Competiton and coexistence

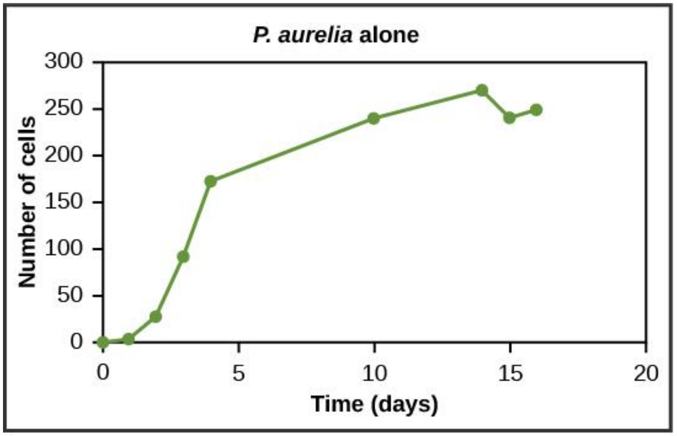
Irena Šímová

Competitive exclusion principle

Two species competing for the same (limited) resource cannot coexist. The species with a slight advantage over another will dominate. This results either in the extinction of the weaker competitor or to a shift towards a different ecological niche.

Georgy F. Gause

The Struggle for Existence (1934)



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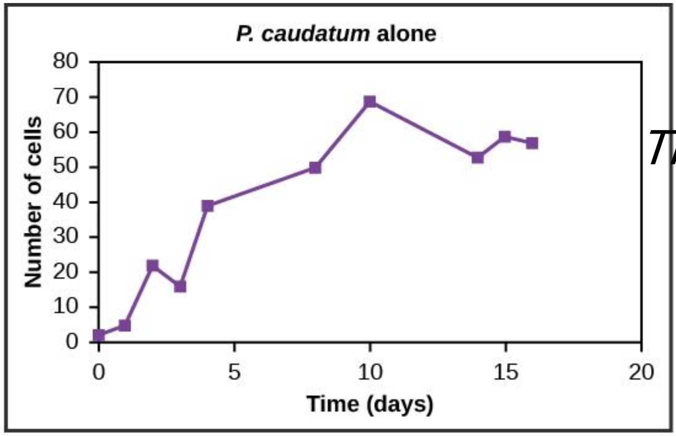

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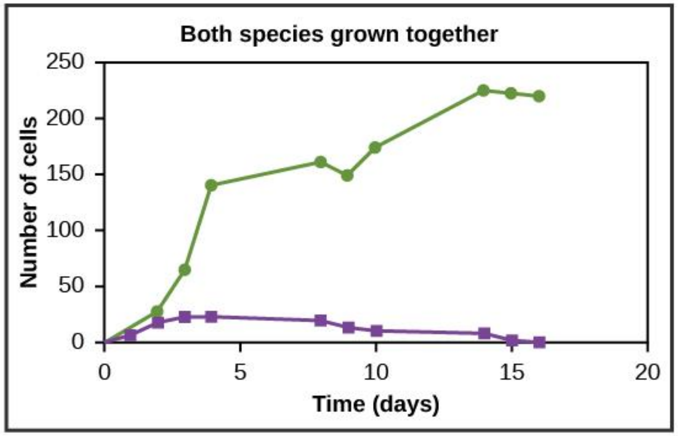
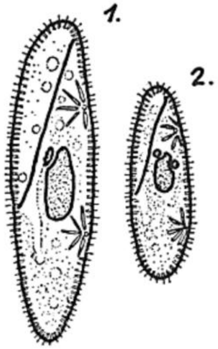


(c)



Paramecium aurelia, P. caudatum

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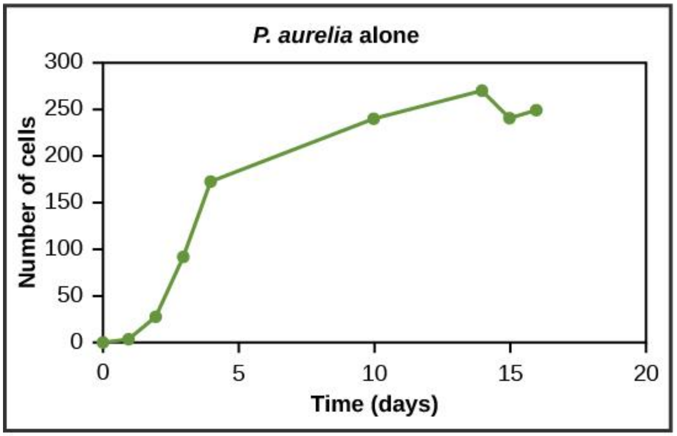

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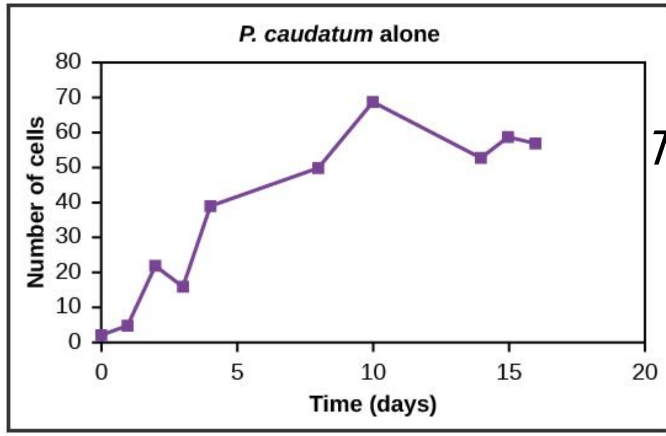

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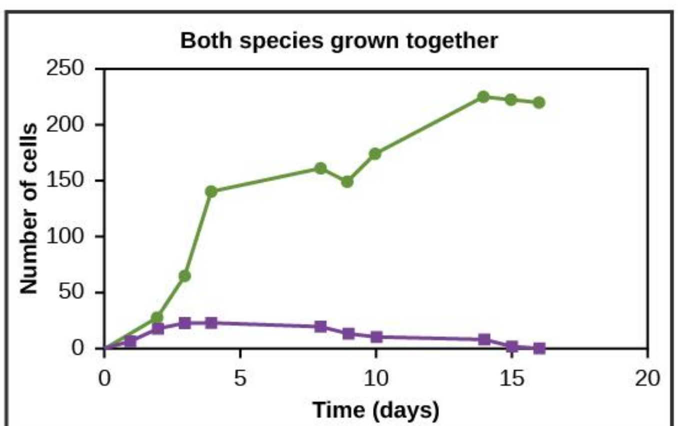

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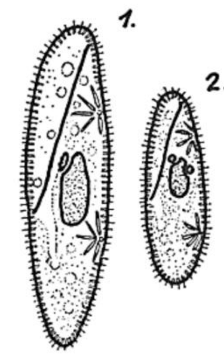


Paramecium aurelia, P. caudatum

only if the ecological factors are constant

Diverse meadow in Krkonoše

Species coexistence and competition

Diverse meadow in Krkonoše

Lupinus invasion

Species coexistence and competition

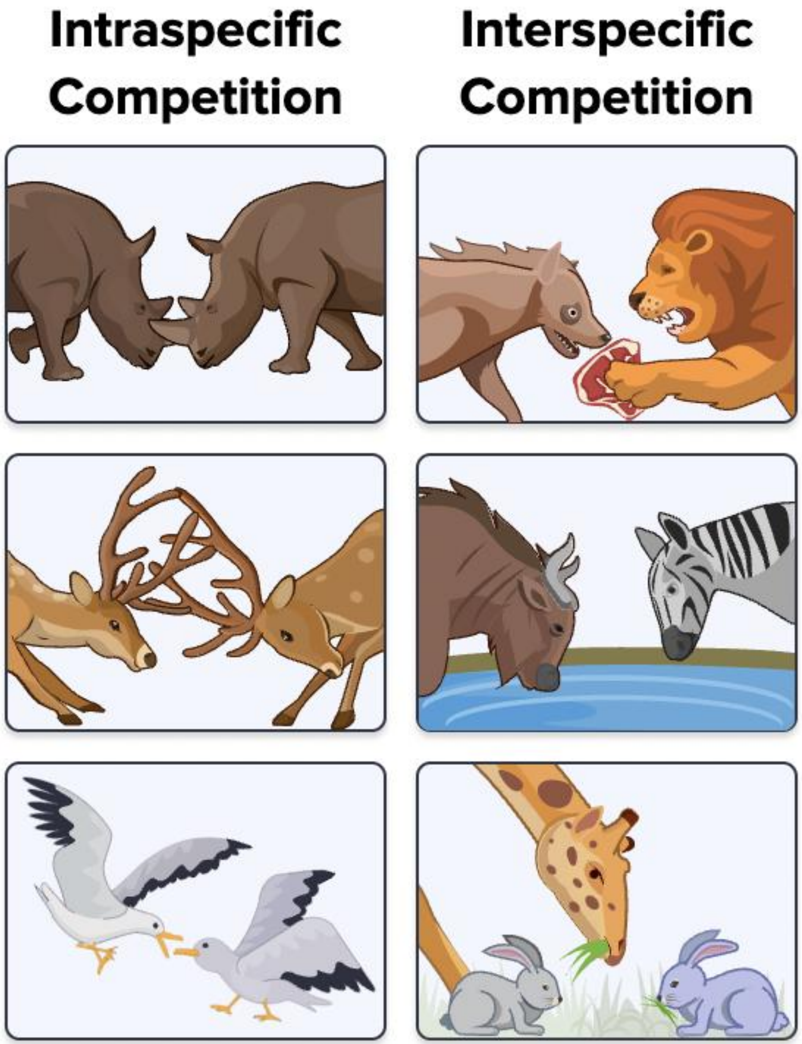
Diverse meadow in Krkonoše

Lupinus invasion

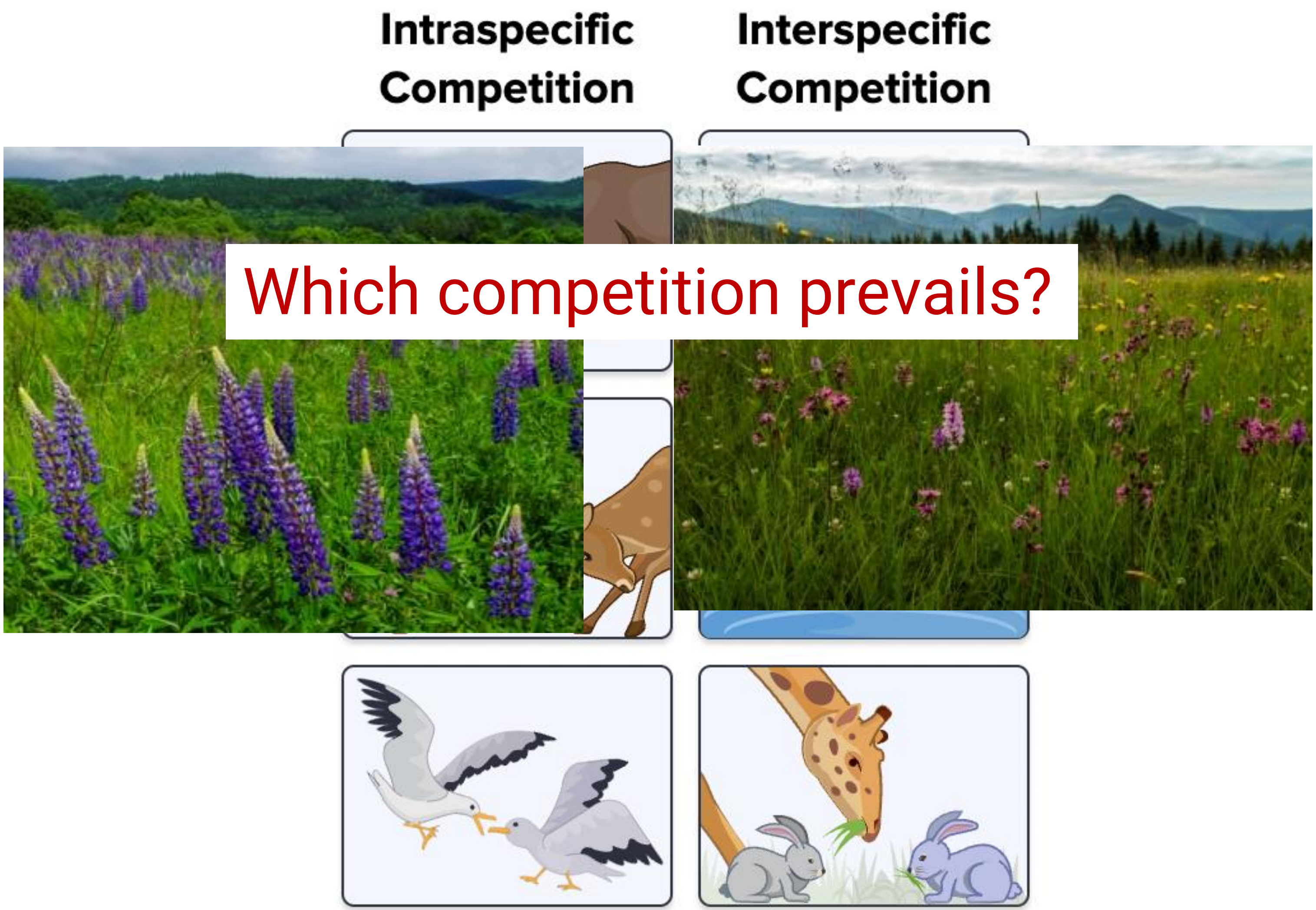
Why can multiple species coexist?

What happens after introducing of non-native species?

The effect of an introduced species depends on two factors: interspecific and intraspecific competition



The effect of an introduced species depends on two factors: interspecific and intraspecific competition



Interspecific vs. Intraspecific competition

Interspecific > Intraspecific

Competitive Exclusion Principle
Greater competition between the two species than within the species

One of the species is completely removed and the other survives

Interspecific vs. Intraspecific competition

Interspecific > Intraspecific

Competitive Exclusion Principle
Greater competition between the two species than within the species

One of the species is completely removed and the other survives

Interspecific < Intraspecific

Stable coexistence
Each species limits its own population growth more than it limits the population growth of its competitors

Negative frequency dependence: the rarer a species becomes in a community, the more its population growth rate increases, buffering it against competitive exclusion.

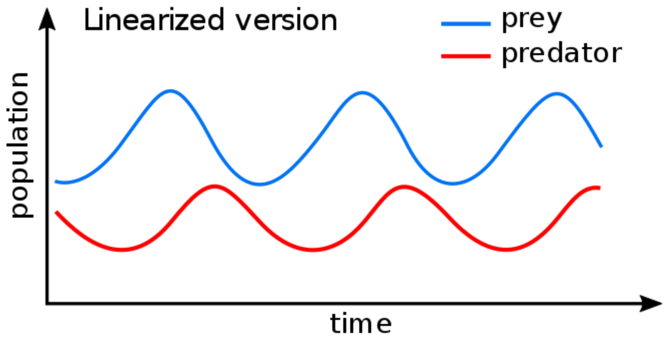
Let's formalize it

LOTKA-VOLTERRA MODEL OF COMPETITION

Alfred Lotka

Vito Volterra

Predator-prey dynamics

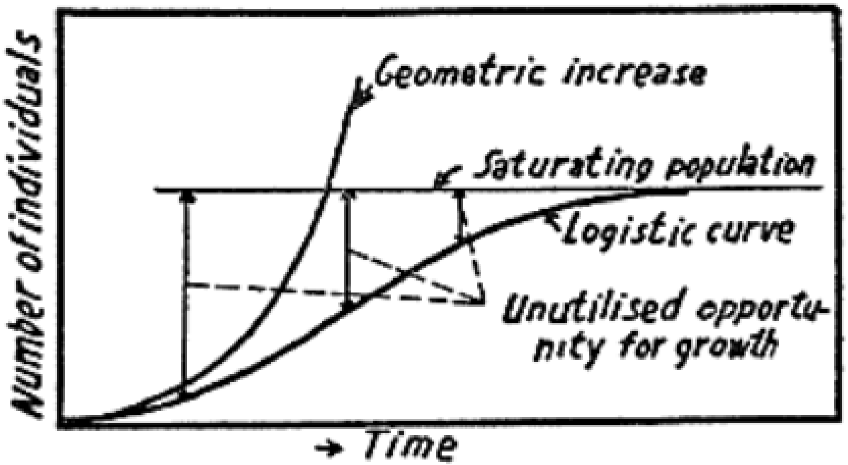


Extended to The competitive Lotka-Volterra equations model

interspecific competition between two species

How the population growth of each species is affected by the presence of the other species

LOTKA-VOLTERRA MODEL OF COMPETITION 1 SPECIES



The total potential number of offspring of all individuals per time

$$\frac{dN}{dt} = bN$$

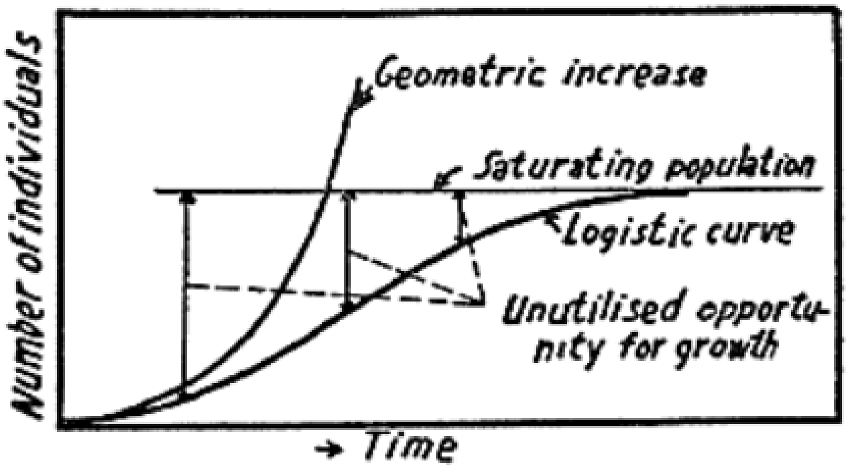
number of organisms (N)

the potential increase from each one of them (b)

Gause 1934

LOTKA-VOLTERRA MODEL OF COMPETITION

1 SPECIES



The total potential number of offspring of all individuals per time

$$\frac{dN}{dt} = bN$$

number of organisms (N)

the potential increase from each one of them (b)

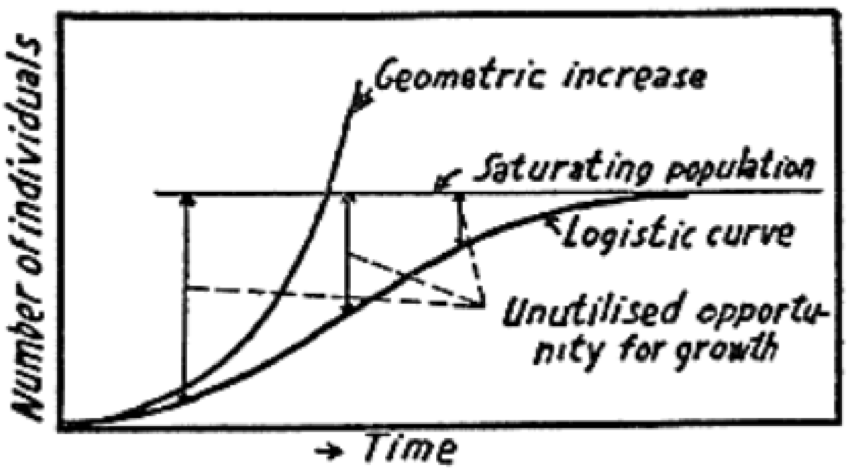
Saturating population (logistic curve)

