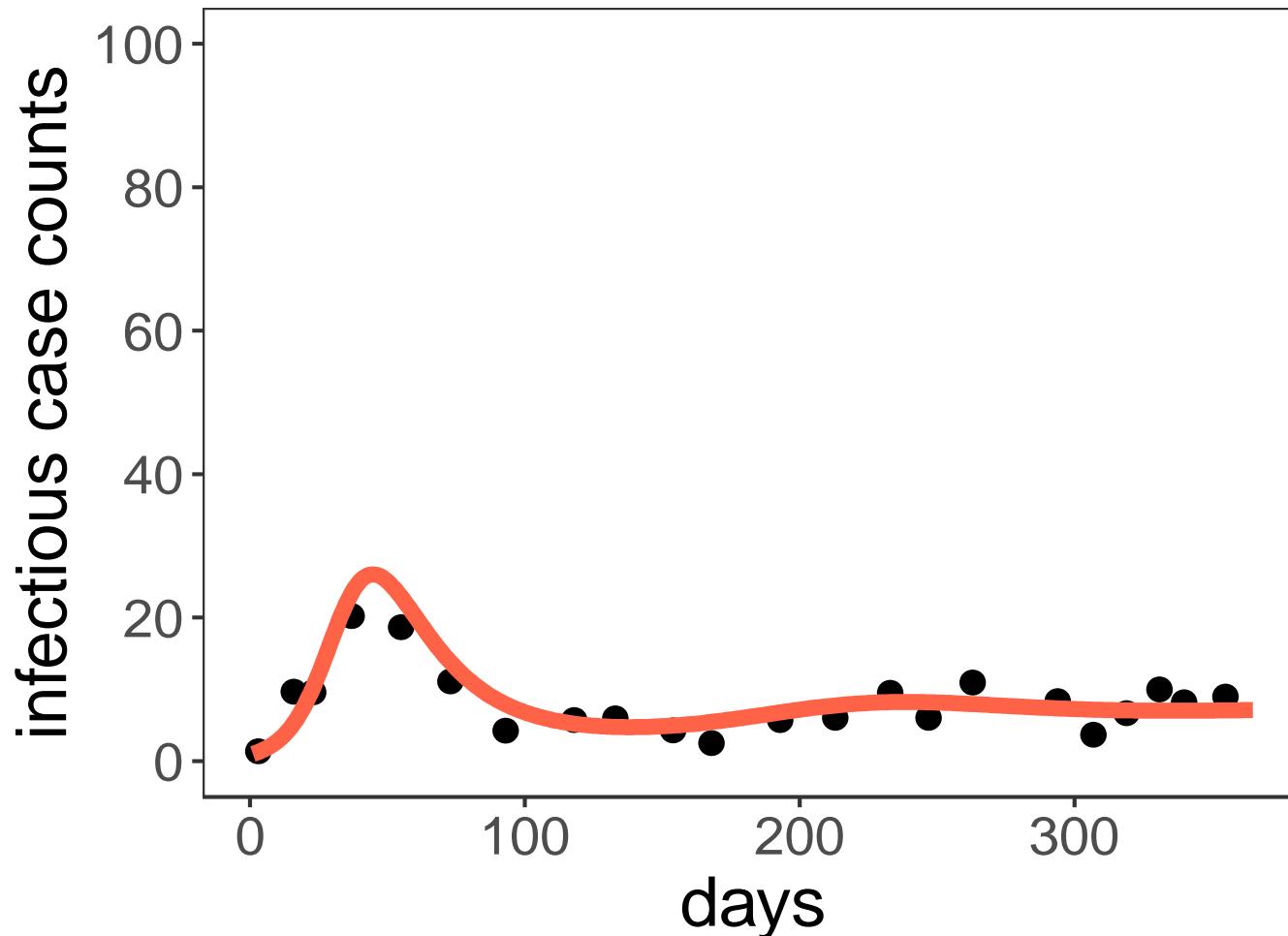
$\gamma$  = recovery rate



We can **estimate epidemic trajectories**  
by fitting SIR models to infectious case  
count data.



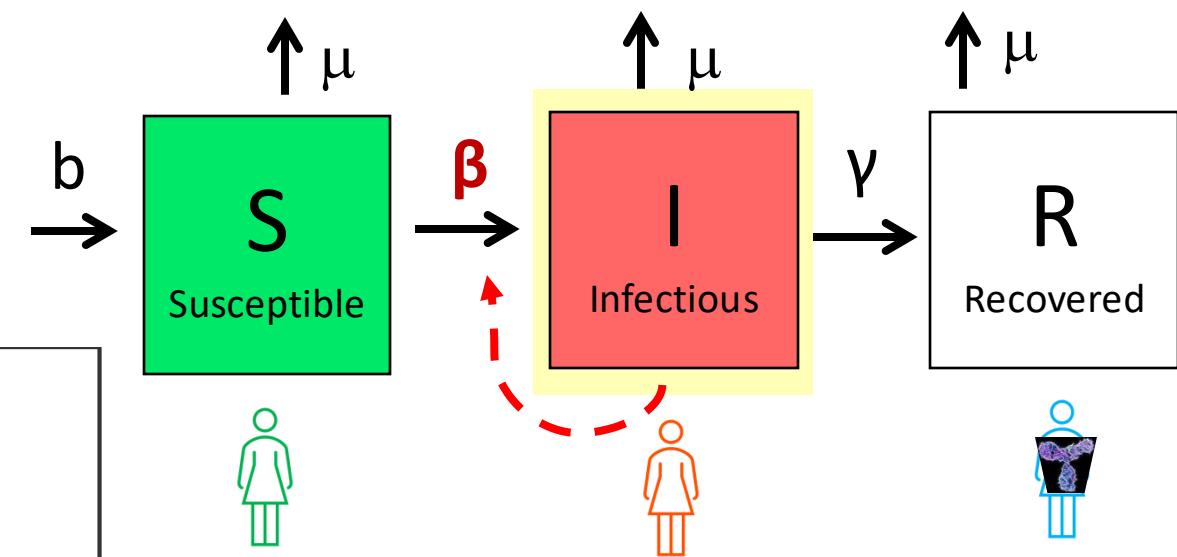
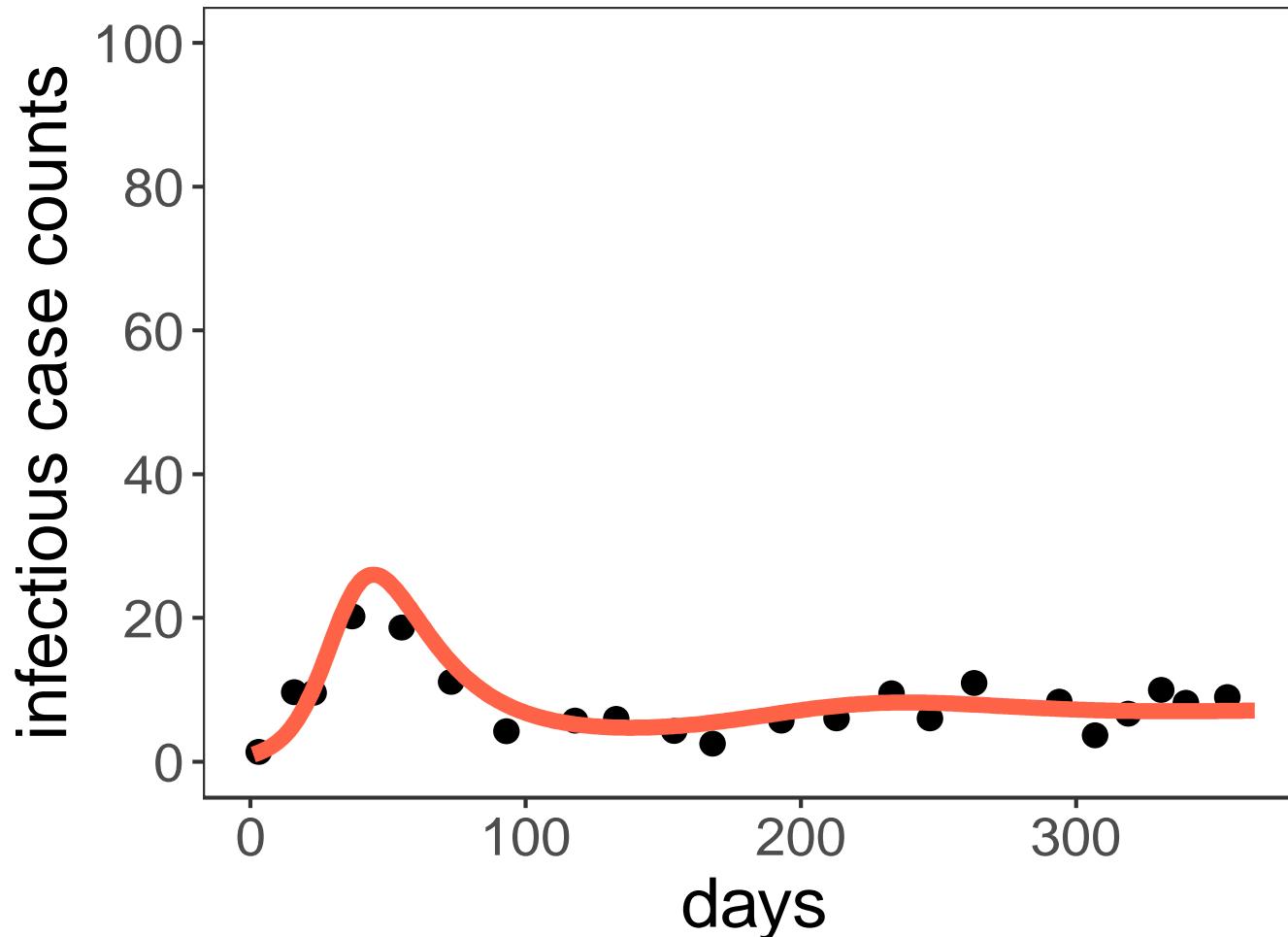
We can **estimate epidemic trajectories**  
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$$R_0 = \frac{\beta}{\gamma + \mu}$$

$b$  = birth rate  
 $\mu$  = death rate  
 $\beta$  = **transmission rate**  
 $\gamma$  = recovery rate

We can **estimate epidemic trajectories**  
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$$R_0 = \frac{\beta}{\gamma + \mu}$$

$$R_E = R_0 \frac{S}{N}$$

$b$  = birth rate  
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 $\beta$  = **transmission rate**  
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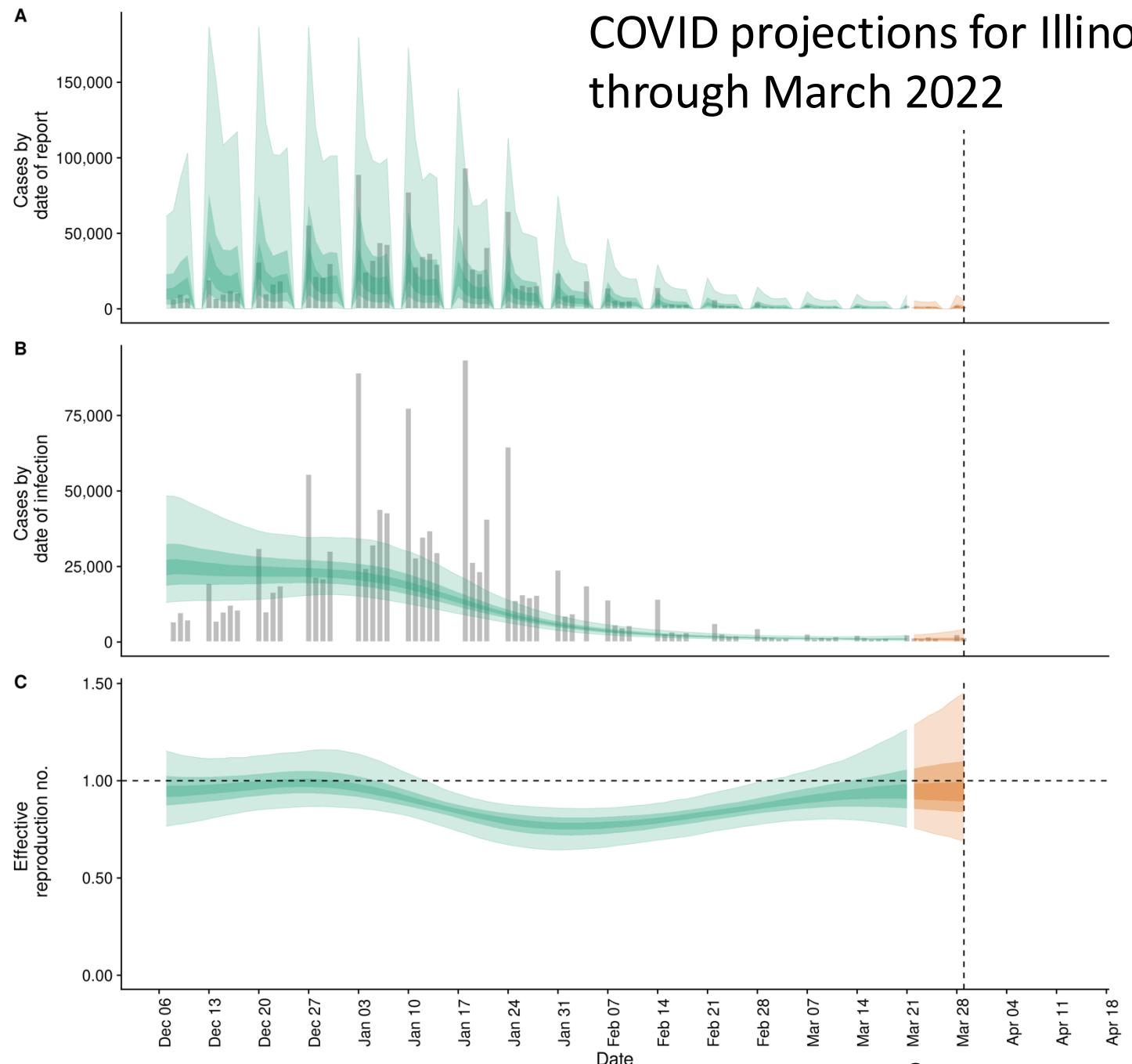
$\approx \lambda$  for a  
*population model*

(epidemics spread @ $R_E > 1$  and decline @ $R_E < 1$ )

# $R_E$ OR $R_t$

- The **effective reproduction number** for a pathogen

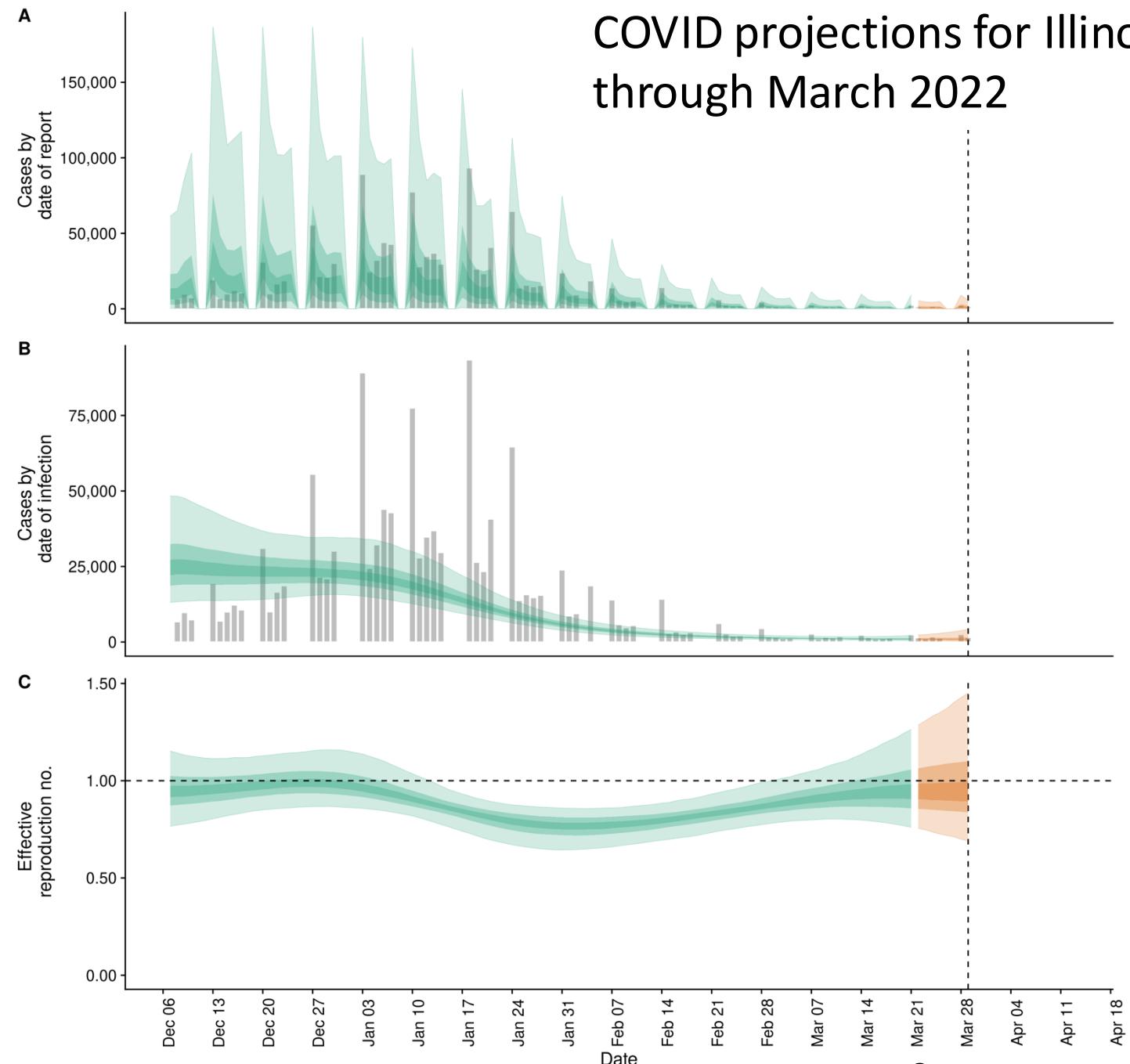
COVID projections for Illinois through March 2022