{Rate of growth or increase per unit of time} = {Potential increase of population per unit of time} * {Degree of realization of the potential increase. Depends on the number of still vacant places.}

Gause 1934

LOTKA-VOLTERRA MODEL OF COMPETITION

1 SPECIES



The total potential number of offspring of all individuals per time

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Saturating population (logistic curve)

{Rate of growth or increase per unit of time} = {Potential increase of population per unit of time} * {Degree of realization of the potential increase. Depends on the number of still vacant places.}

$$\frac{dN}{dt} = bn\frac{K-N}{K}$$

how near the already accumulated size of the population (N) approaches the maximal population (K) that can exist in the given environment

Gause 1934

Lotka-Volterra model of competition

2 species

LOTKA-VOLTERRA MODEL OF COMPETITION

2 SPECIES

{ Rate of growth of the first species in a mixed population } = { Potential increase of the populaton of the first species } * { Degree of realization of the potential increase. Depends on the number of still vacant places. }

{ Rate of growth of the second species in a mixed population } = { Potential increase of the populaton of the second species } * { Degree of realization of the potential increase. Depends on the number of still vacant places. }

Gause 1934

$$\frac{d\mathrm{N}_1}{dt} = b_1 N_1 \frac{K_1 - (N_1 + \alpha_{12} N_2)}{K_1}$$

$$\frac{d\mathrm{N}_2}{dt} = b_2 N_2 \frac{K_2 - (N_2 + \alpha_{21} N_1)}{K_2}$$

α_{12} : the effect of species2 on species1 (how many places suitable for species1 are occupied by species2)

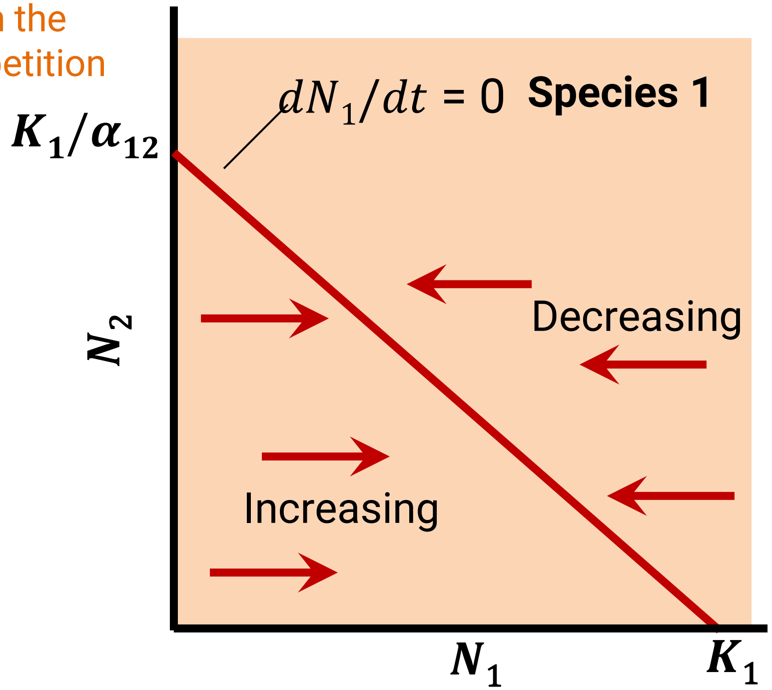
α_{21} : the effect of the species1 on species2

Gause 1934

LOTKA-VOLTERRA MODEL OF COMPETITION

2 SPECIES

maximum possible number of species2 given the competition



maximum number of species1 possible in the absence of species2

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - a_{12} N_2}{K_1} \right)$$

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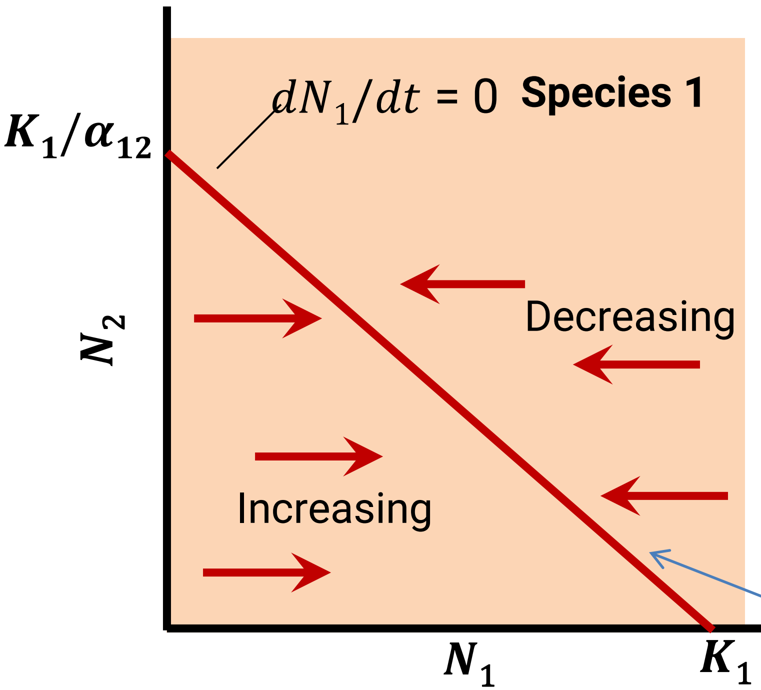
LOTKA-VOLTERRA MODEL OF COMPETITION

2 SPECIES



zero net growth isocline (ZNGI)

Equilibrium when dN/dt = 0

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - a_{12} N_2}{K_1} \right)$$

$$\mathrm{N}_1 = K_1 - a_{12} N_2$$

Solutions when N_2=0 (K1) and N_1=0 ($K1/\alpha_{12}$)

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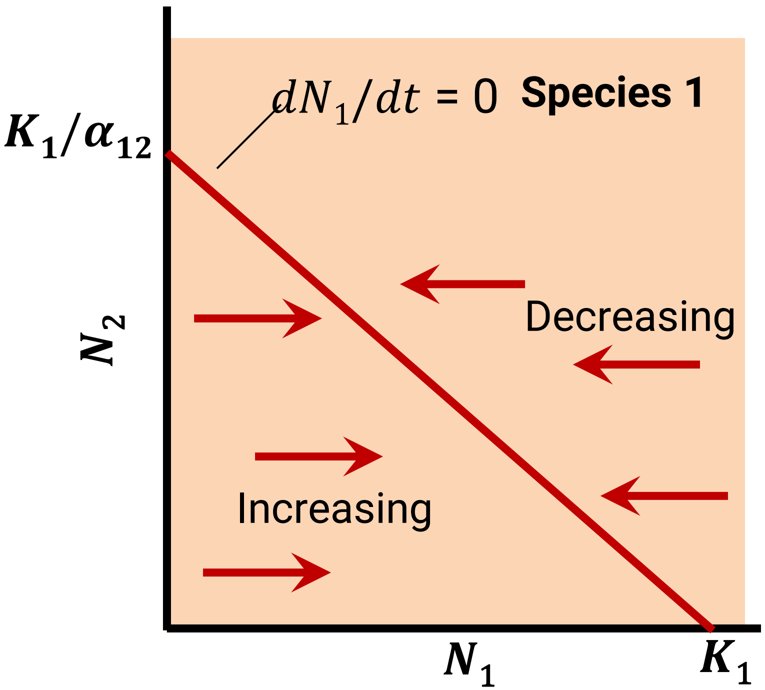
LOTKA-VOLTERRA MODEL OF COMPETITION

2 SPECIES



$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - a_{12} N_2}{K_1} \right)$$

α_{12}: the effect of species2 on species1 (competition coefficient),

$\boldsymbol{\alpha_{12}} = 0$ … one individual of species2 has the same competitive effect of one ind. species1 $(K_1/\alpha_{12} = K_1)$

$\boldsymbol{\alpha_{12}} > 1$ … one individual of species2 is more competitive than one of species1 $(K_1/\alpha_{12} < K_1)$

$\boldsymbol{\alpha_{12}} < 1$ … one individual of species2 is less competitive than one of species1 $(K_1/\alpha_{12} > K_1)$

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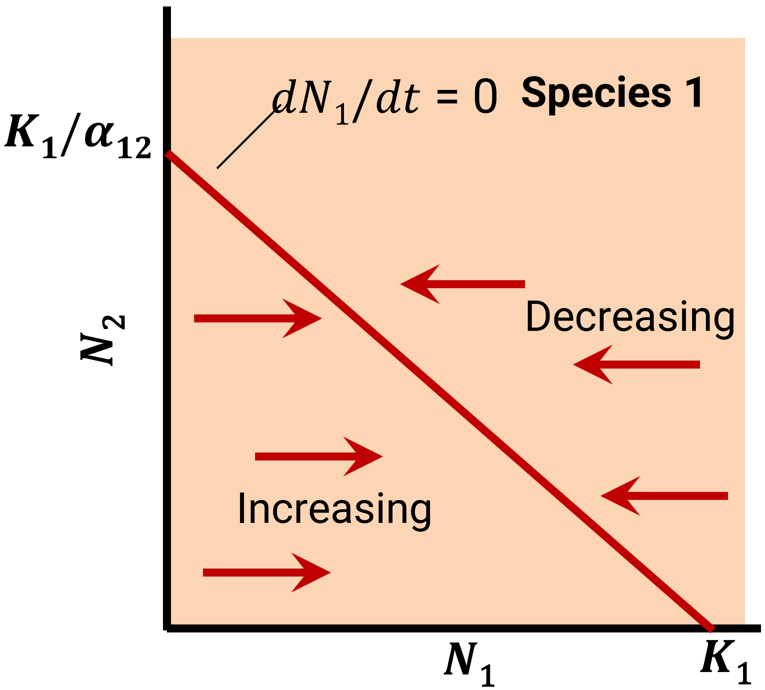
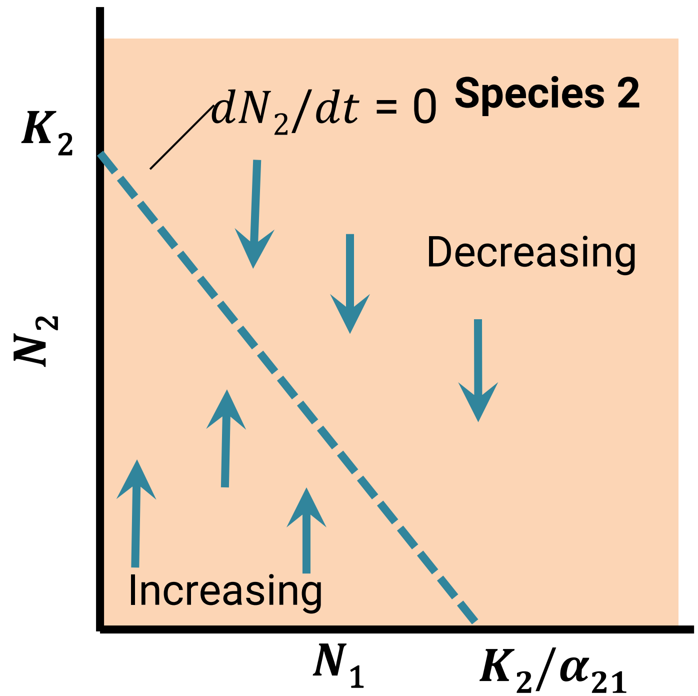
LOTKA-VOLTERRA MODEL OF COMPETITION 2 SPECIES





$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - a_{12} N_2}{K_1} \right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - a_{21} N_1}{K_2} \right)$$

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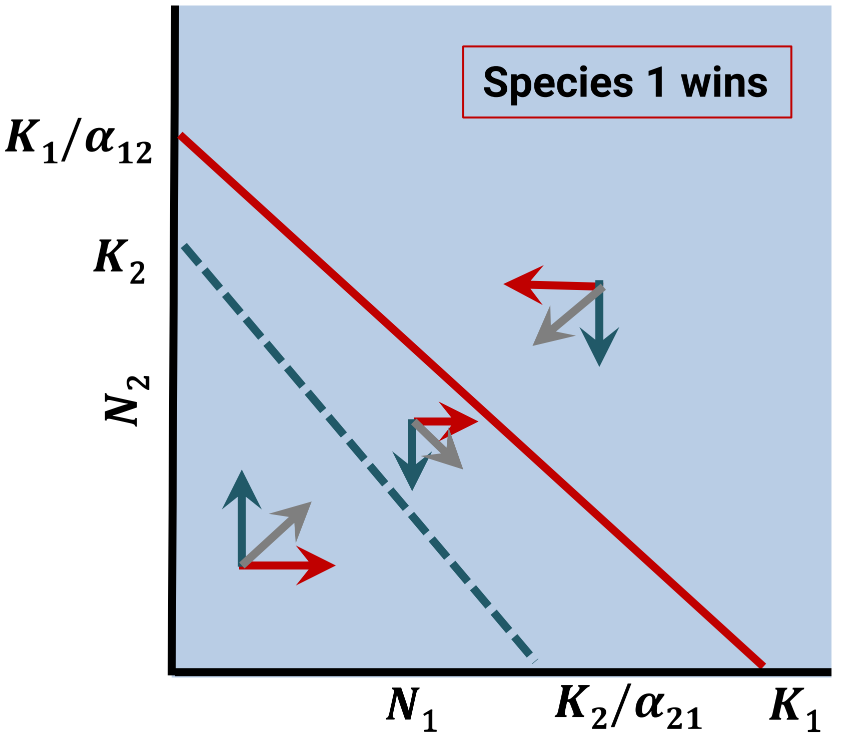
LOTKA-VOLTERRA MODEL OF COMPETITION

2 SPECIES

4 SCENARIOS

$K_1/\alpha_{12} > K_2$ and $K_2/\alpha_{21} < K_2$



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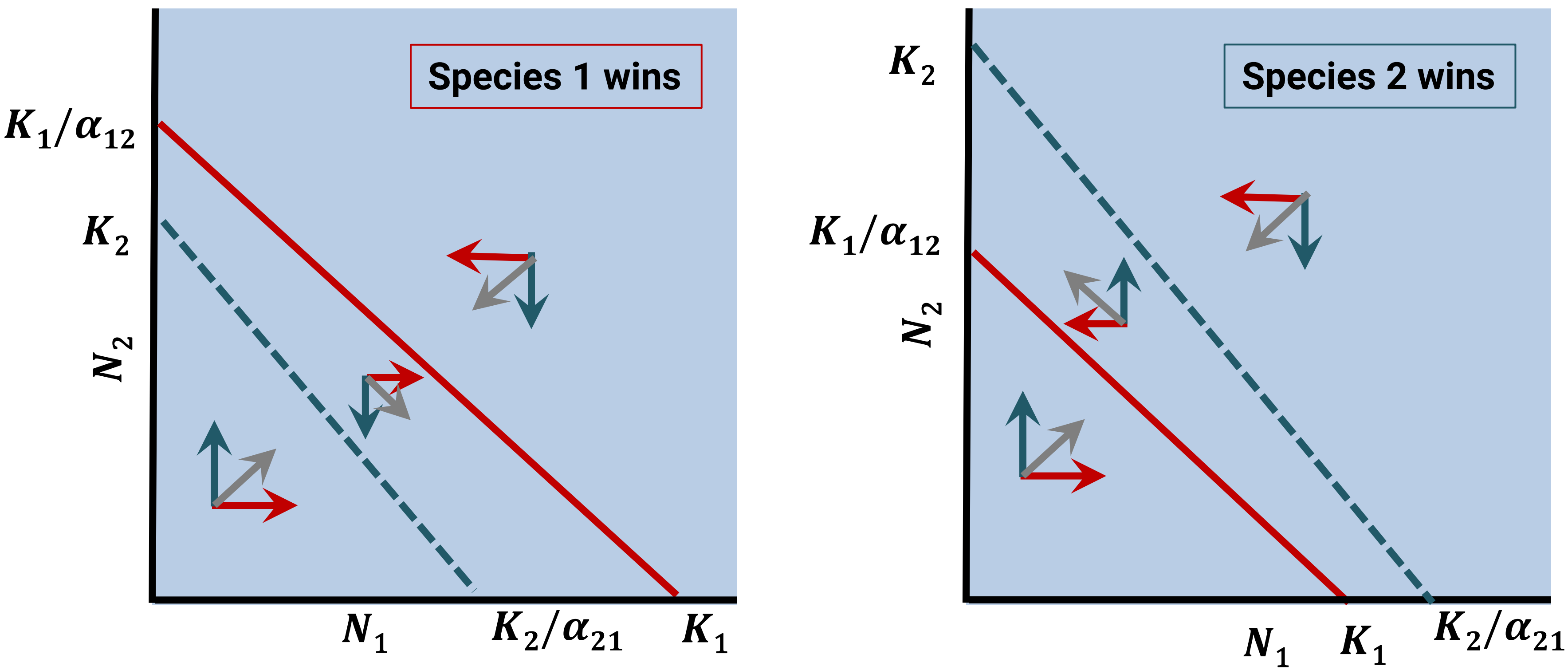
Lotka-Volterra model of competition

2 species

4 scenarios

$K_1/\alpha_{12} > K_2$ and $K_2/\alpha_{21} < K_2$

$K_1/\alpha_{12} < K_2$ and $K_2/\alpha_{21} > K_2$



Dominance control

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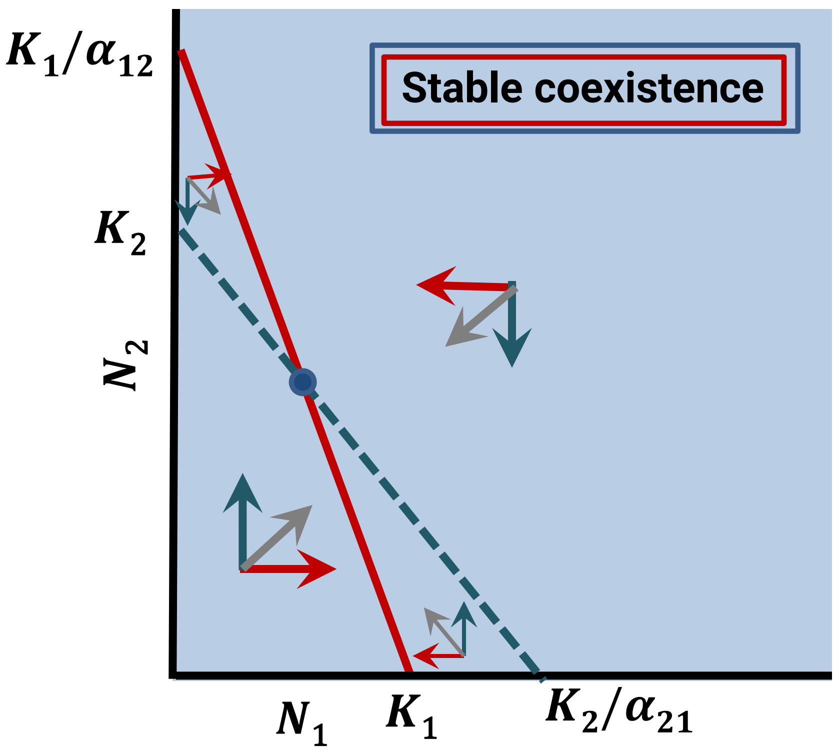
Lotka-Volterra model of competition

2 SPECIES

4 SCENARIOS

$K_1/\alpha_{12} > K_2$ and $K_2/\alpha_{21} > K_2$



α < 1 (high K/α) higher intraspecific competition
α > 1 (low K/α) higher interspecific competition

K1 < K2/(effect on species2)
lower K1 … higher intraspecific competition
higher K2/(effect on species2) … lower interspecific competition
intraspecific competition > interspecific competition

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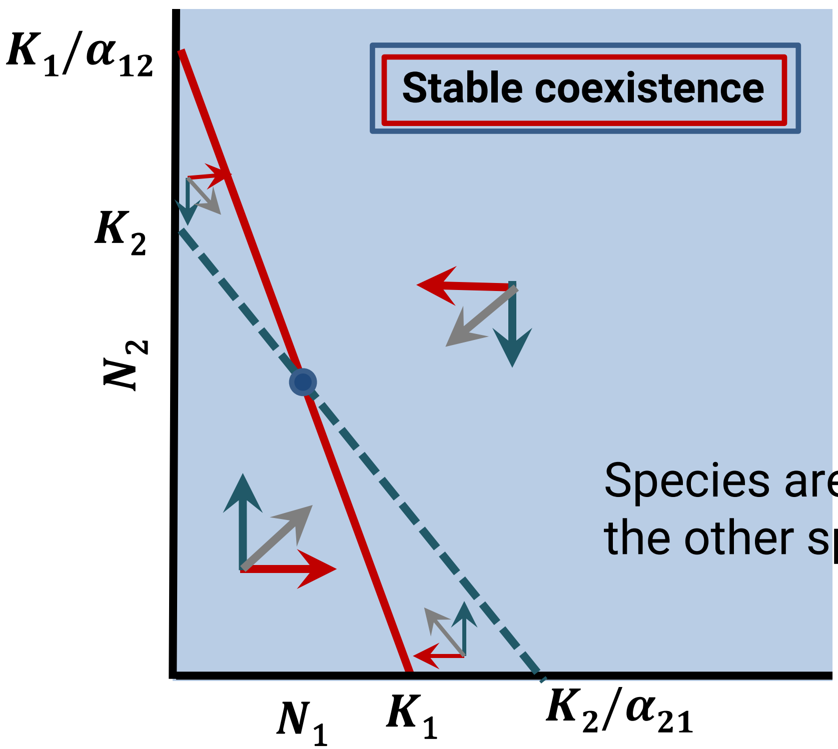
LOTKA-VOLTERRA MODEL OF COMPETITION

2 SPECIES

4 SCENARIOS

$K_1/\alpha_{12} > K_2$ and $K_2/\alpha_{21} > K_2$



Species are limiting themselves more than they limit the other species

K1 < K2/(effect on species2)
lower K1 … higher intraspecific competition
higher K2/(effect on species2) … lower interspecific competition
intraspecific competition > interspecific competition

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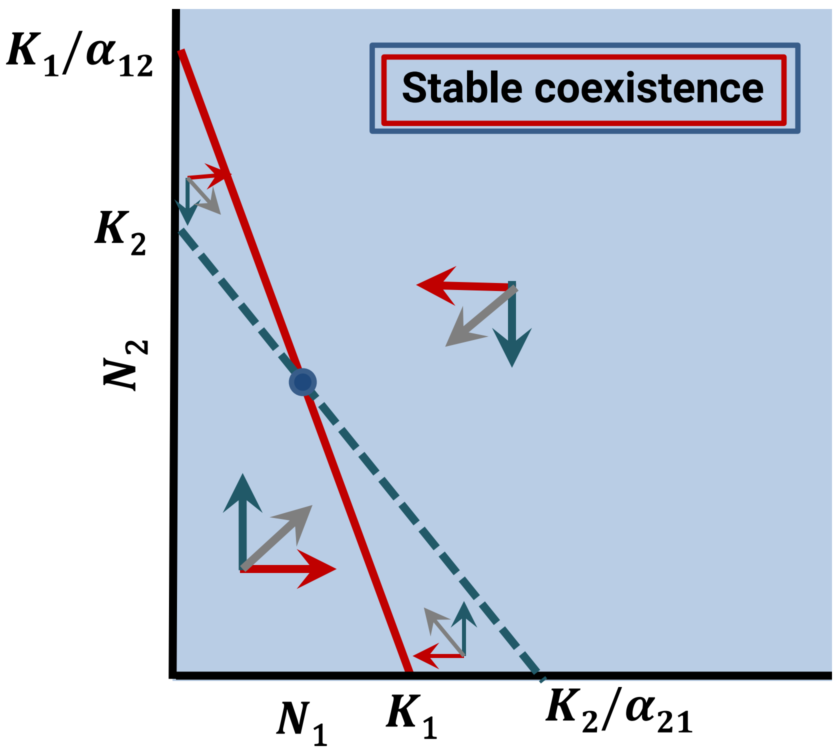
Lotka-Volterra model of competition

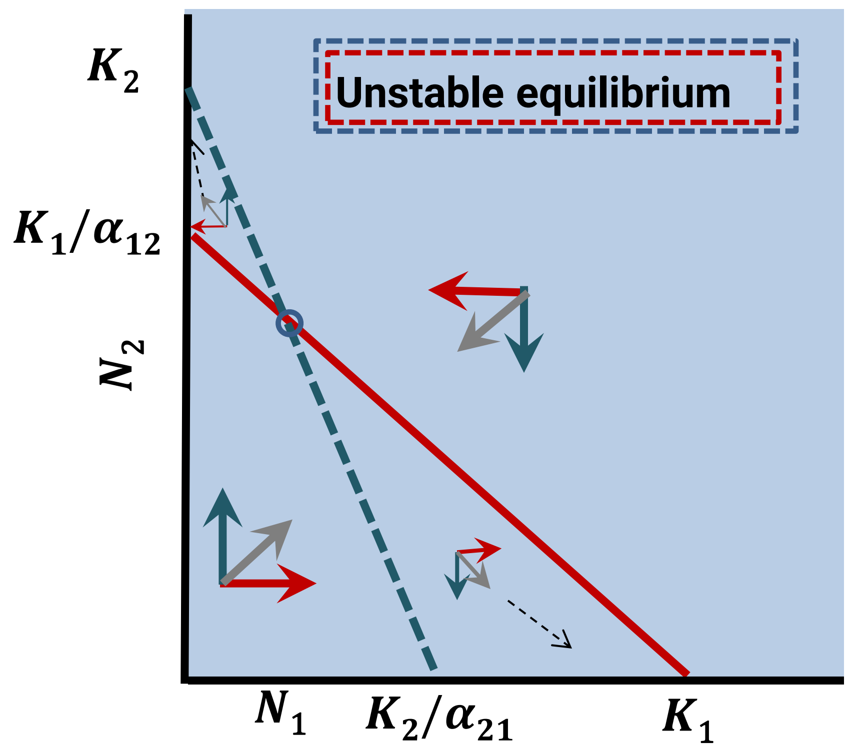
2 SPECIES

4 SCENARIOS

$K_1/\alpha_{12} > K_2$ and $K_2/\alpha_{21} > K_2$



$K_1/\alpha_{12} < K_2$ and $K_2/\alpha_{21} < K_2$



Interspecfic competition > Intraspecific

Founder control

K1 < K2/(effect on species2)
lower K1 … higher intraspecific competition
higher K2/(effect on species2) … lower interspecific competition
intraspecific competition > interspecific competition

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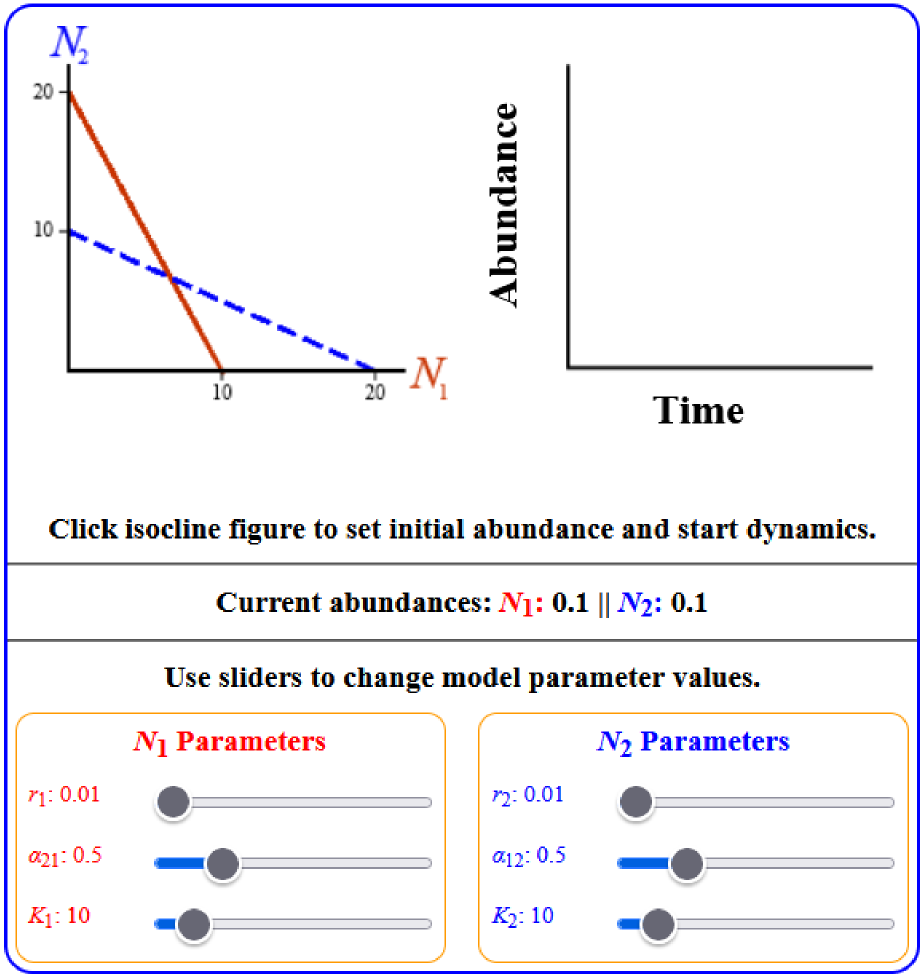
https://communityecologybook.org/LVComp.html



Lotka-Volterra model of competition SUMMARY

Four possible outcomes depending on *K* (carrying capacity of each species) and alpha (the effect of one species on the other):

Trivial equilibria (**dominance control**)

One species drives the other out (competitive exclusion)

K individuals of the winning species

Stable equilibrium

Adding or removing individuals of one or both species returns back to the same equilibrium point; both species will continue to coexist

Unstable equilibrium (**founder control**)

Adding or removing individuals of one or both species results in one of two possible outcomes (depending on the initial abundances):

- Species 1 wins
- Species 2 wins

Stably coexisting species must exhibit negative frequency dependence: tend to increase when rare; decline when common

Proc. Natl. Acad. Sci. USA
Vol. 87, pp. 9610–9614, December 1990
Ecology

Invasion resistance arises in strongly interacting species-rich model competition communities

TED J. CASE

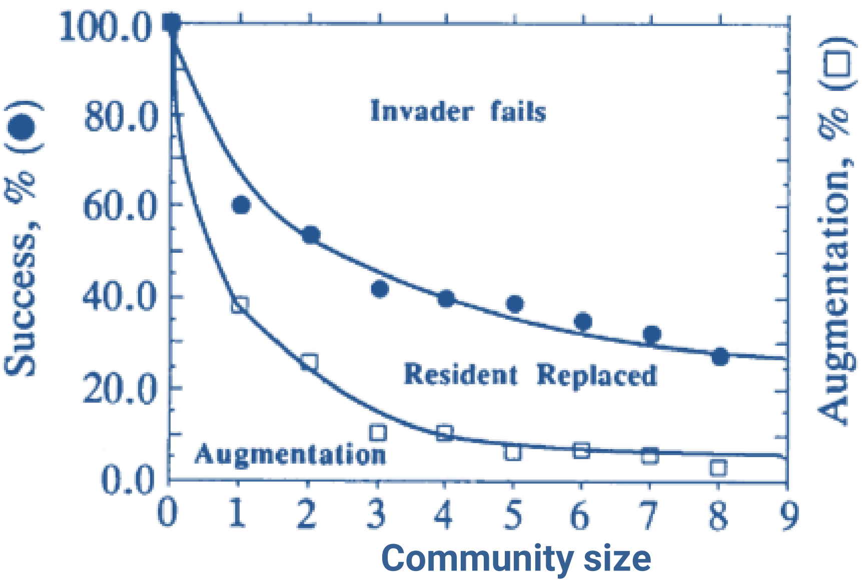
Department of Biology, C-016, University of California at San Diego, La Jolla, CA 92093

Communicated by Thomas W. Schoener, September 4, 1990

Simulation of the invasion process

The probability of colonization success for an invader decreases with community size and the average strength of competition

Species-rich communities limit the invasion possibilities ("activation barrier")



Augmentation (the community absorbs invader, that coexist with other species)

Case studies

Ecology Letters

Letters | Full Access

Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition

Peter B. Adler, Danielle Smull, Karen H. Beard, Ryan T. Choi, Tucker Furniss, Andrew Kulmatiski, Joan M. Meiners, Andrew T. Tredennick, Kari E. Veblen

Evidence based on pairs of interacting plants

Intraspecific competition is stronger than interspecific competition for most pairs of co-occurring species

Why is competitive exclusion is rarely observed in nature?

The paradox of plankton
(Hutchinson 1961)

According to the competitive exclusion principle, only a small number of plankton species should be able to coexist on the limited resources.

But in reality, large numbers of plankton species coexist within small regions of open sea

Why is competitive exclusion is rarely observed in nature?

Why is competitive exclusion is rarely observed in nature?

Resource partitioning (Tilman)

Niche differentiation

Differential responses to spatial and temporal environmental variation (Chesson)

Species–specific natural enemies (Janzen, Connell)

…

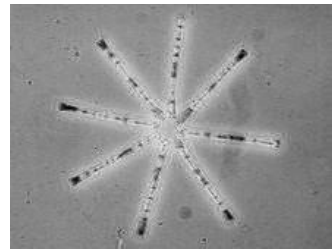
Why is competitive exclusion is rarely observed in nature?

Resource partitioning (species utilizing the same resources)

WHY IS COMPETITIVE EXCLUSION IS RARELY OBSERVED IN NATURE?

Resource partitioning (utilizing the same resources)

Cyclotella



Asterionella

Resources:
silica (for their glass-like shells) and **phosphate** (for growth and reproduction).

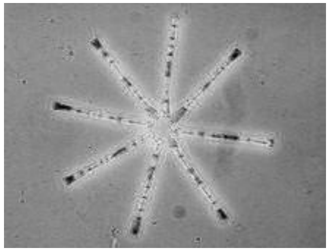
Cyclotella needs less silica but more phosphate
Asterionella needs more silica but less phosphate

Who wins when phosphate / silica is limited?

When the coexistence is possible?

Resource partitioning (utilizing the same resources)

Cyclotella



Asterionella

Resources:
silica (for their glass-like shells) and **phosphate** (for growth and reproduction).

Competition Outcome:

When **phosphate is abundant but silica is scarce**, **Cyclotella** outcompetes Asterionella because it can survive with less silica and dominates the ecosystem.

When **silica is abundant but phosphate is scarce**, **Asterionella** outcompetes Cyclotella because it is better at using limited phosphate.

If both resources are supplied in balanced proportions, the two species can coexist.

Competition for Resources

David Tilman

Professor of Ecology, University of Minnesota & Professor, Bren School UCSB
Verified email at umn.edu

ecology sustainability biodiversity diet-health agriculture

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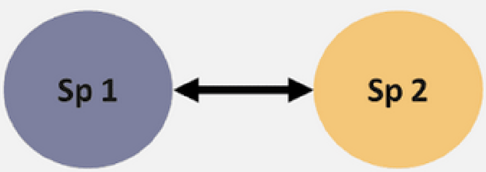
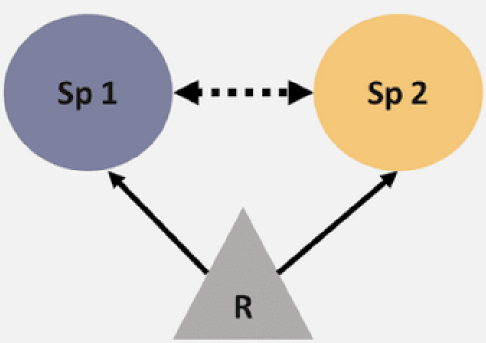
Competition for Resources

Resource: a component of the environment consumed by the population and its increase in the environment contributes to an increase in growth rate of the population

Examples for plants: photosynthetically active radiation, nutrients in the soil, pollinators
For animals: food, nesting places,…



Interference or Contest Competition: Individuals or populations behave in a way that reduces exploitation efficiency of another individual or population (direct). Lotka-Volterra

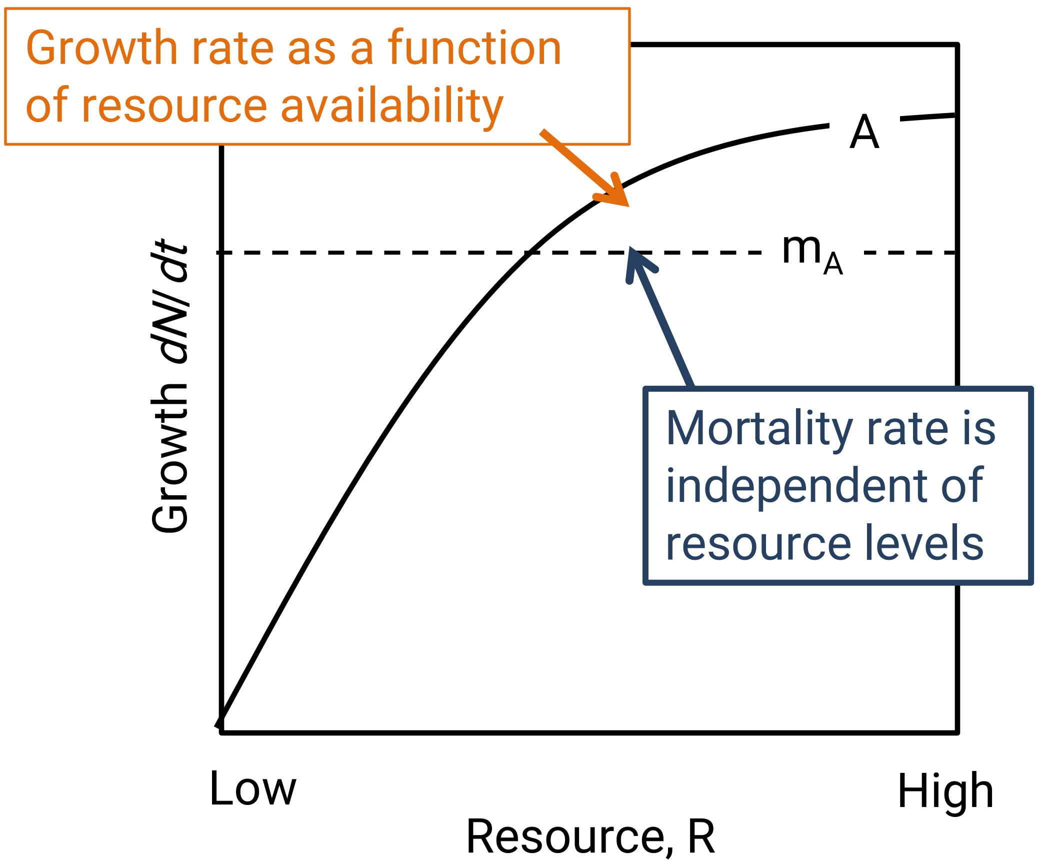


Exploitation or Scramble Competition: Individuals or populations depress one another through use of a shared resource (indirect).