# $R_E$ OR $R_t$

- The **effective reproduction number** for a pathogen
- Defined as: the number of new cases caused by one infectious case in a **partially susceptible** population

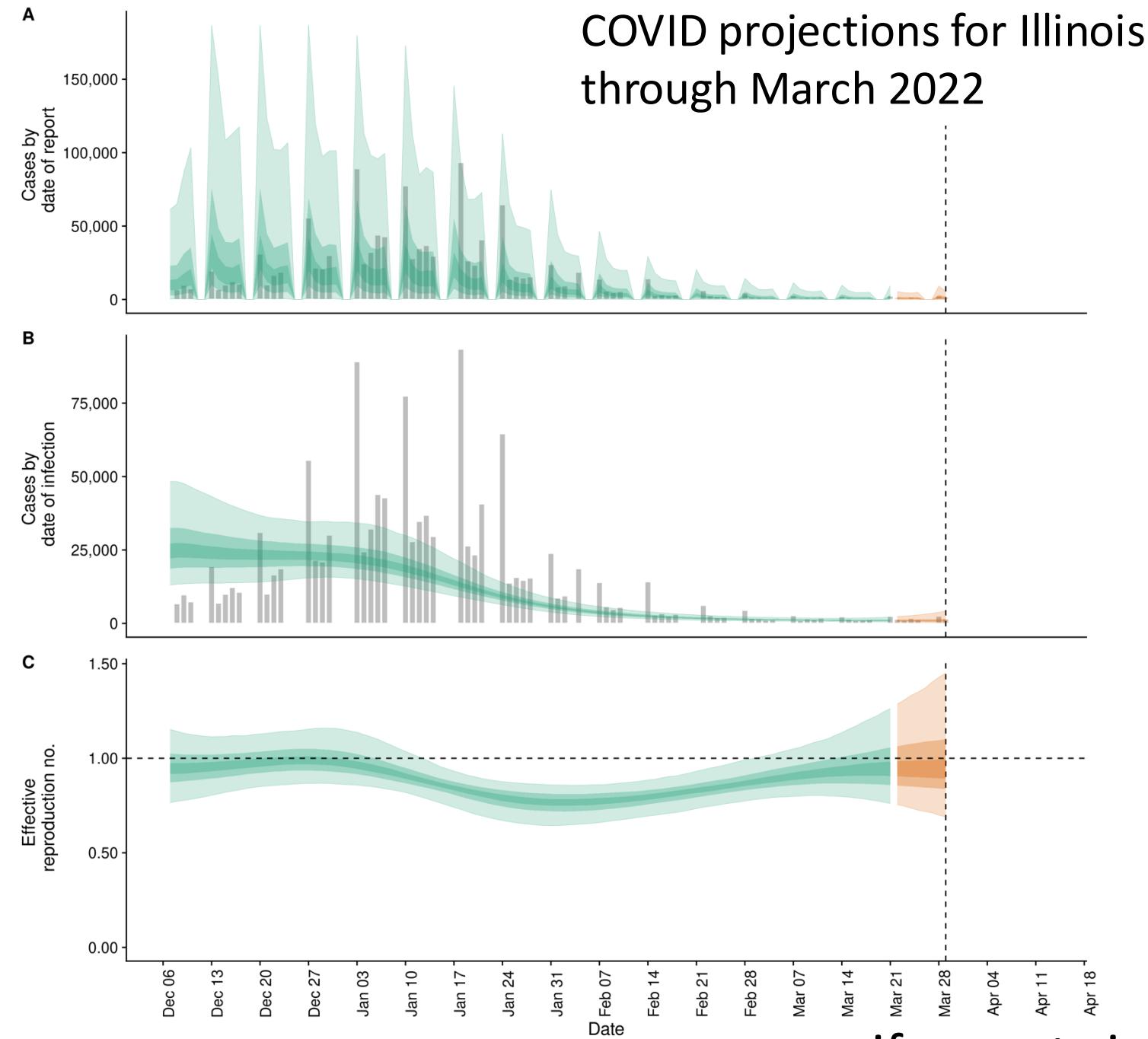
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# $R_E$ OR $R_t$

- The **effective reproduction number** for a pathogen
- Defined as: the number of new cases caused by one infectious case in a **partially susceptible** population
- Calculated as  $R_0 * \text{proportion susceptible}$

$$R_E = R_0 \frac{S}{N}$$

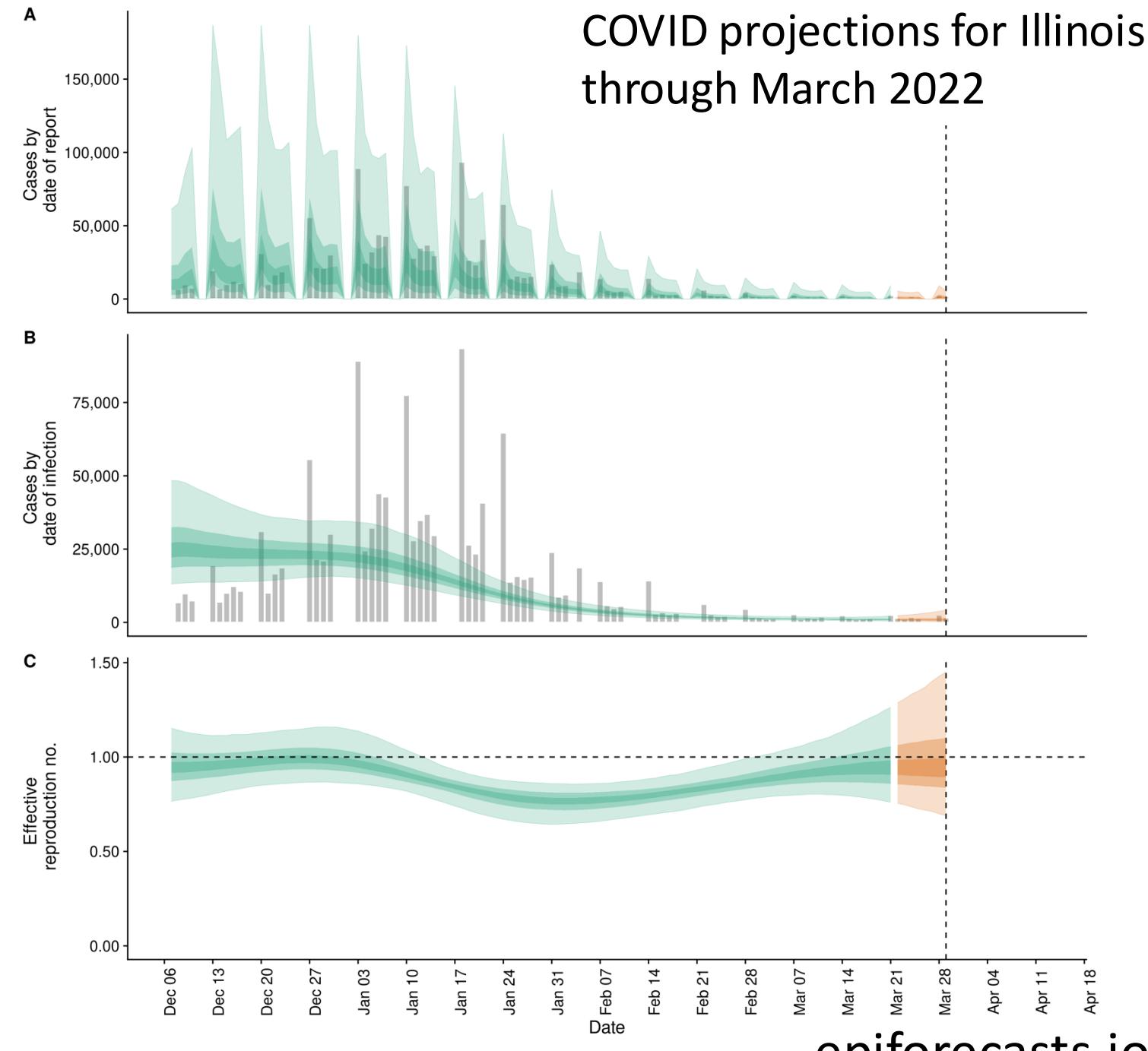


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- Gives a realistic pulse of the current pace of the epidemic!