Tilman

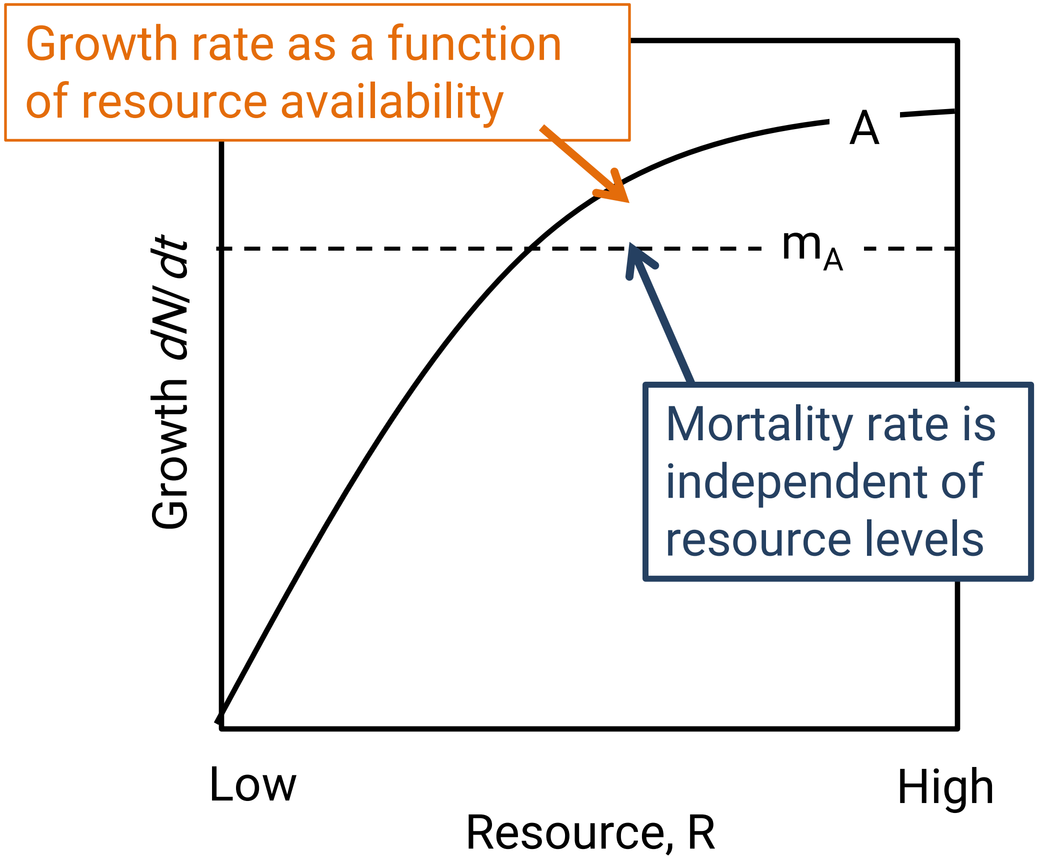
Competition for Resources

Dynamics of *1 resource* (*R*) and *1 consumer* species population (*N*)



COMPETITION FOR RESOURCES

Dynamics of *1 resource* (*R*) and *1 consumer* species population (*N*)



Dynamical equation of the consumer population:

If R availability is constant:

$$dN/dt = N * (uR - m)$$

mortality (*d*) is independent of R
natality (*u*) is a function R

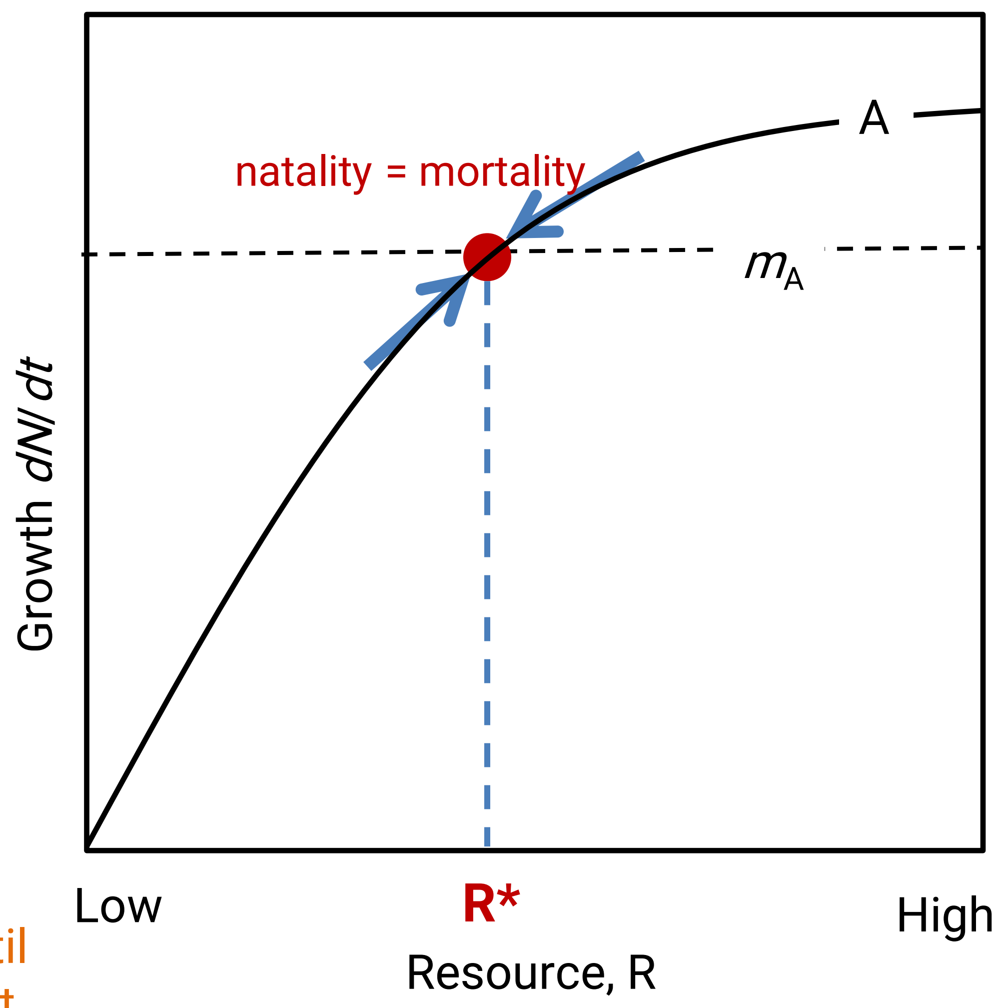
If R use efficiency changes with R:
Michaelis-Menten relationship:

$$dN/dt = N * (uR/(k + R) - m)$$

k - half-saturation constant

COMPETITION FOR RESOURCES

Dynamics of *1 resource* (*R*) and *1 consumer* species population (*N*)



Resources are drawn down to reach a balance between resource uptake and release

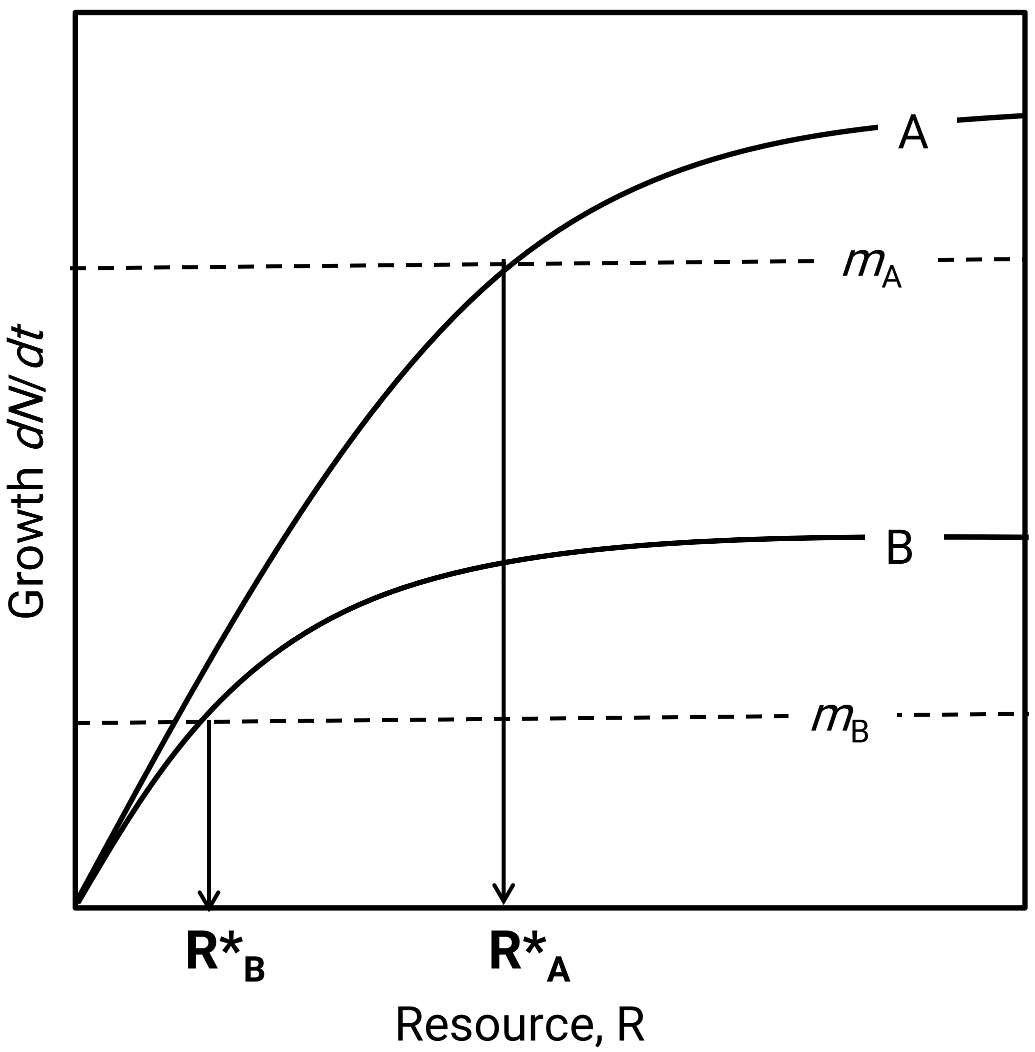
Below R*, mortality increases releasing more resource into the environment until the equilibrium point is reached

Competition for resources

Dynamics of *1 resource* (*R*) and *2 consumers*

Dynamics of *1 resource* (*R*) and *2 consumers*

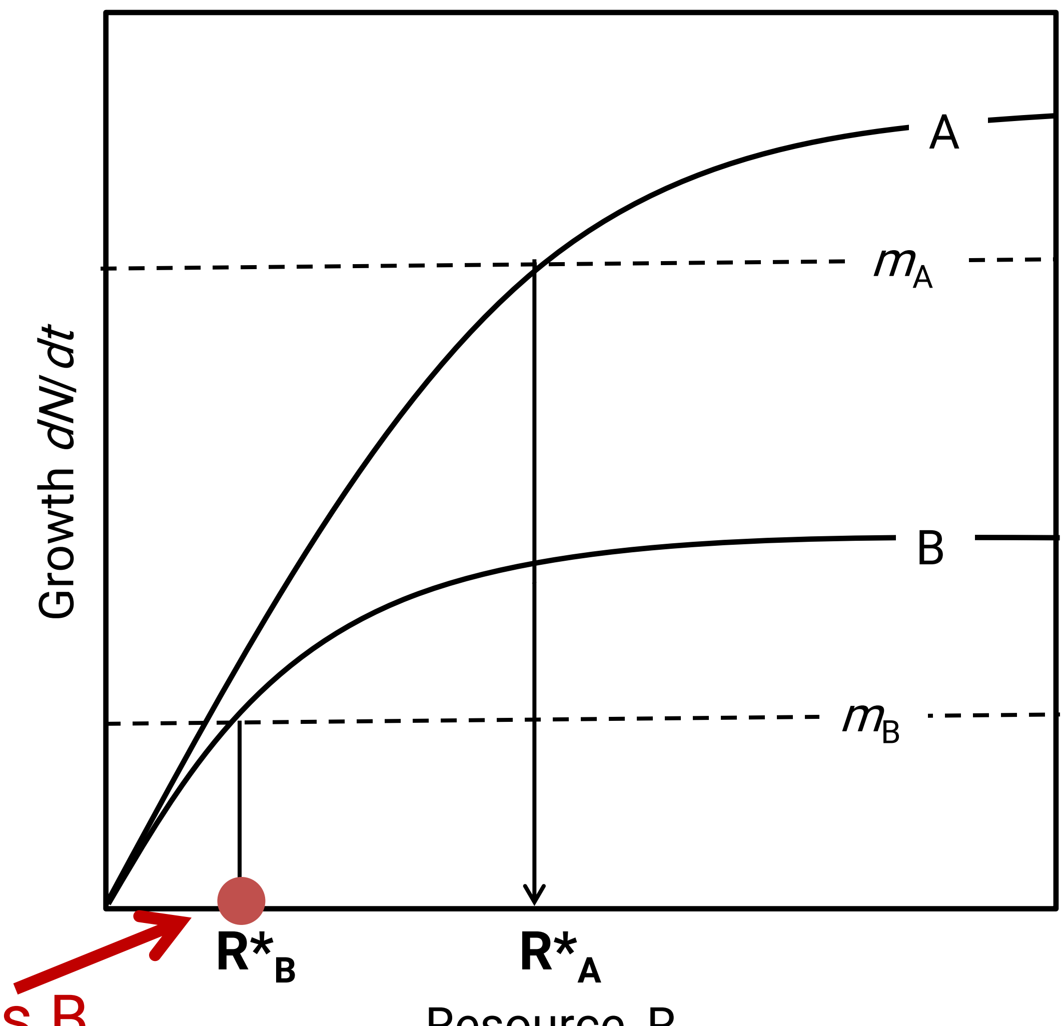
Who will win?



Dynamics of *1 resource* (*R*) and *2 consumers*

Who will win?

Only one species can exist, if there is one limiting resource



Species B

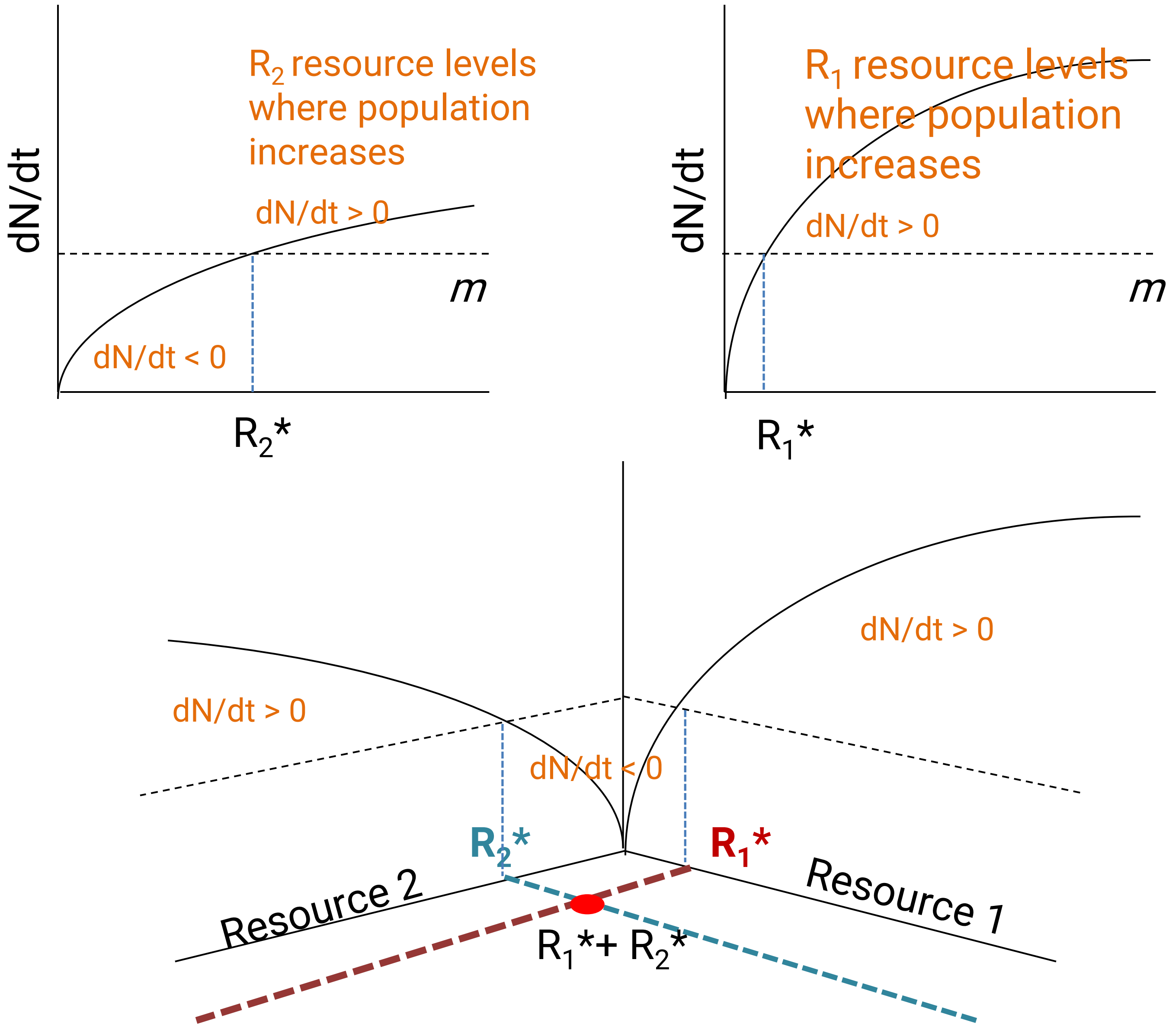
having zero growth at the resource level when species A has negative growth