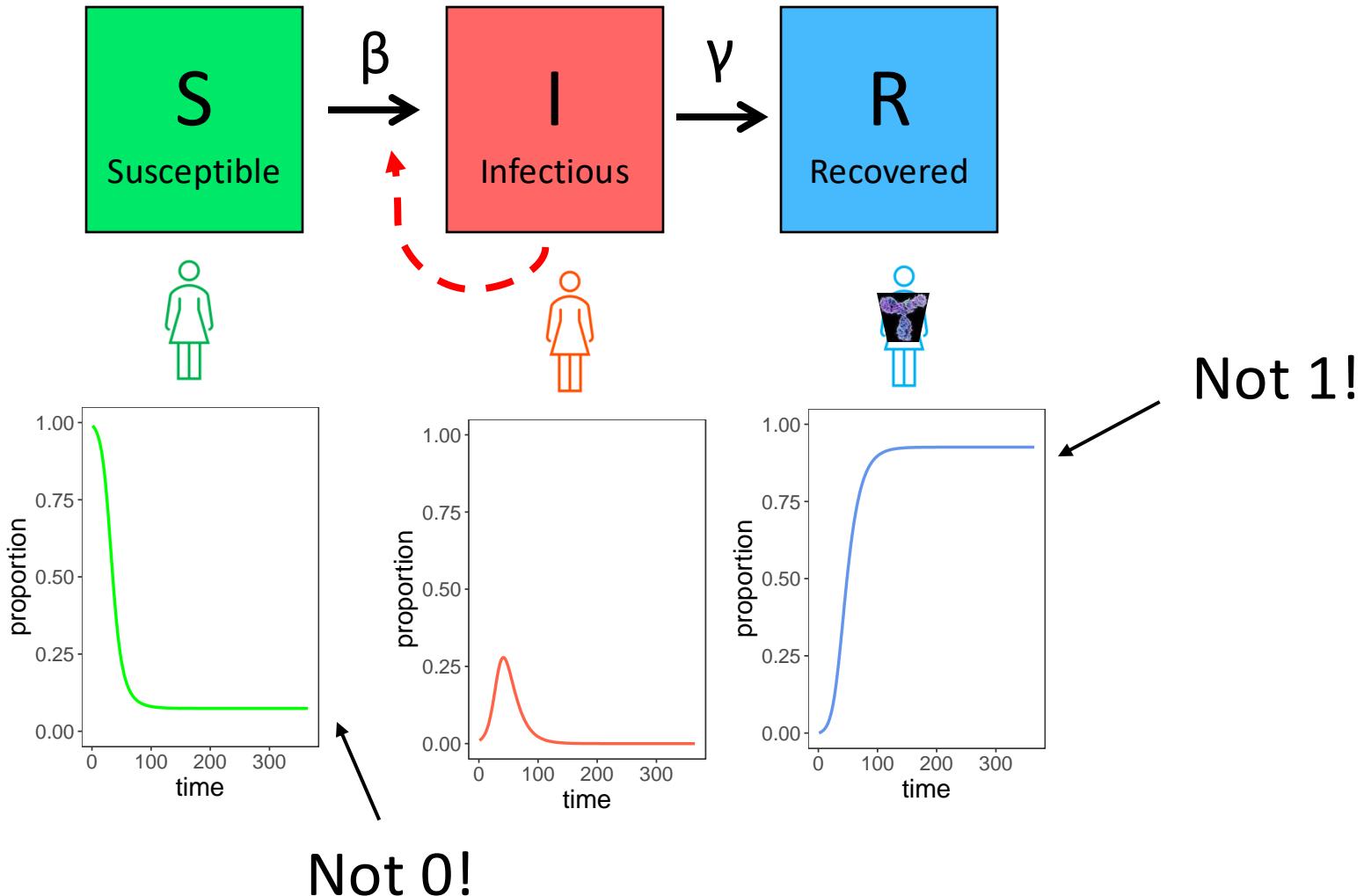


No matter the dynamics, not everyone gets infected before the epidemic ends!

$$\frac{dS}{dt} = -\beta SI$$

$$\frac{dI}{dt} = \beta SI - \gamma I$$

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$\beta$  = transmission rate

$\gamma$  = recovery rate

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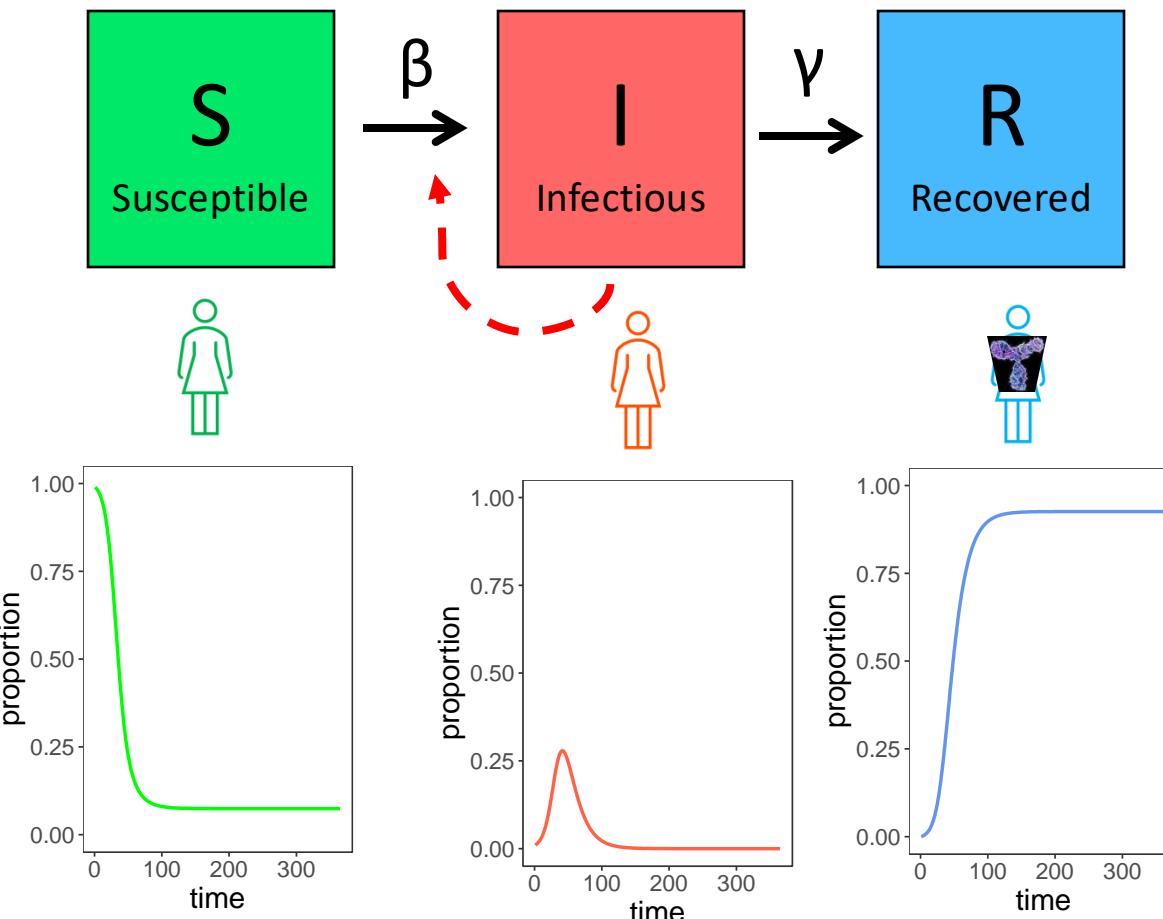
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- The epidemic does not end because all individuals have been infected and have either died or recovered.
- Rather, finding new susceptibles becomes more difficult and  $R_E < 1$