Competition for resources

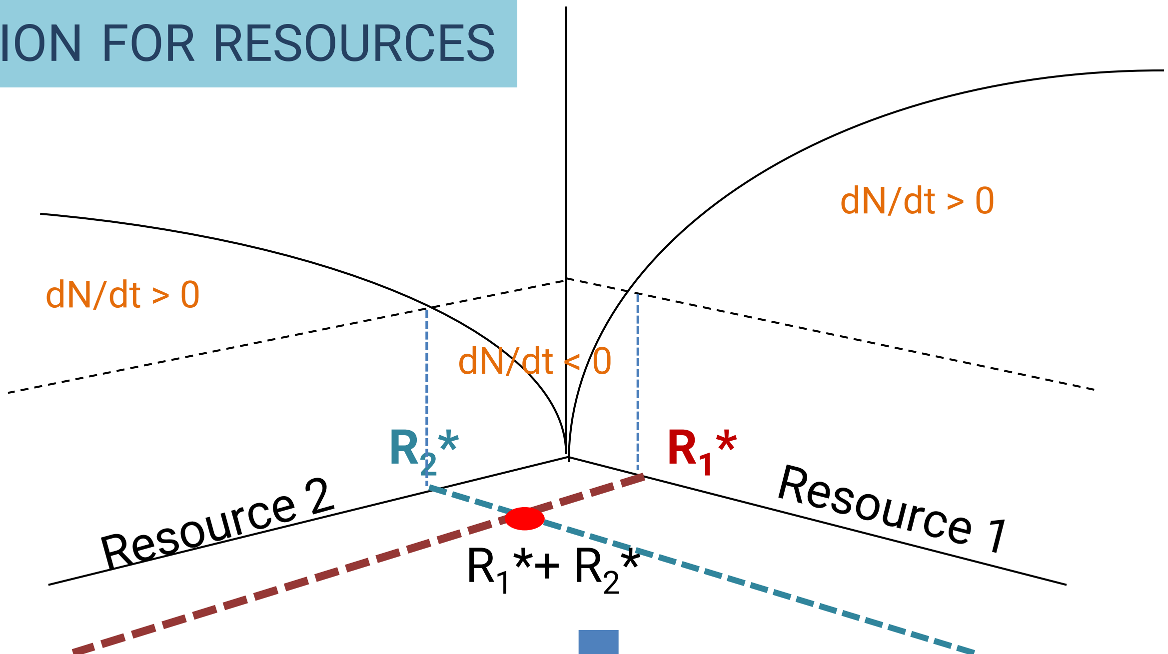
Dynamics of *2 resources* (*R*) and *1 consumer*

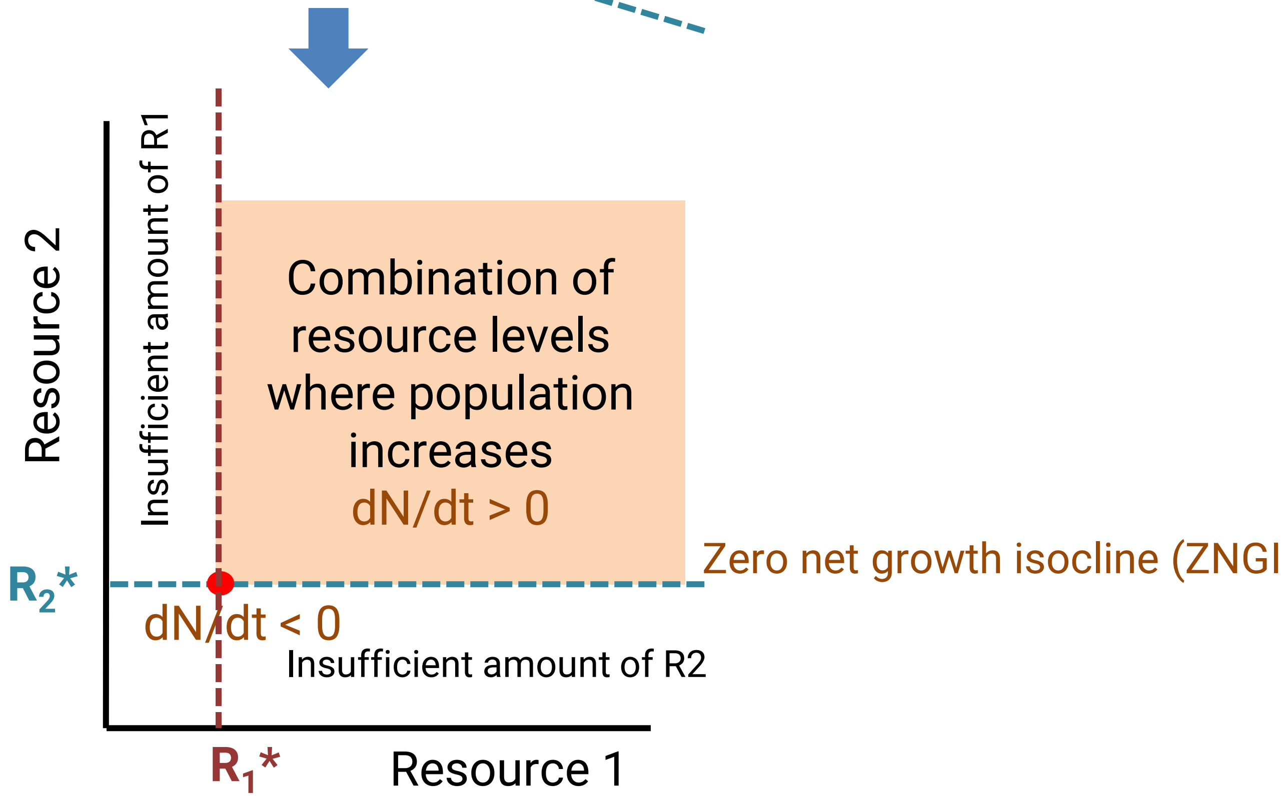
COMPETITION FOR RESOURCES

Dynamics of *2 resources* (*R*) and *1 consumer*



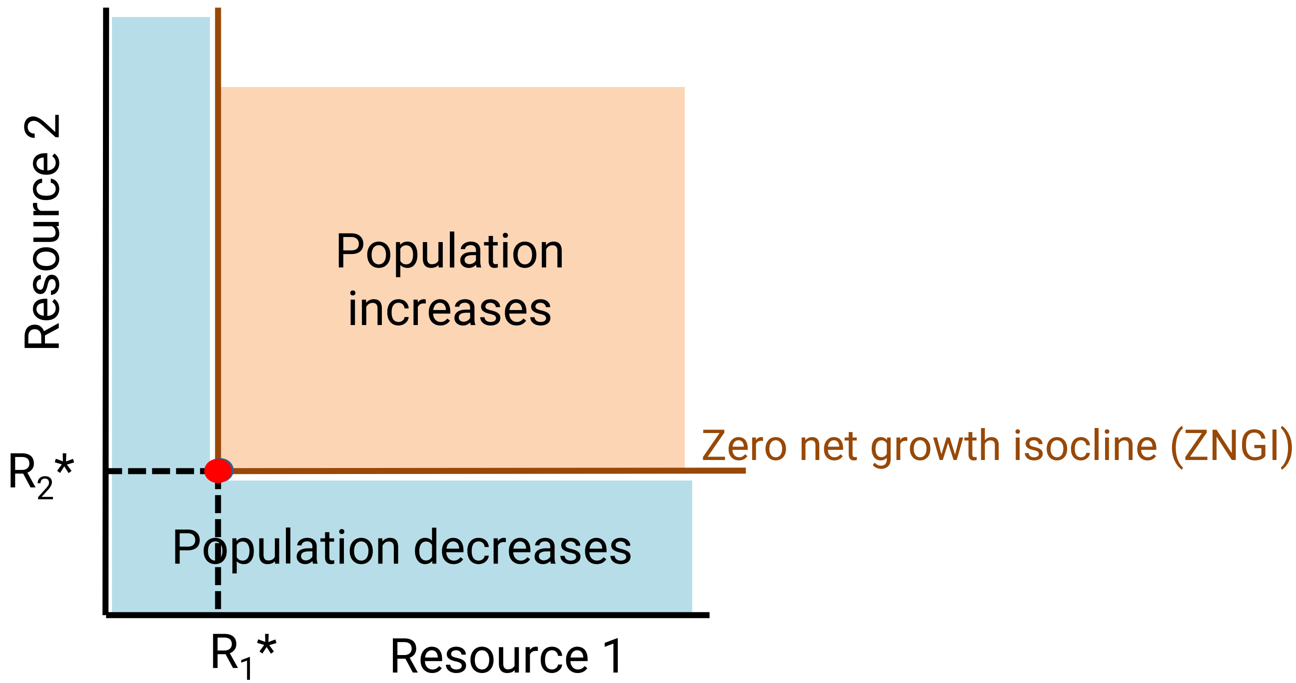
Competition for resources





Competition for resources

Dynamics of *2 resources* (*R*) and *1 consumer*

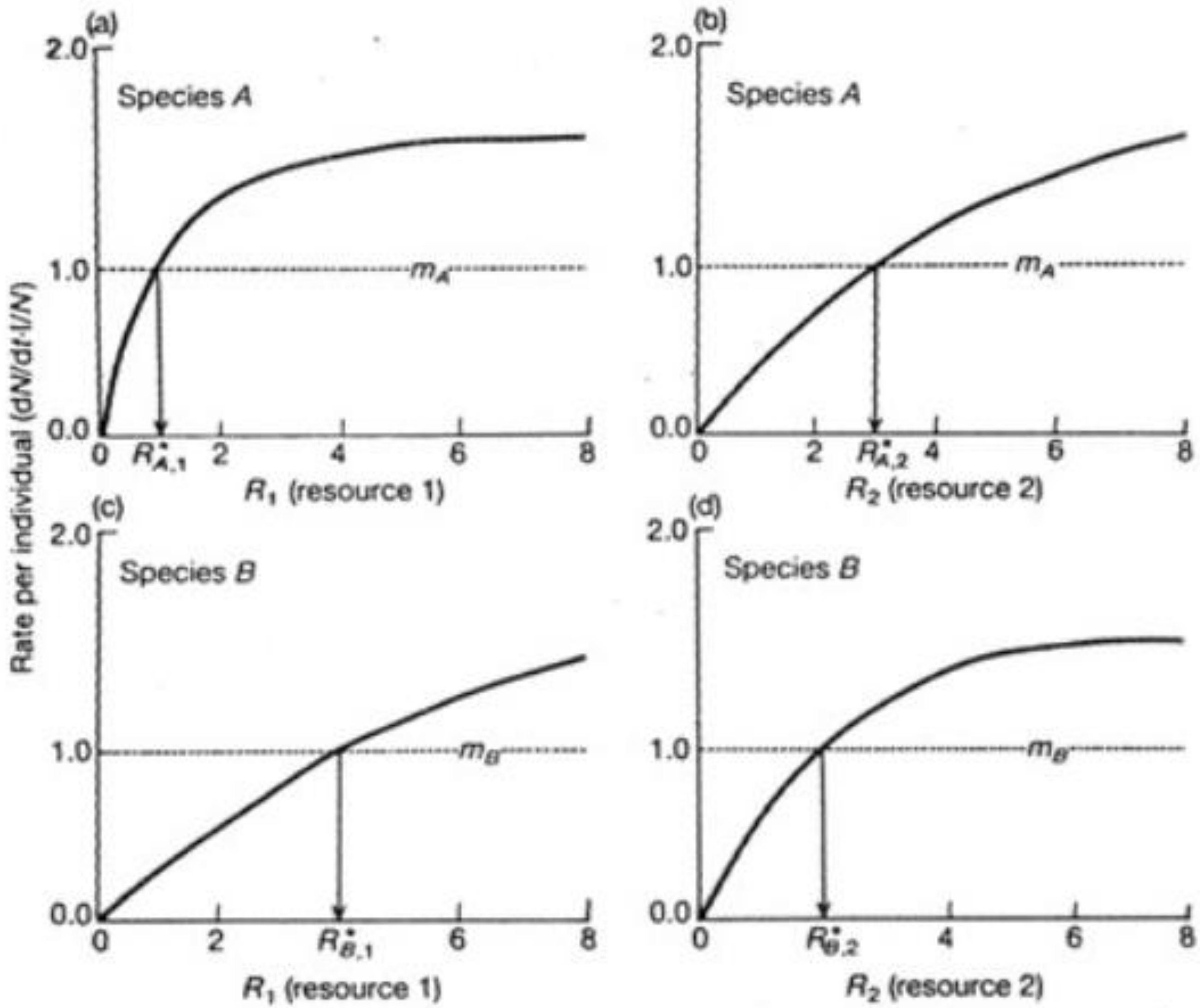


Competition for resources

Dynamics of *2 resources* (*R*) and *2 consumers (N)*

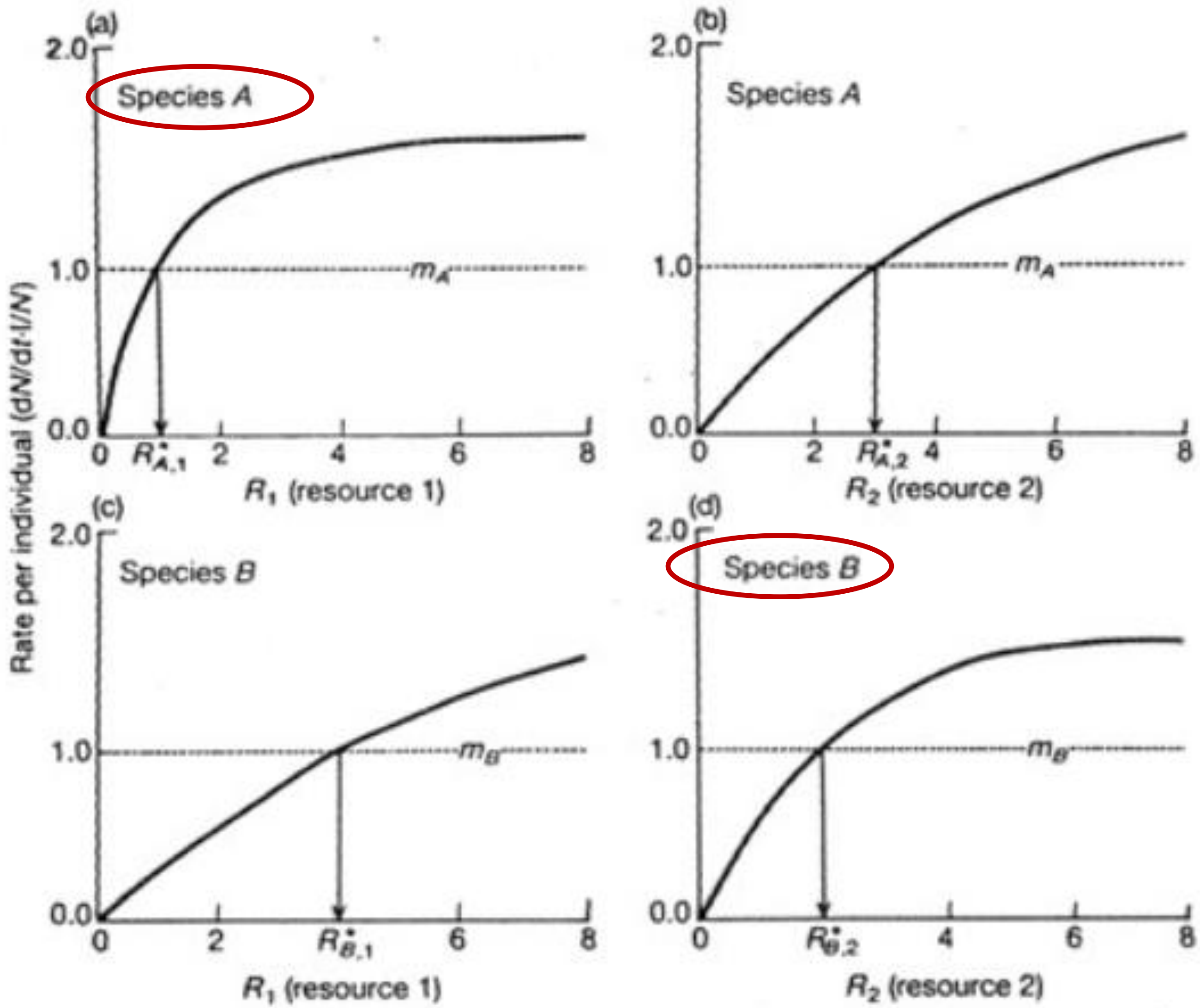
Dynamics of *2 resources* (*R*) and *2 consumers* (*N*)

Who wins?



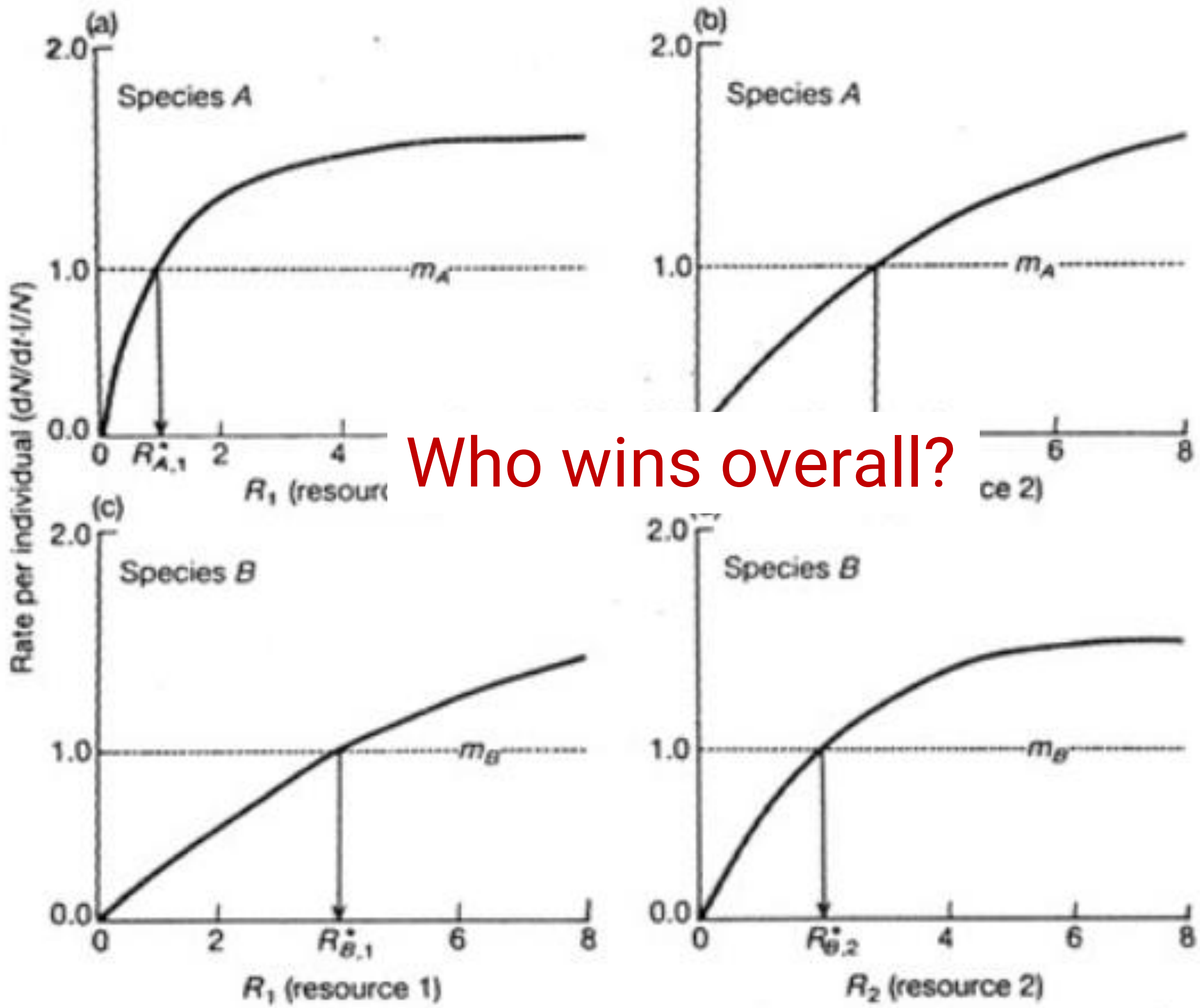
Dynamics of *2 resources* (*R*) and *2 consumers* (*N*)

Who wins?



Dynamics of *2 resources* (*R*) and *2 consumers (N)*

Who wins?

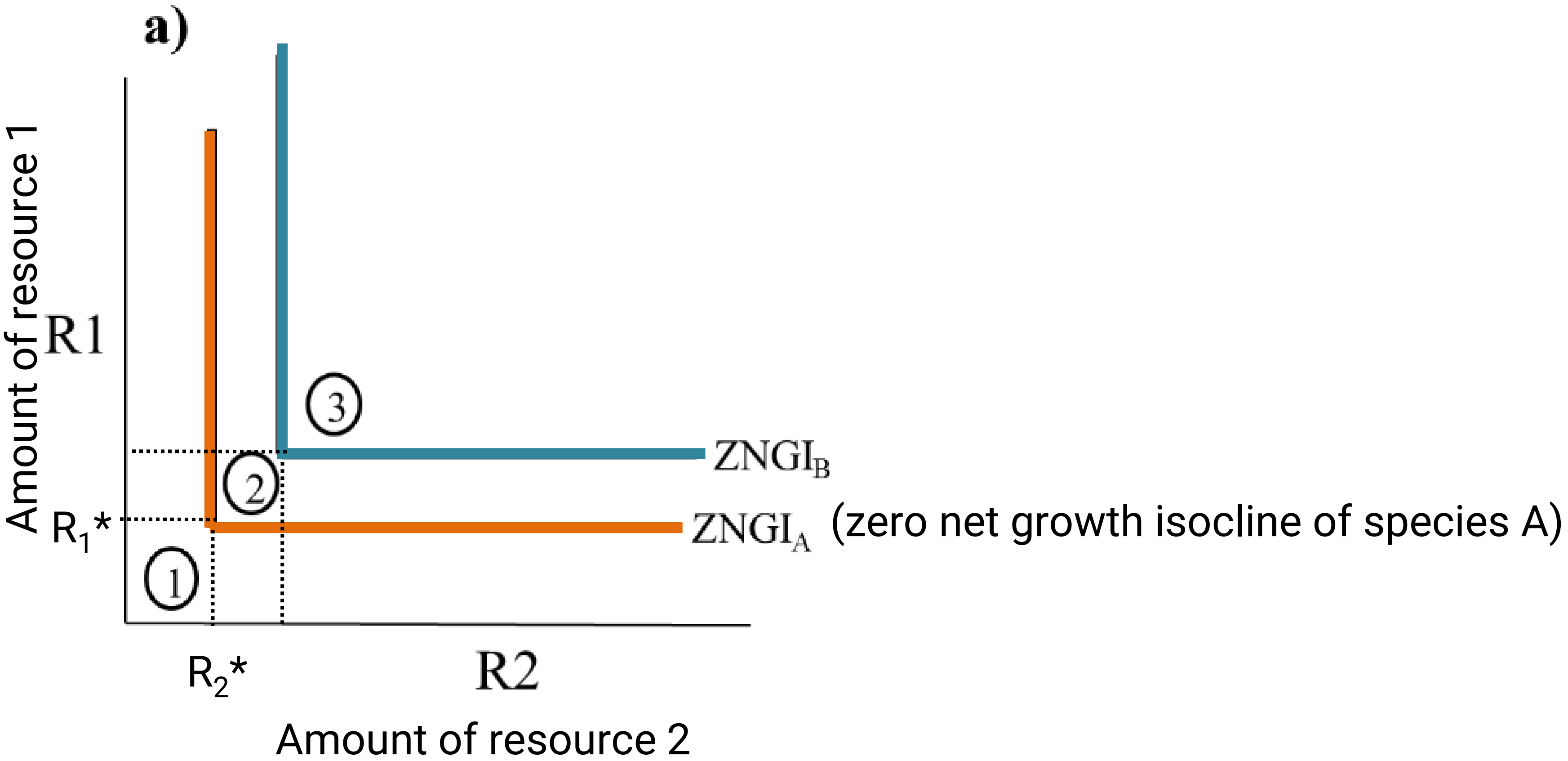


Who wins overall?

Depends on the position of the ZNGIs

COMPETITION FOR RESOURCES

Dynamics of *2 resources* (*R*) and *2 consumers (N)*



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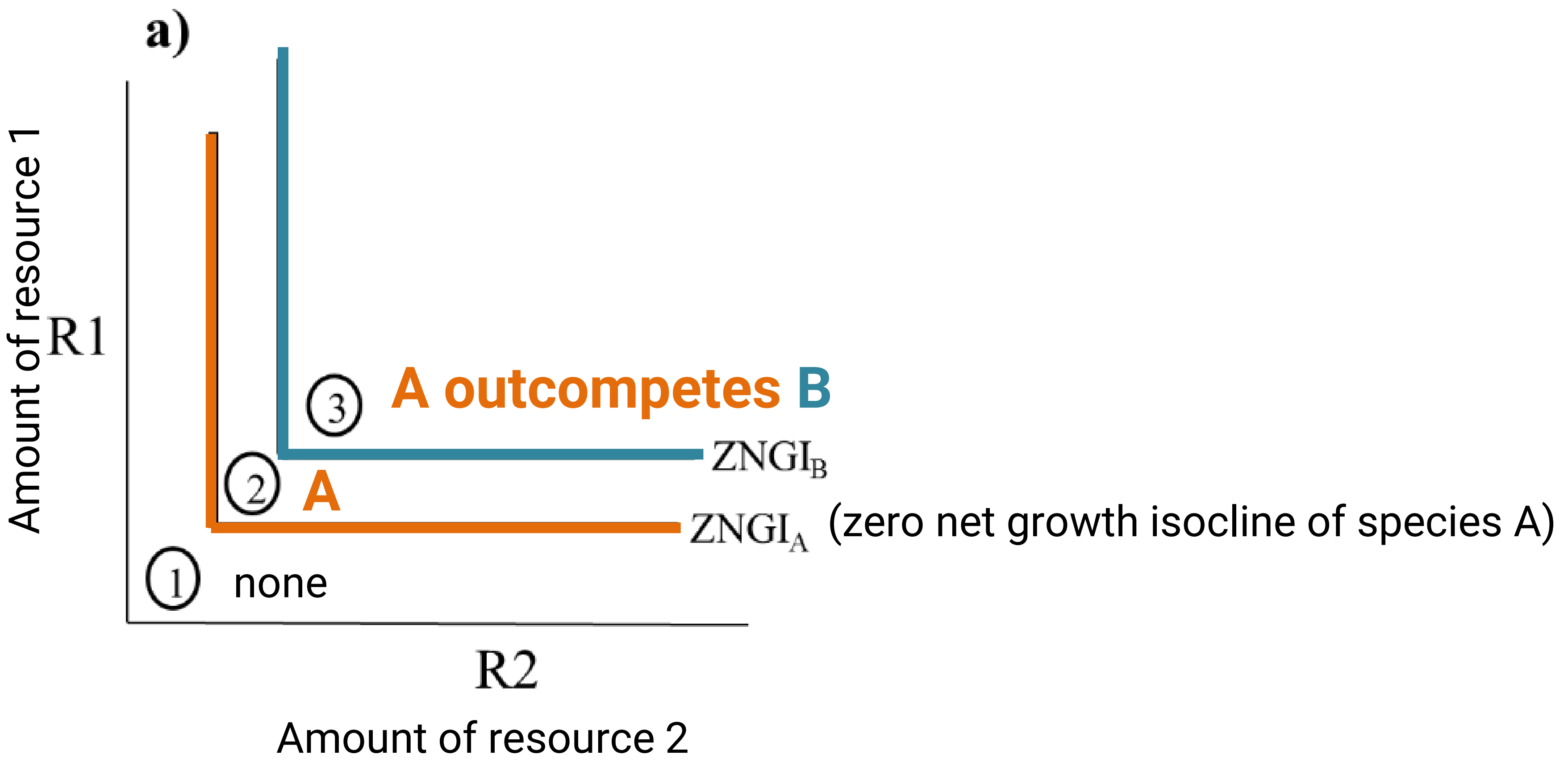

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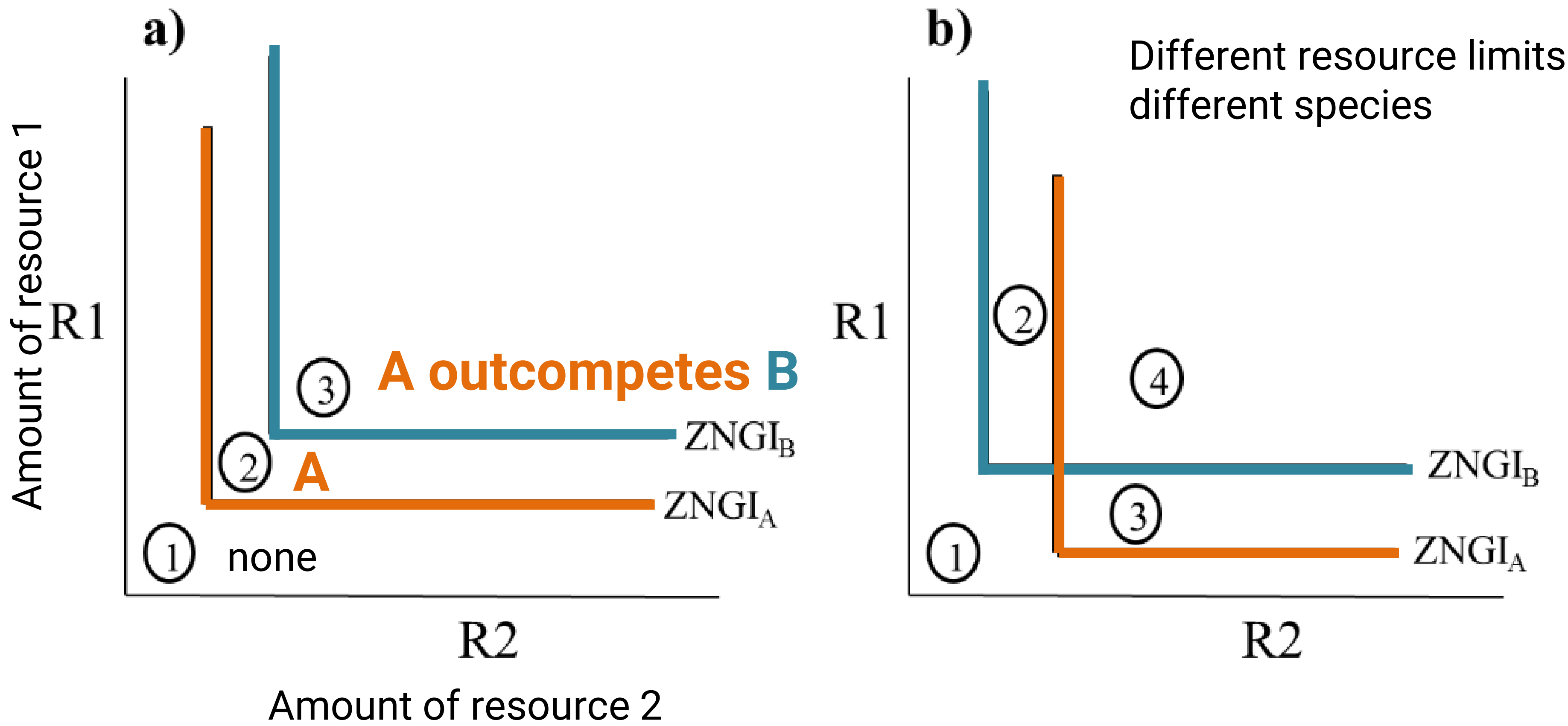

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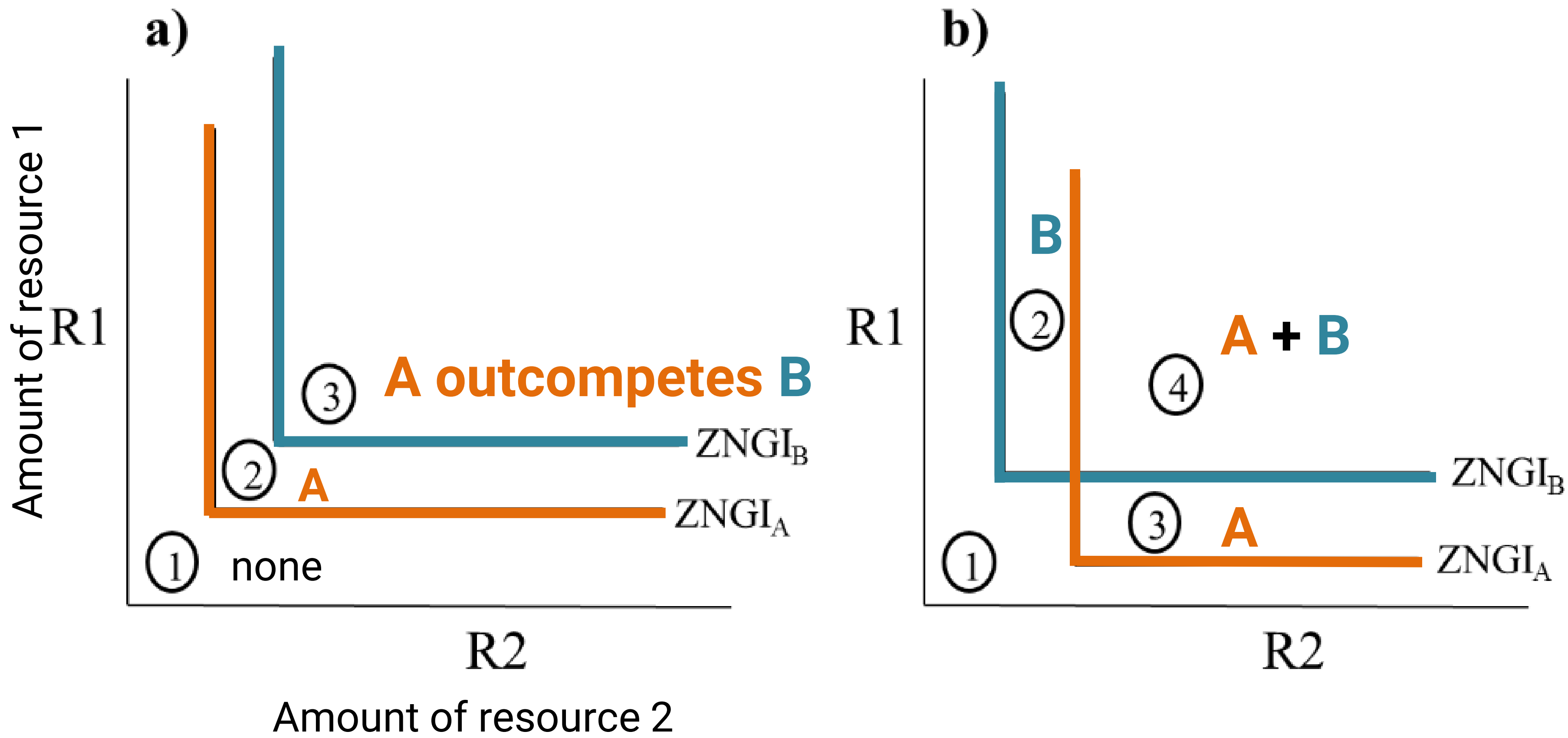

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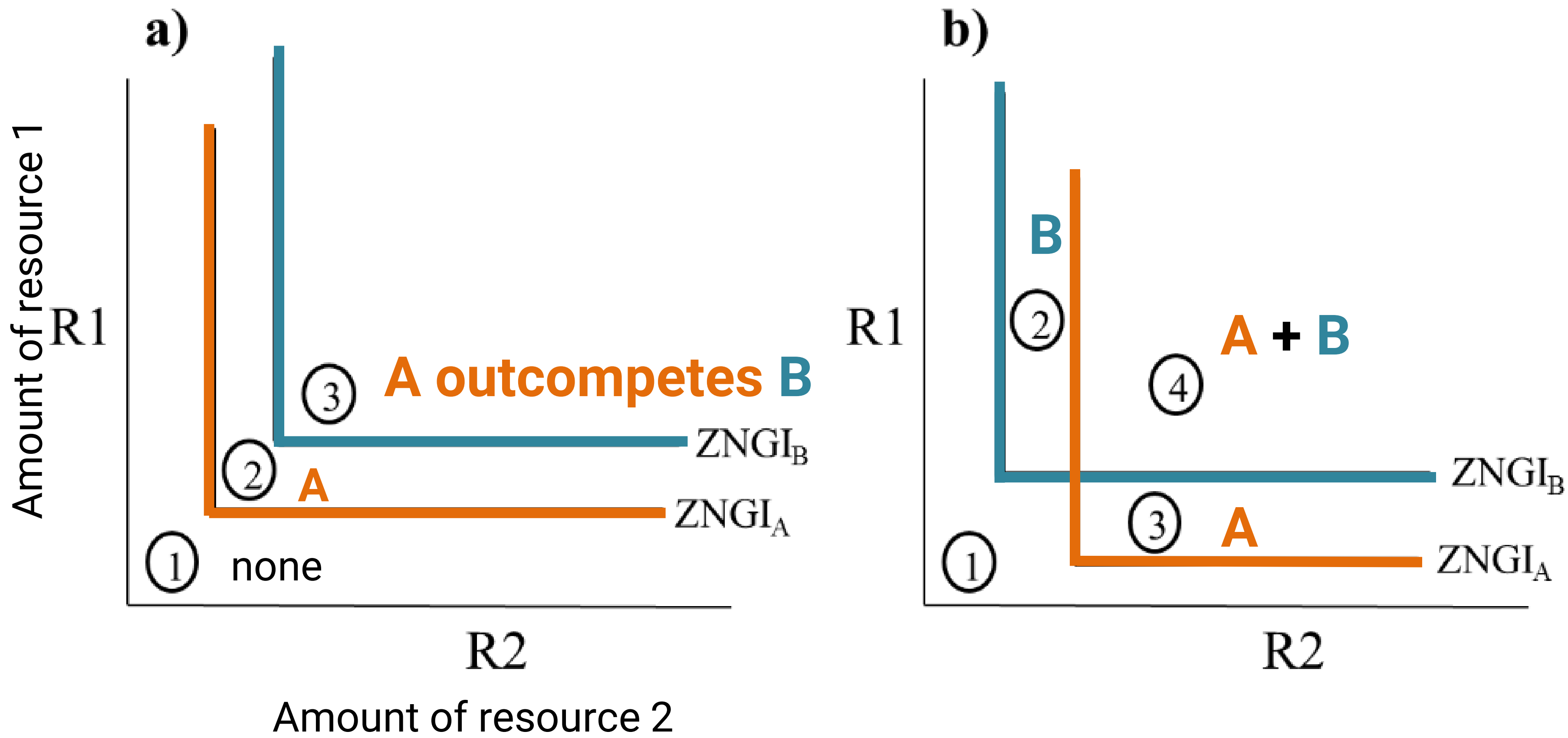


Coexistence depends ALSO on resource consumption by each species and whether a species consumes more of the resource that is more limiting for it.