**Public health interventions** can be employed to reduce both  $R_0$  and  $R_E$

## **$R_0$** interventions

- Social distancing
- Masking
- Limits to gathering sizes
- Drugs that shorten the infectious period



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## **$R_E$** interventions

- Vaccination

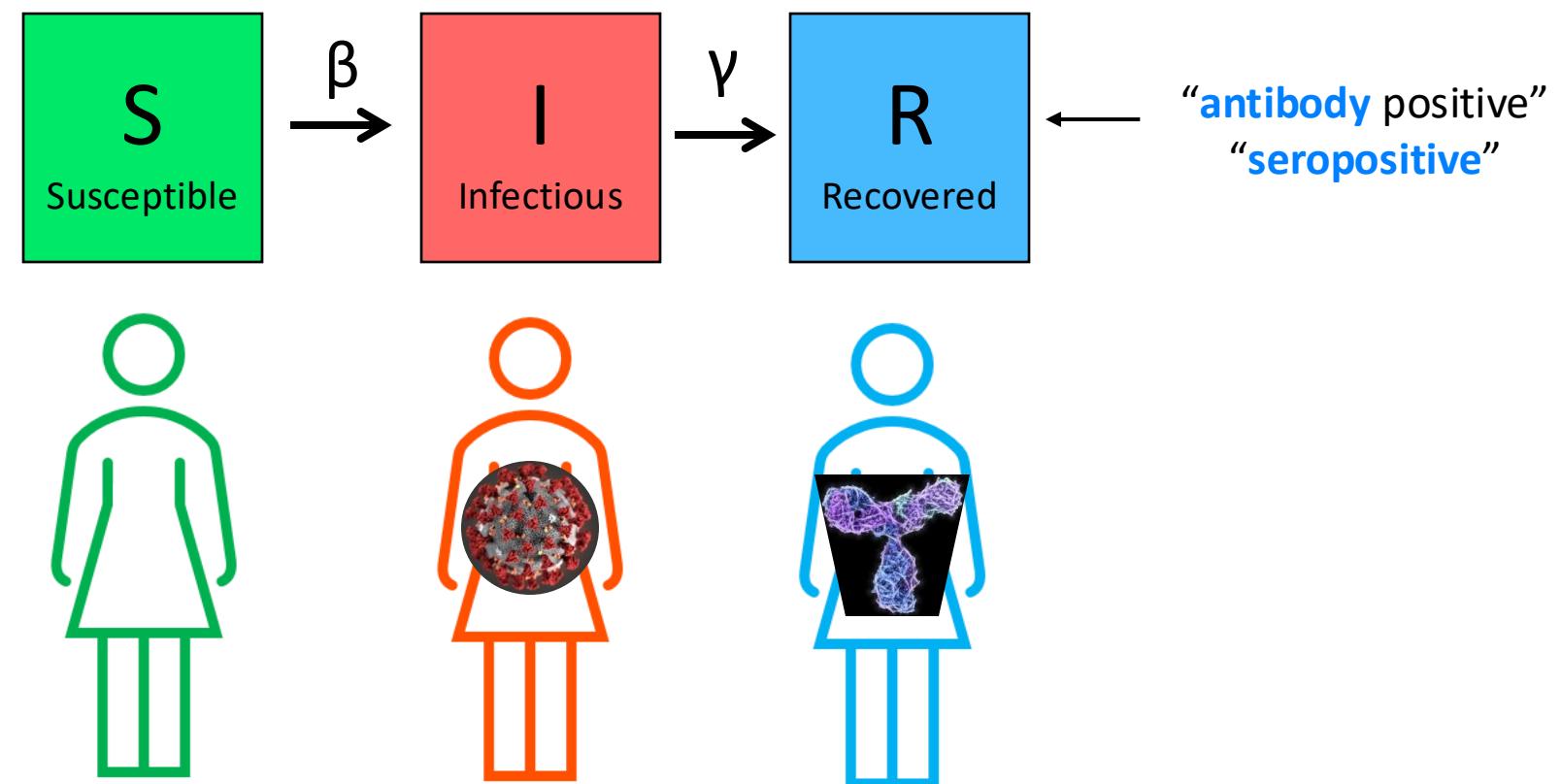


# Mathematics of Vaccination

- Goal: **Reduce  $R_E < 1$**  by removing individuals from the susceptible population.

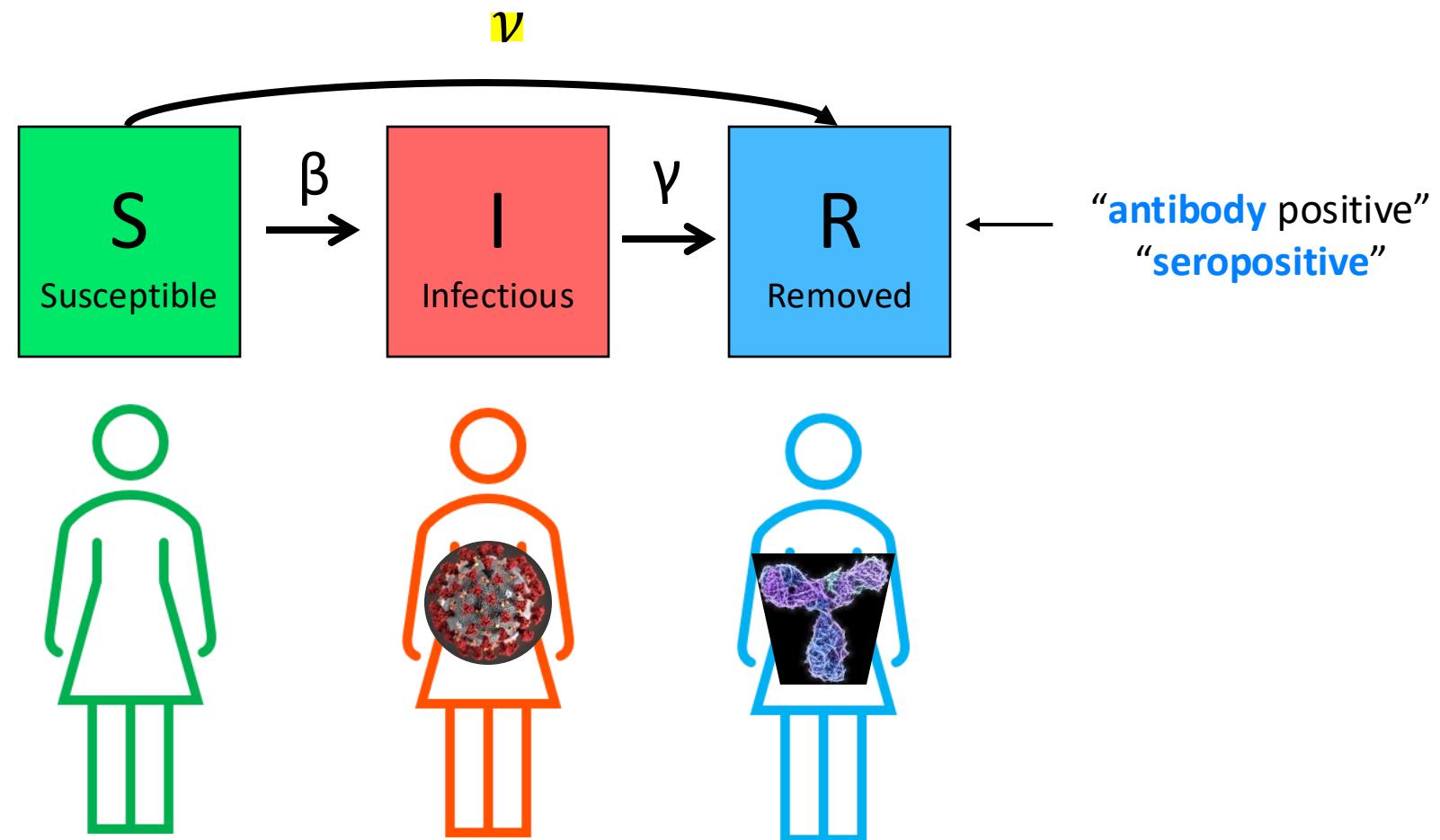
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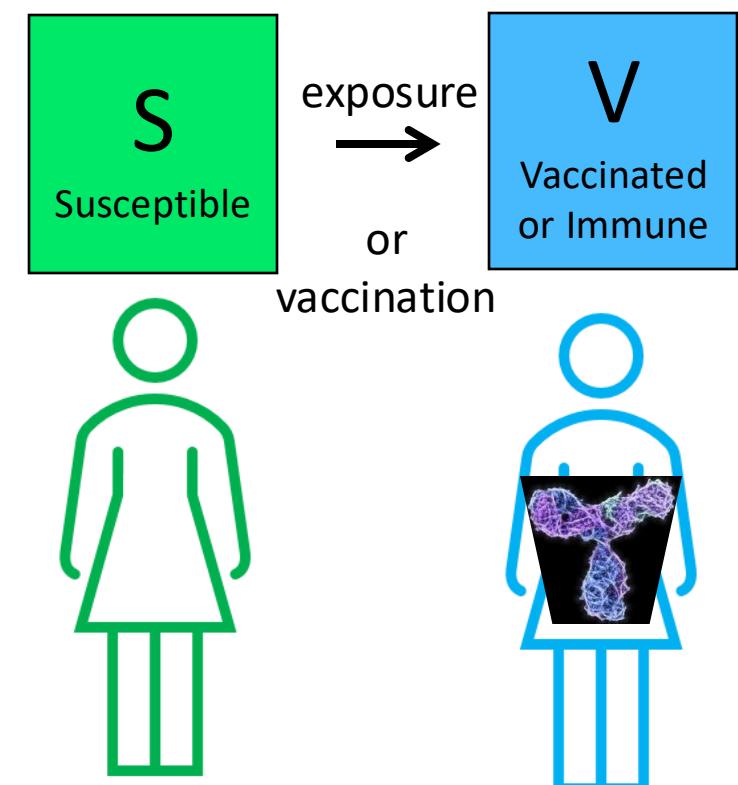
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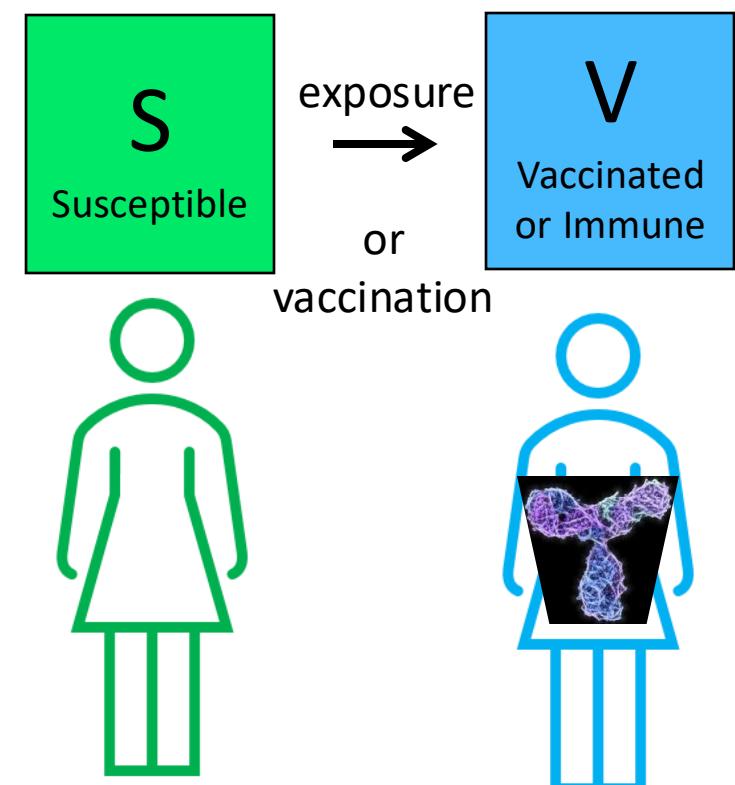
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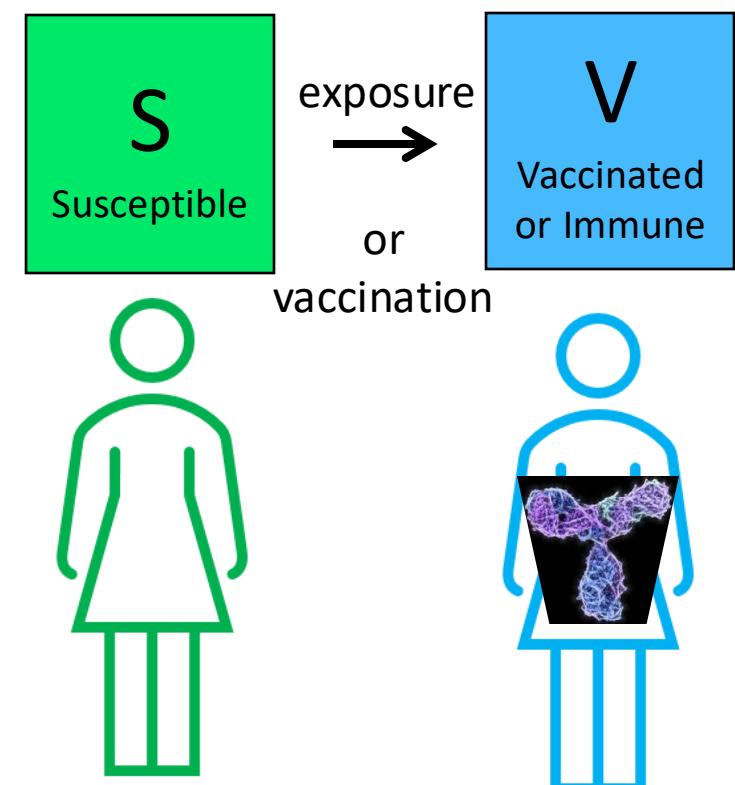
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Prop. Susceptible + Prop. Vaccinated = 1.



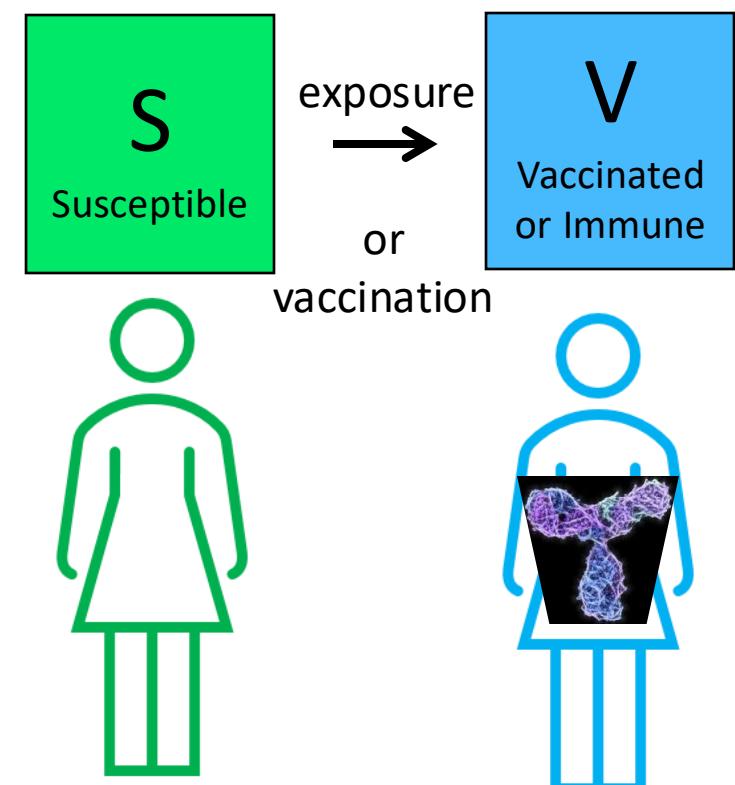
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- Remember,  $R_E = R_0 P_S$  or  $R_E = R_0(1 - P_V)$