Dynamics of *2 resources* (*R*) and *2 consumers* (*N*)

Two parameters affecting species competition

1. resource level (*R*)
2. resource consumption rate (*w*)

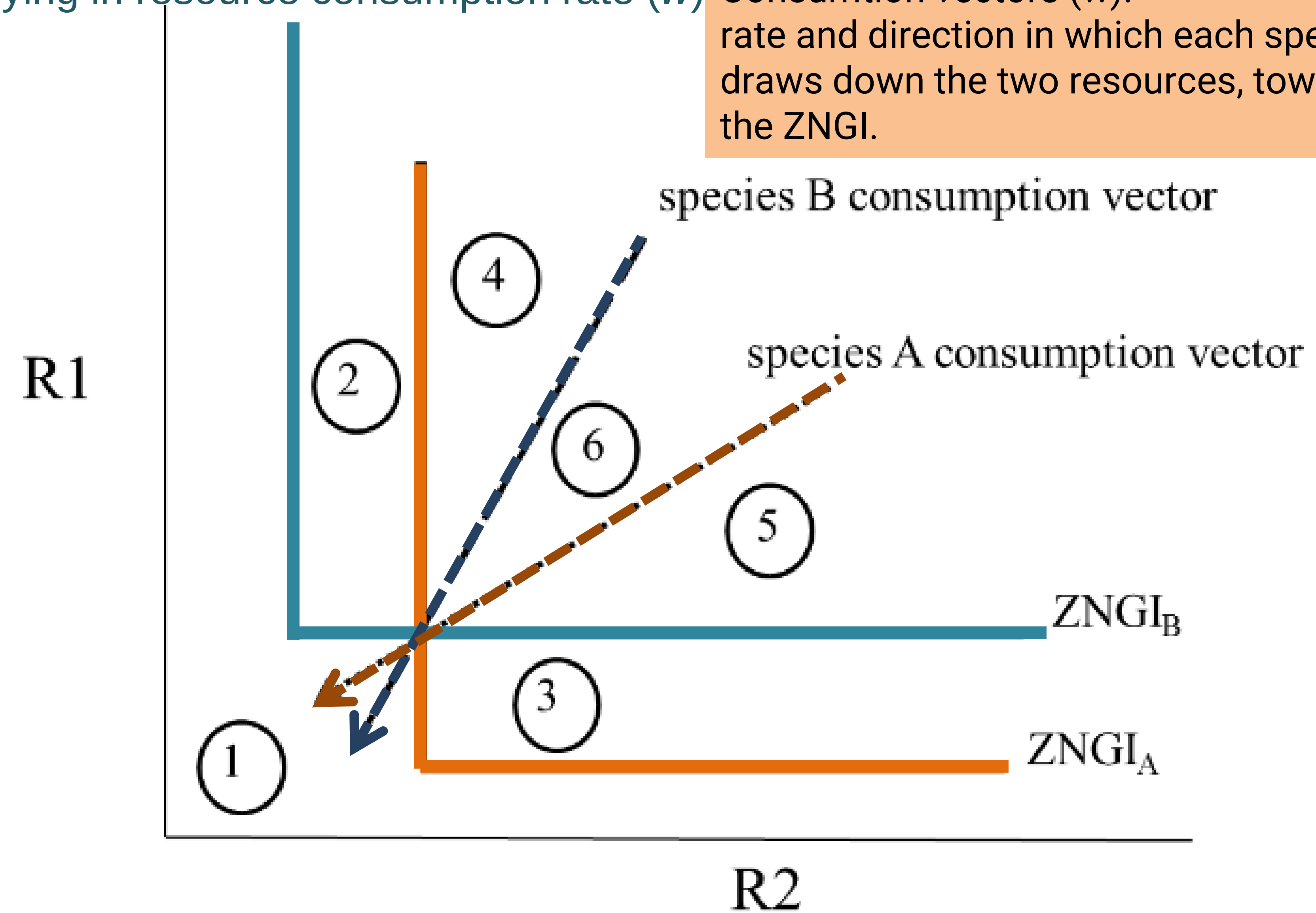
Competition for resources

Dynamics of *2 resources* (*R*) and *2 consumers* varying in resource consumption rate (*w*)

Competition for resources

Dynamics of *2 resources* (*R*) and *2 consumers* varying in resource consumption rate (*w*)

Consumtion vectors (w):
rate and direction in which each species draws down the two resources, towards the ZNGI.



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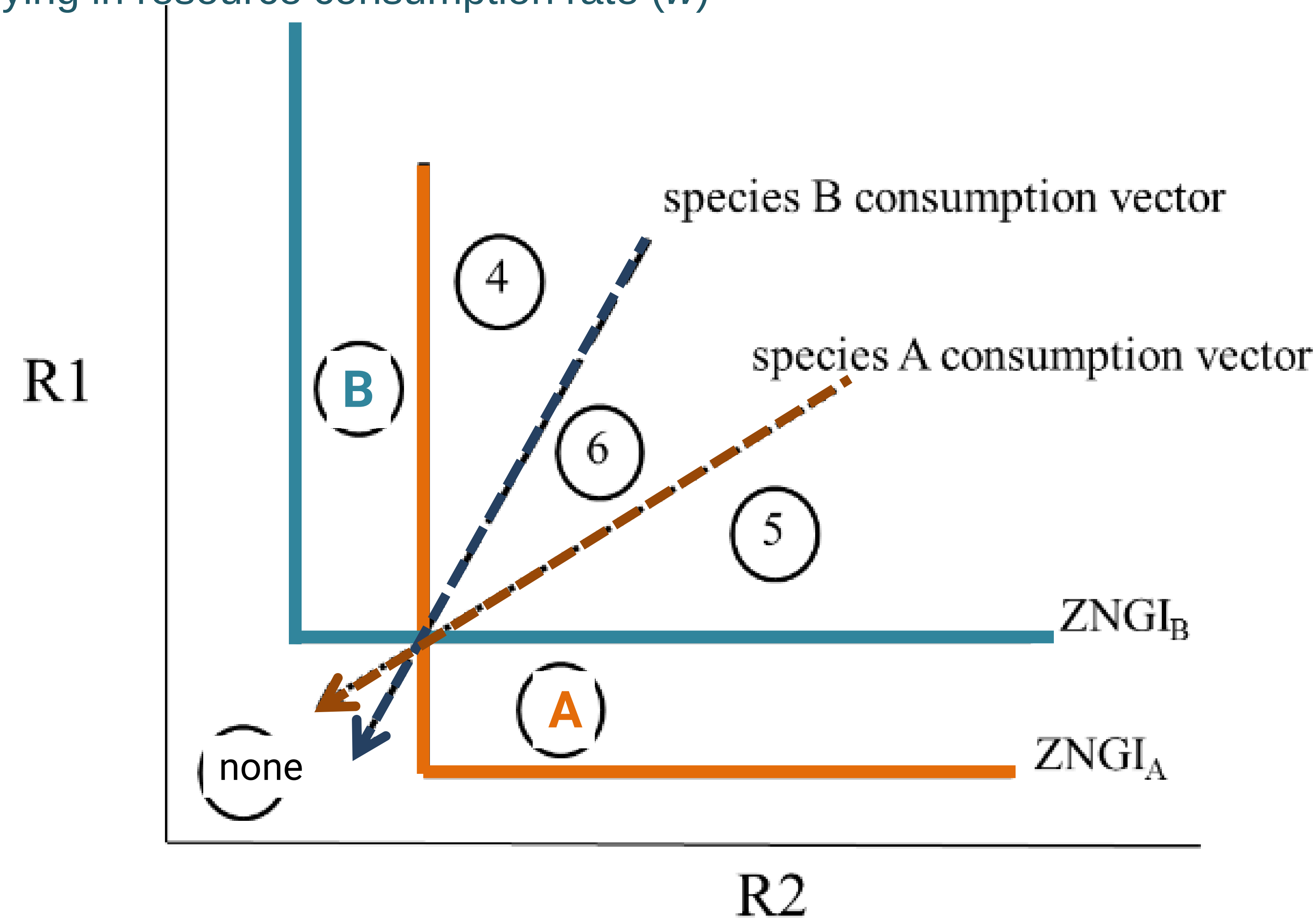

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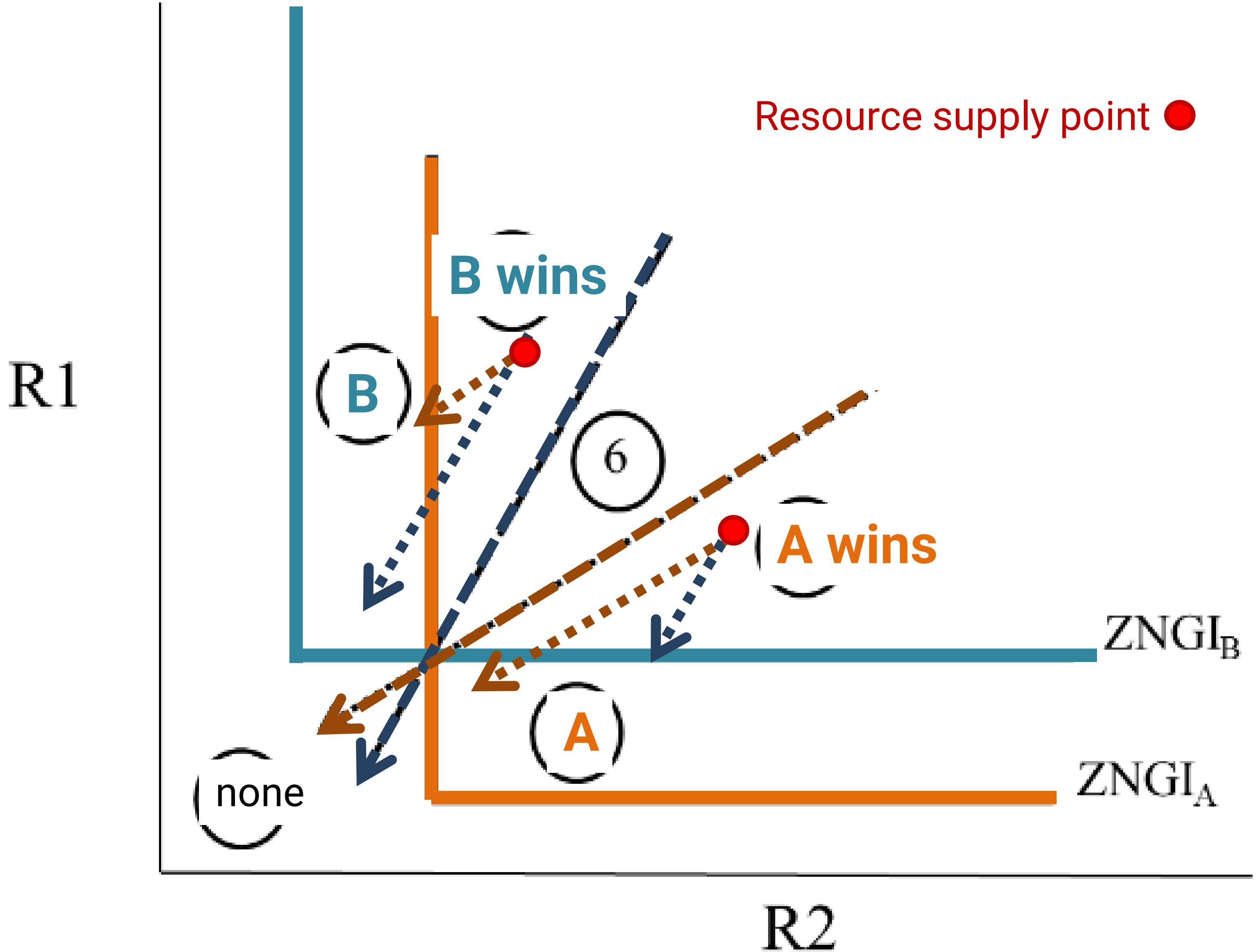

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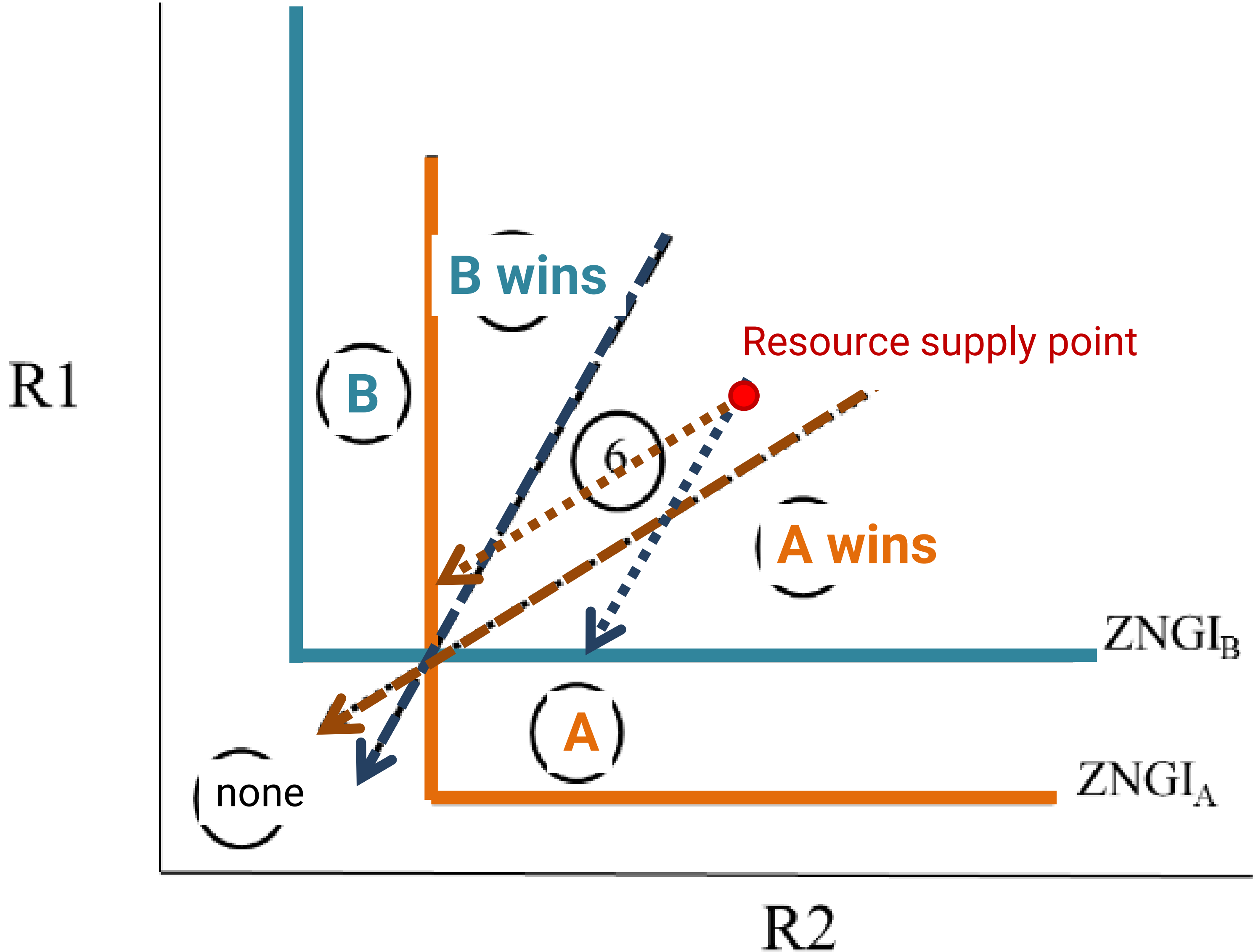

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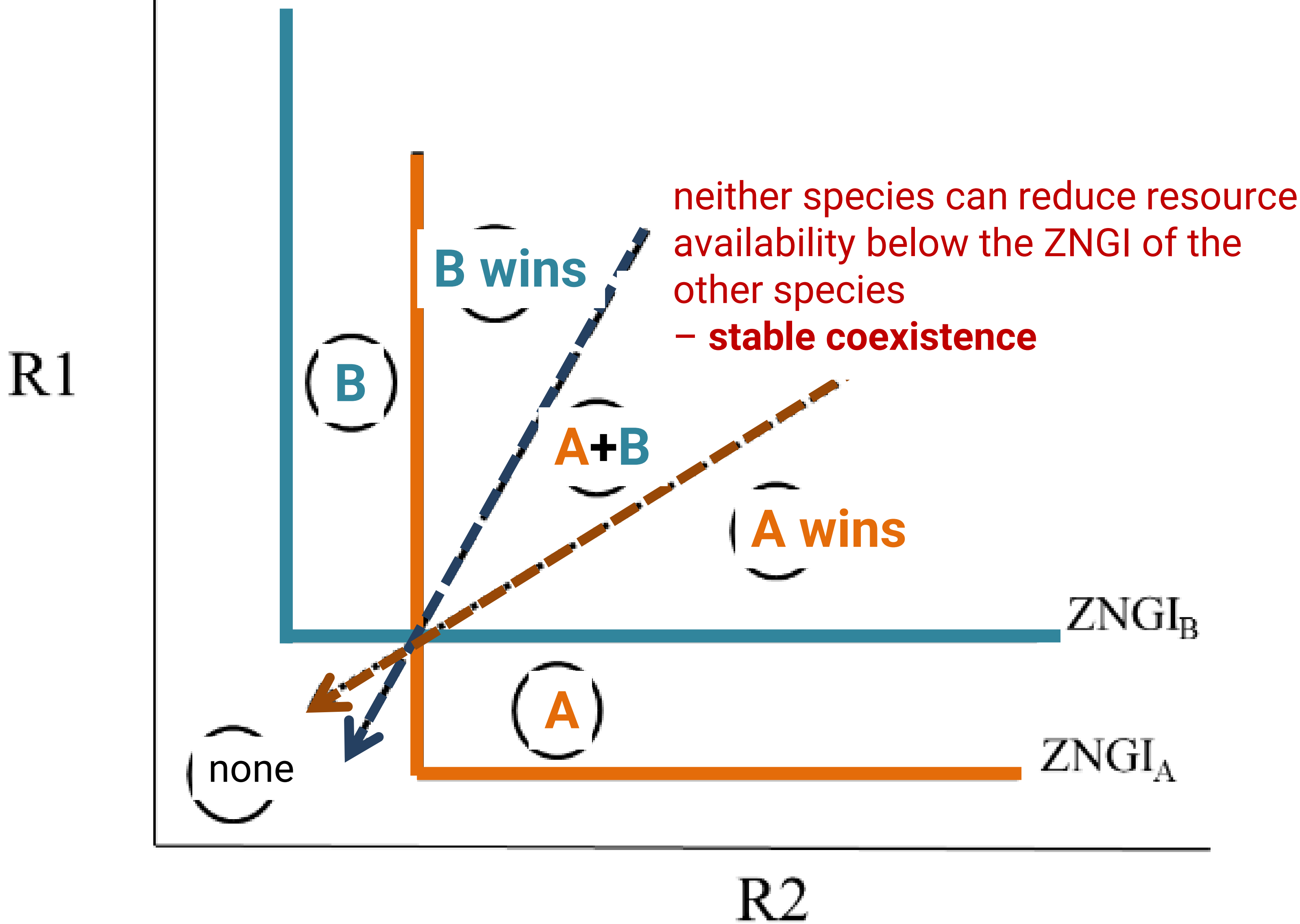