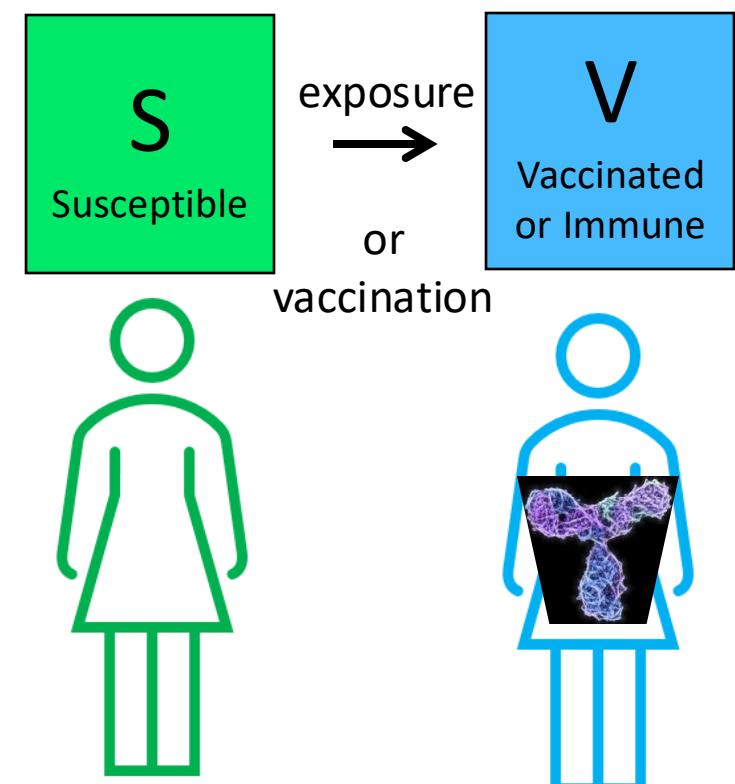
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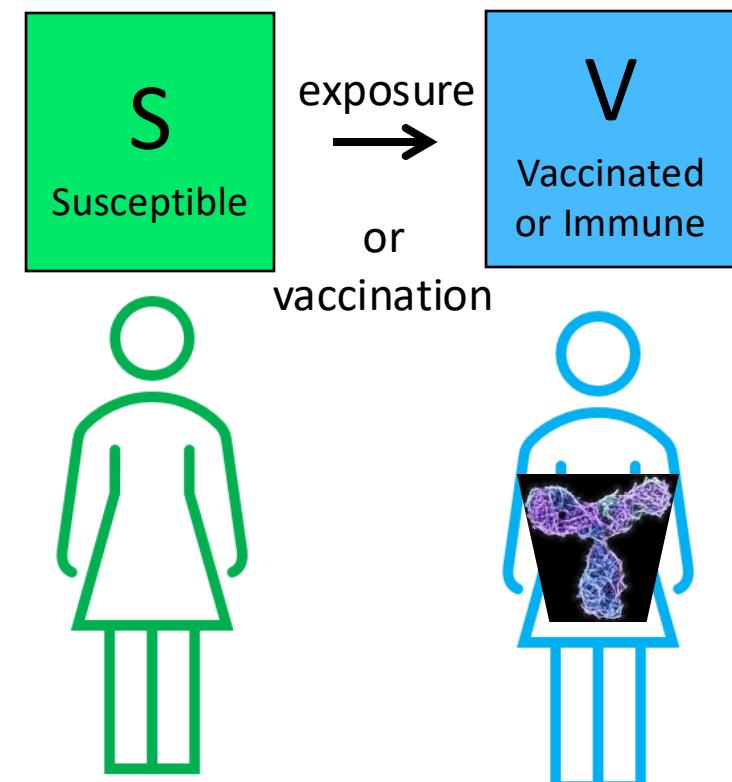
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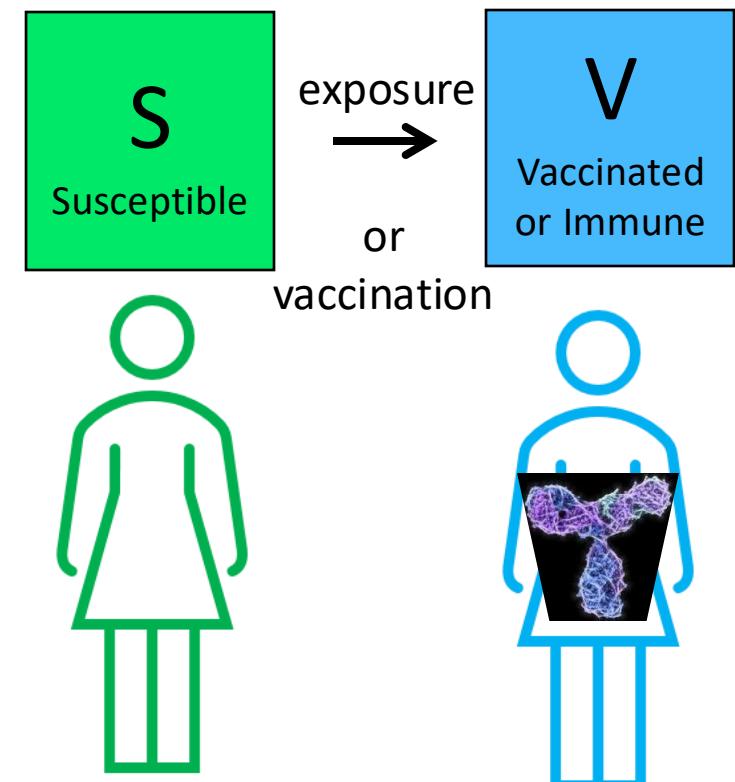
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- Rearranging,  $P_V > 1 - \frac{1}{R_0}$
- **This is the herd immunity threshold.**
- Even susceptibles will not become infected because the disease will not spread ( $R_E < 1$ ).



# Extra

# *Population Biology*

Conservation Biology

Disease Ecology



# *Population Biology*

Conservation Biology

- Goal:

- protect **populations** from extinction

Disease Ecology



# *Population Biology*

## Conservation Biology

- Goal:
  - protect **populations** from extinction
- Concept:
  - **Minimum Viable Population** size (MVP)

## Disease Ecology



# *Population Biology*

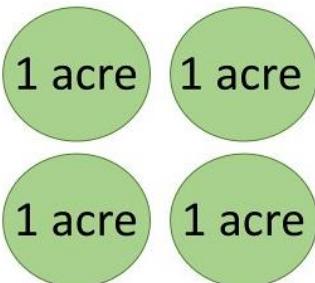
## Conservation Biology

- Goal:
  - protect **populations** from extinction
- Concept:
  - **Minimum Viable Population** size (MVP)
- Approach:
  - protected area **reserves**

Single Large



Several Small



## Disease Ecology

# *Population Biology*

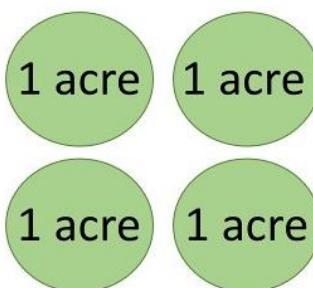
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- Goal:
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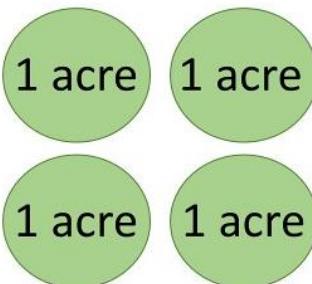
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- Concept:
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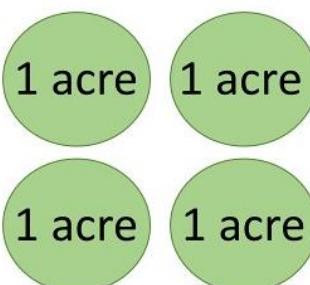
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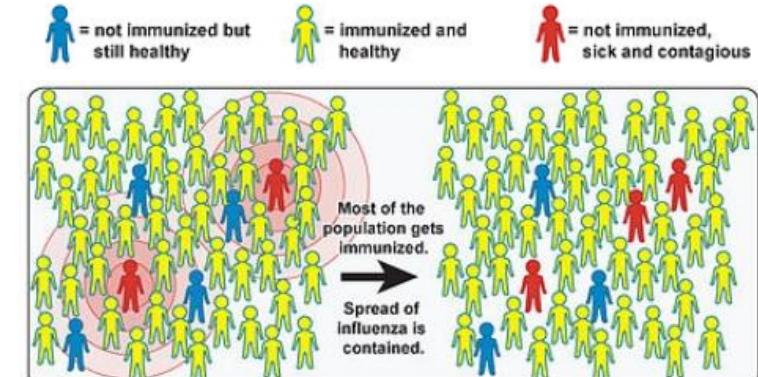


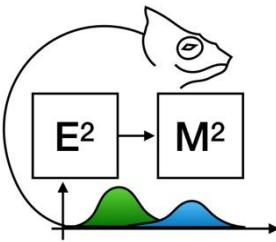
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## Disease Ecology

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- Concept:
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- Approach:
  - sanitation
  - **vaccination**





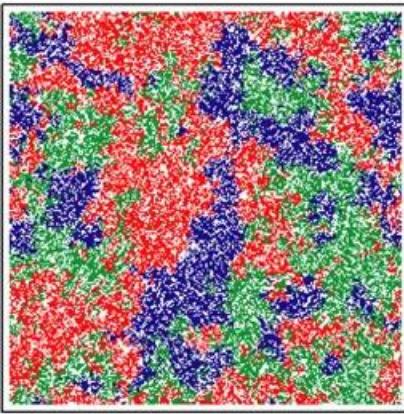
# E<sup>2</sup>M<sup>2</sup>: Ecological and Epidemiological Modeling in Madagascar



December 16, 2022  
**E2M2.org**

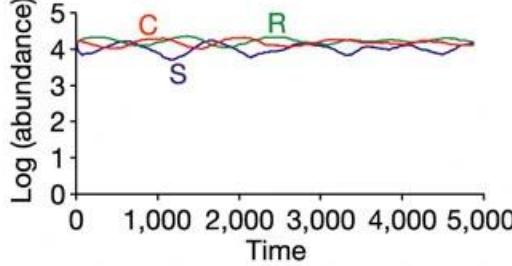
# Sometimes **stochasticity** and **space** are all you need to ensure **coexistence** in a competitive environment

a Time step 3,000

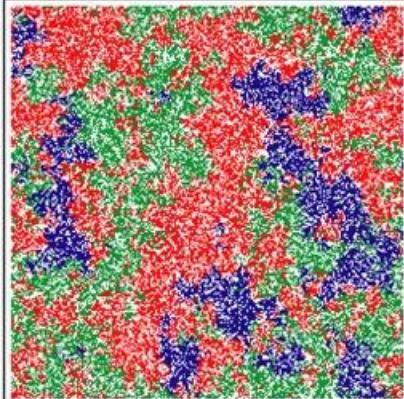


c

Local neighbourhood

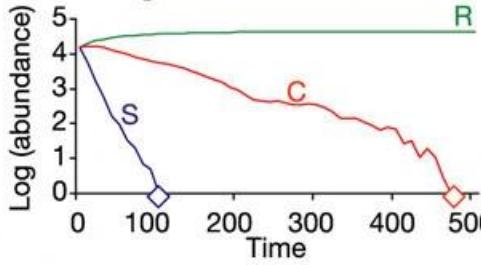


b Time step 3,200

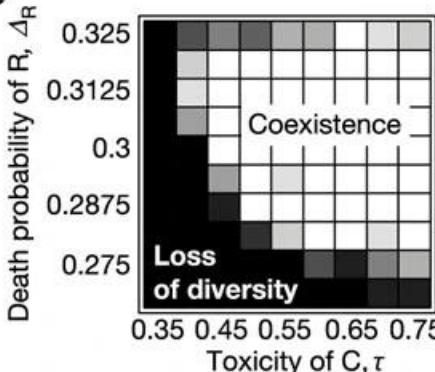


d

Global neighbourhood



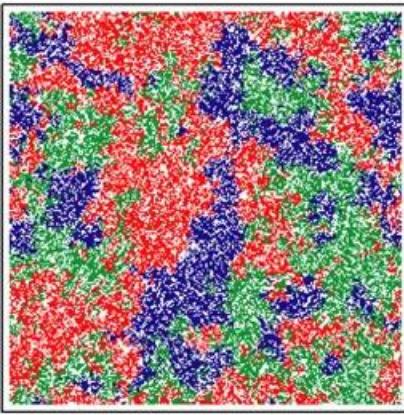
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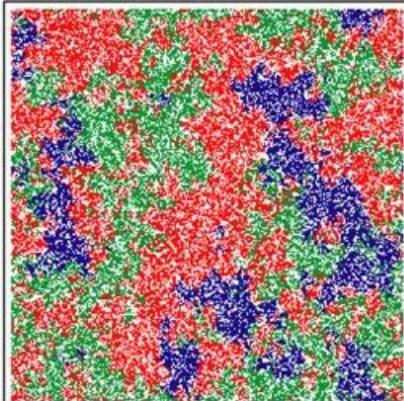
- Kerr et al. modeled a community of 3 strains of *E. coli* with **overlapping resource requirements** (C, R, and S), occupying distinct spatial patches in a metapopulation.

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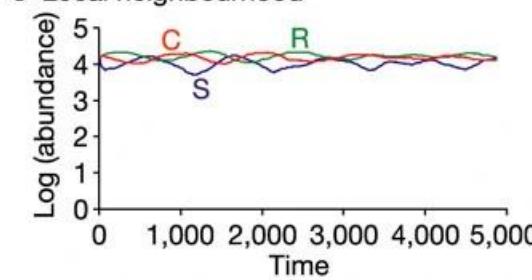


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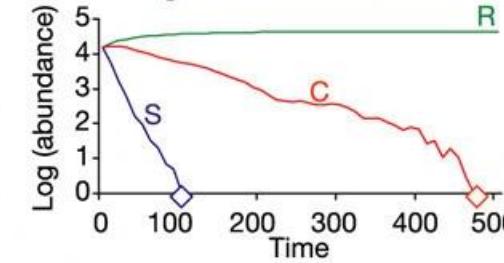
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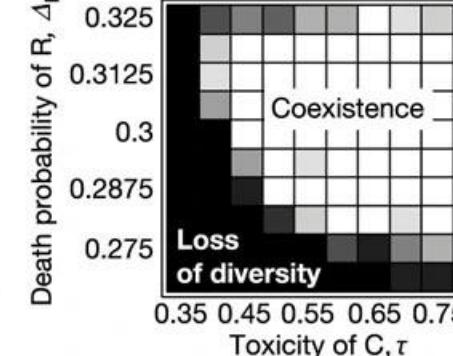


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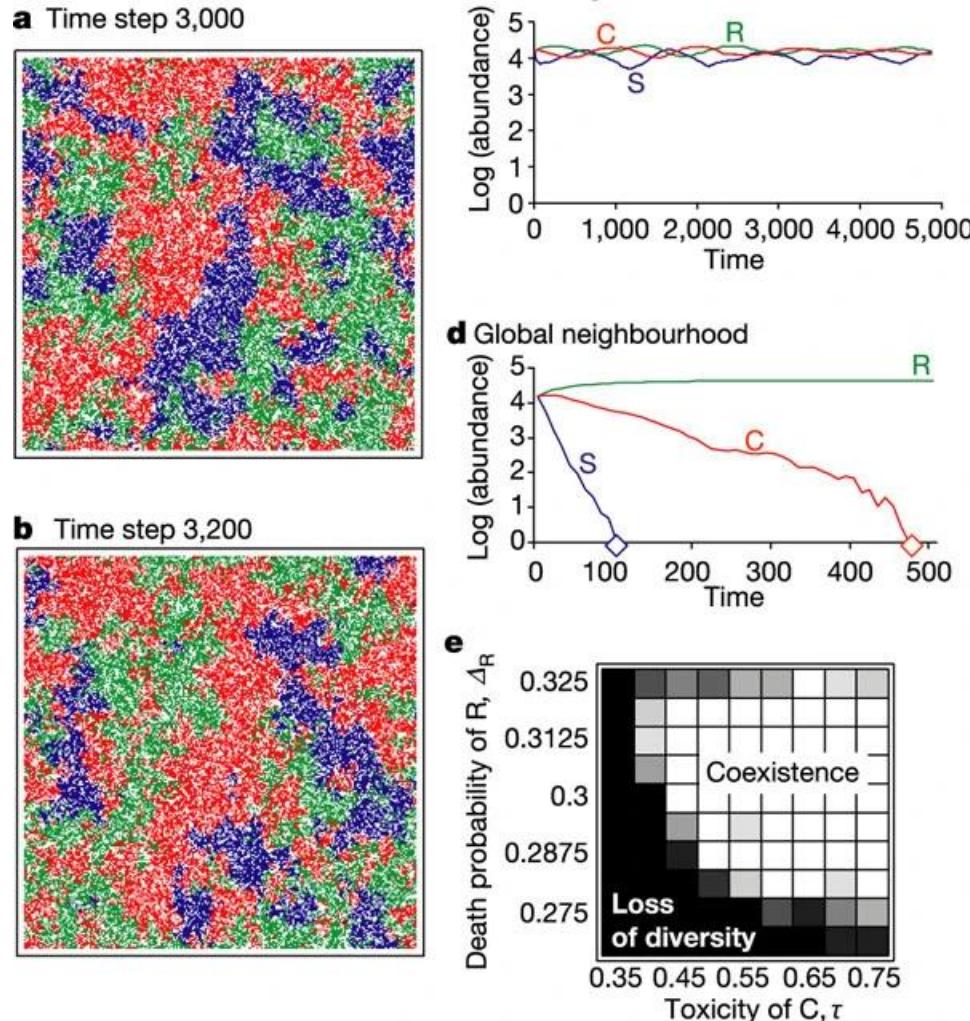


e



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

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- The authors modeled a community of 3 strains of *E. coli* with **overlapping resource requirements** (C,R, and S), occupying distinct spatial patches in a metapopulation.
- They produced simulations allowing for a perfectly mixed population (global neighborhood), or a population in which dispersal (mixing) happened only locally.
- **Local interactions allowed for the coexistence of all three strains** (in theory). What about experimentally?

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