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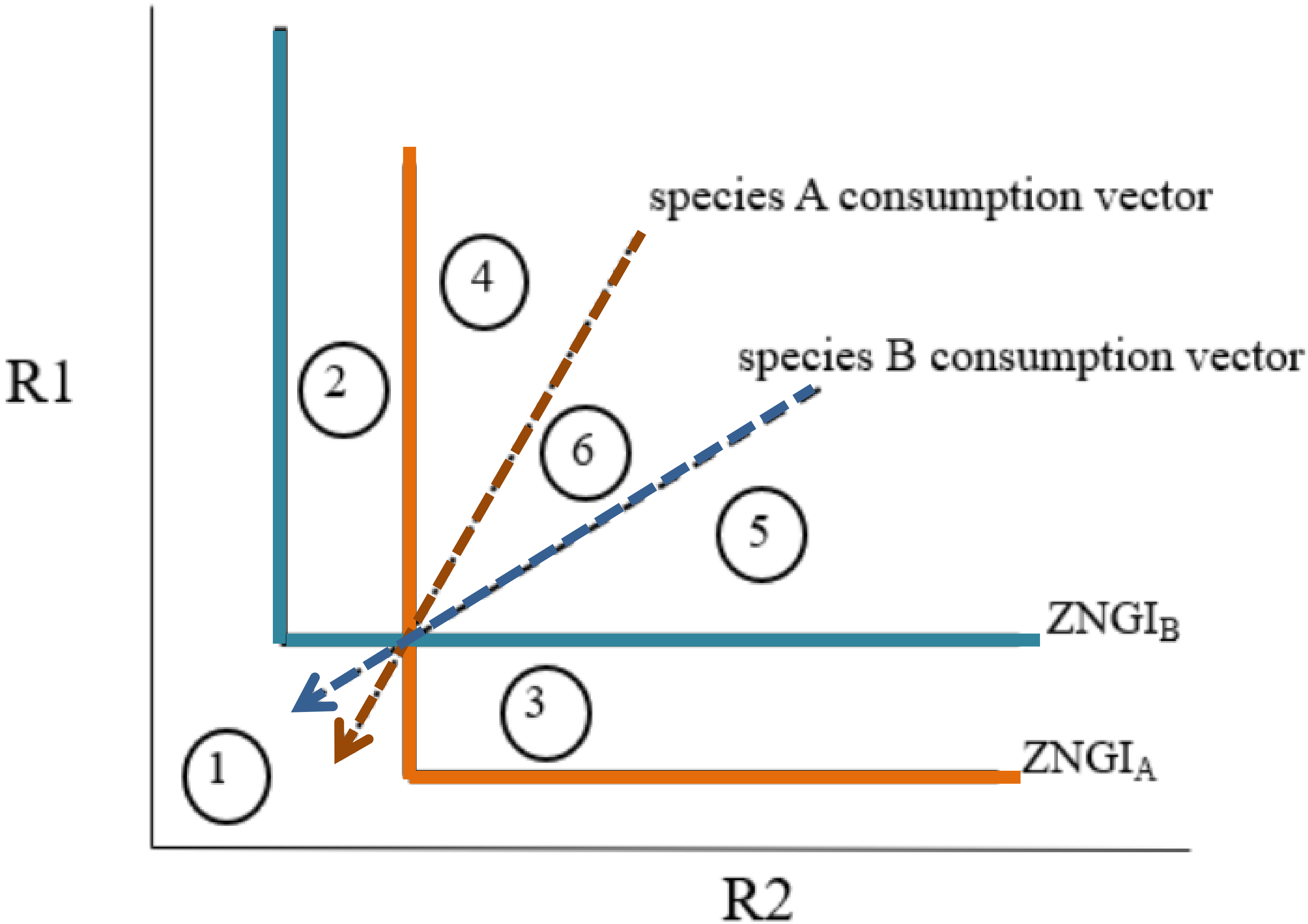

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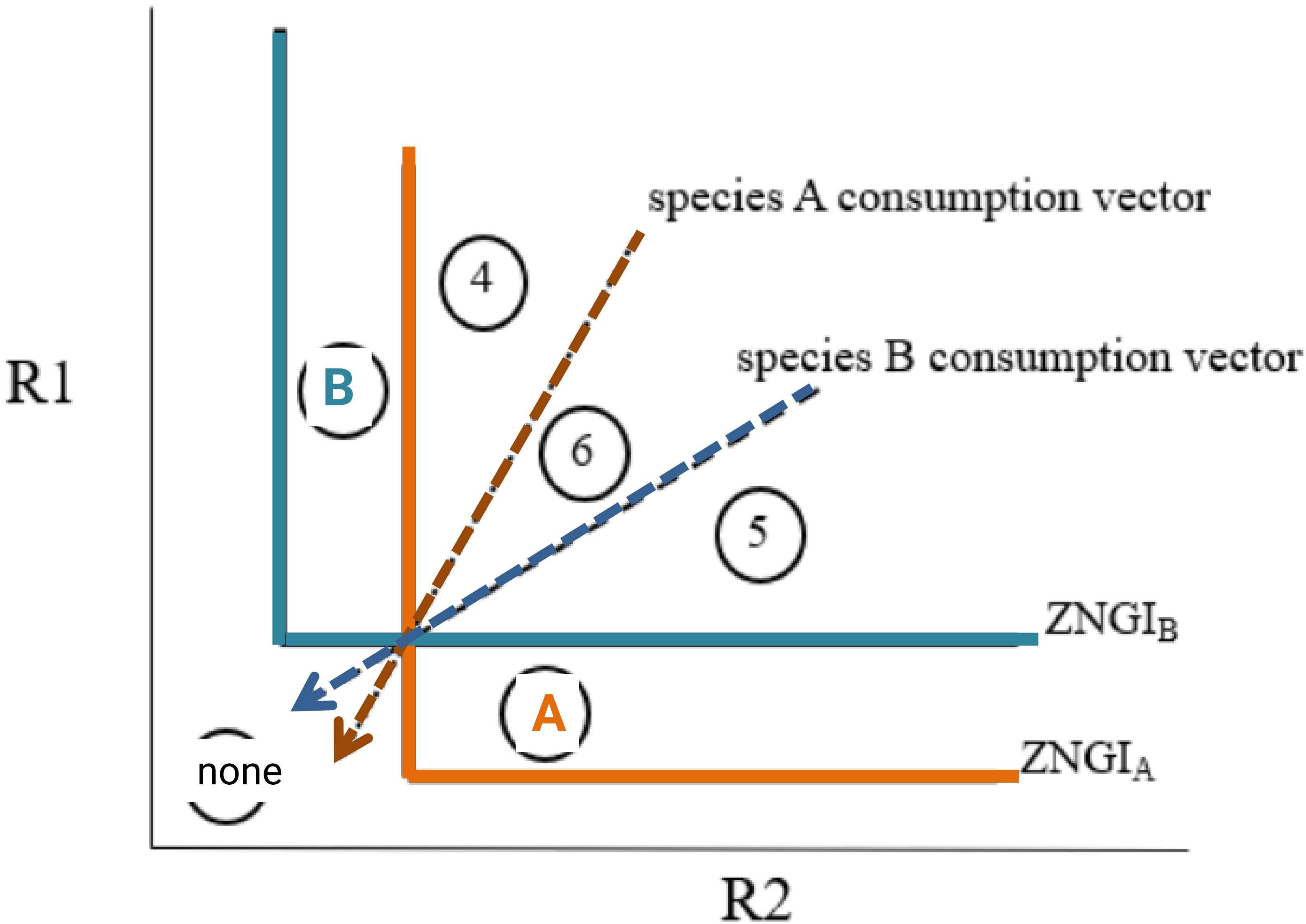

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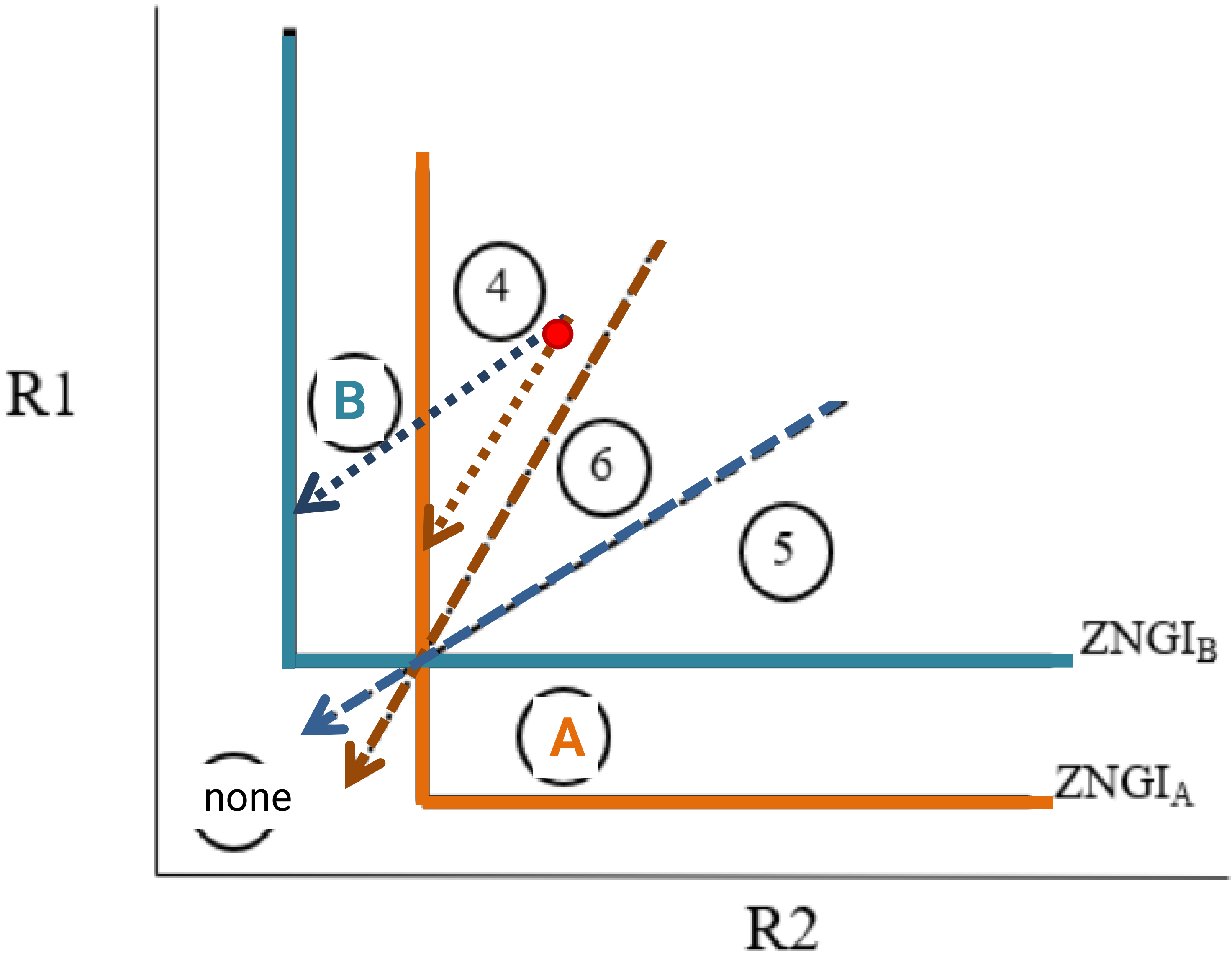

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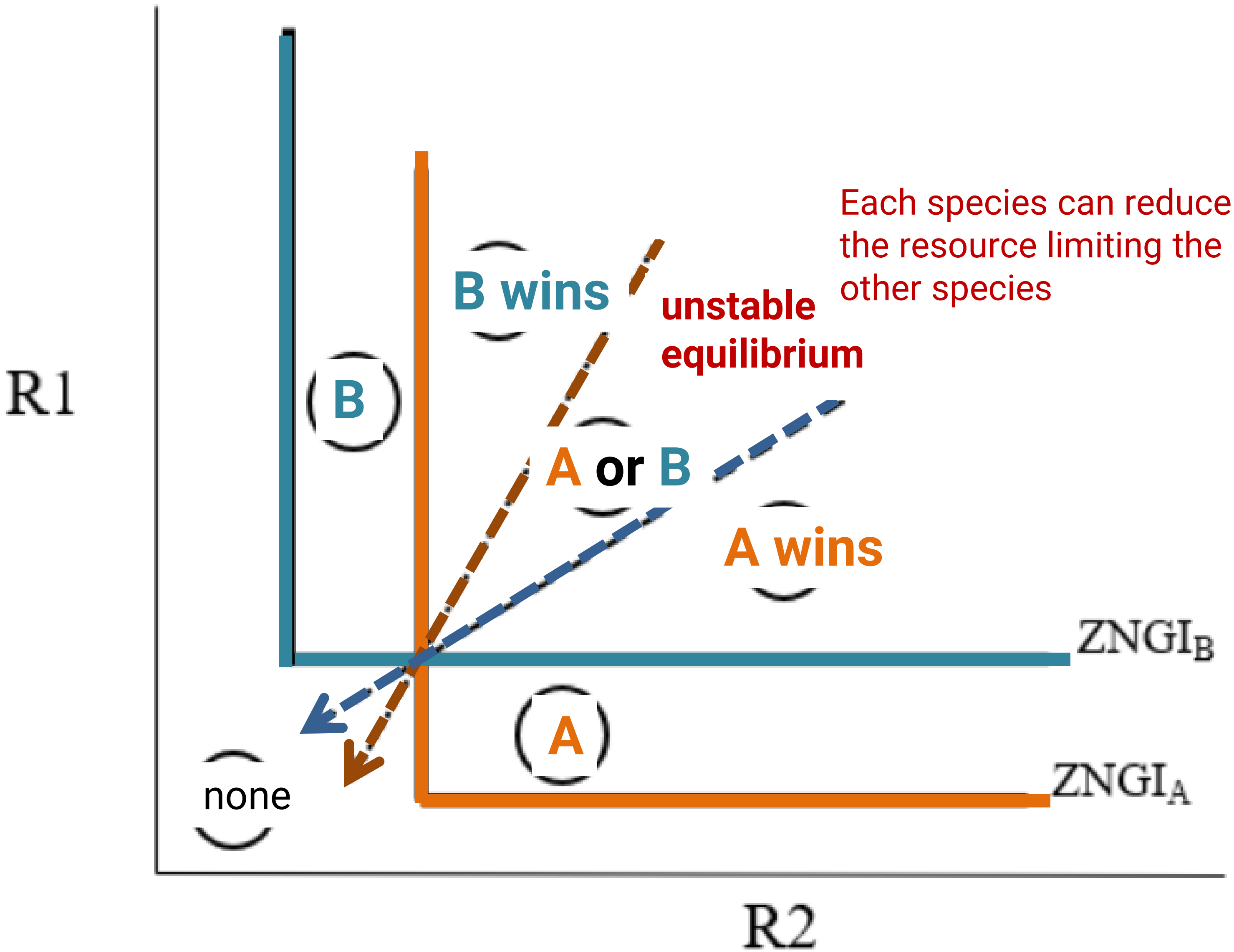

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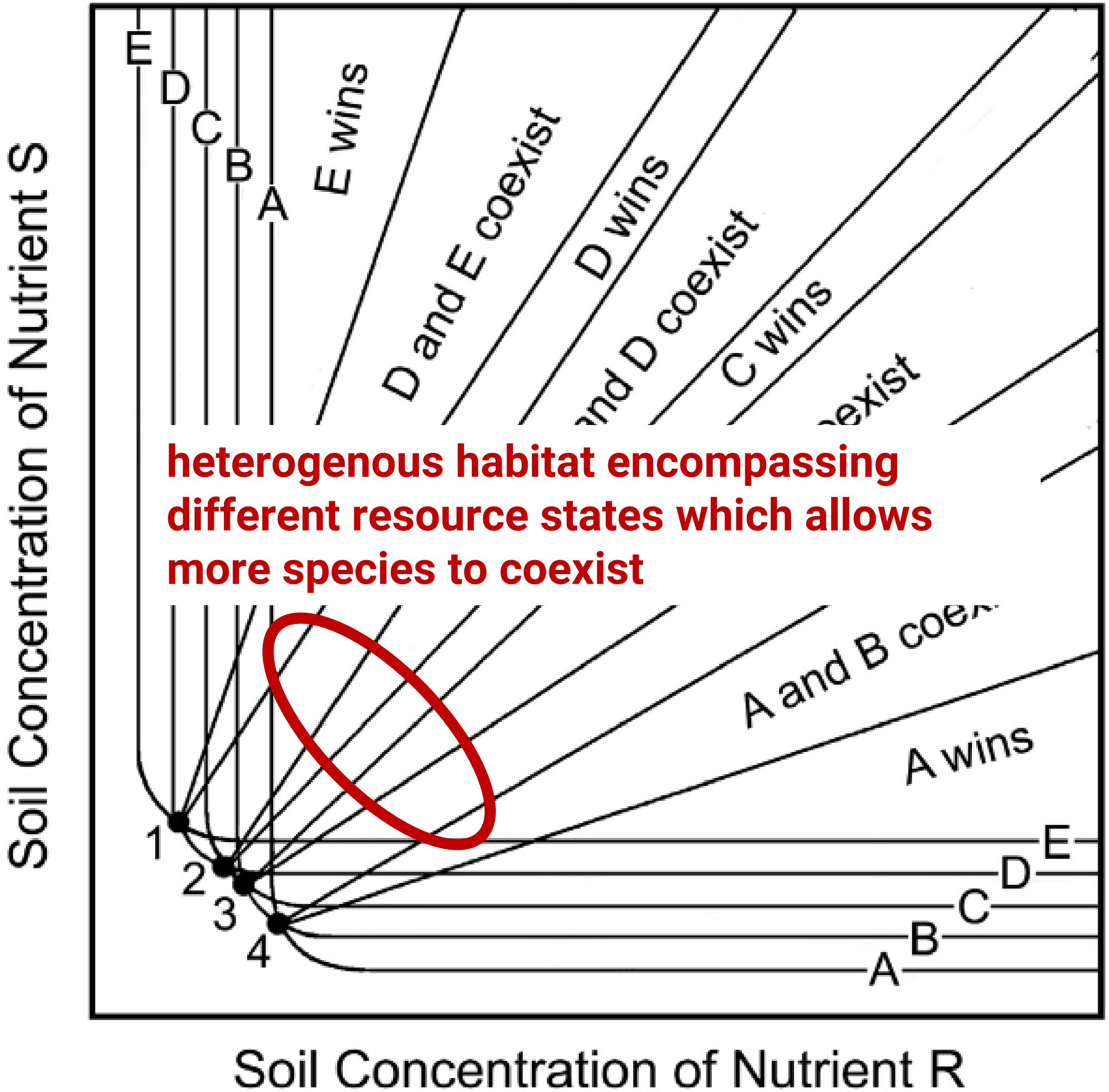
Competition for resources

Multiple species



Multiple species

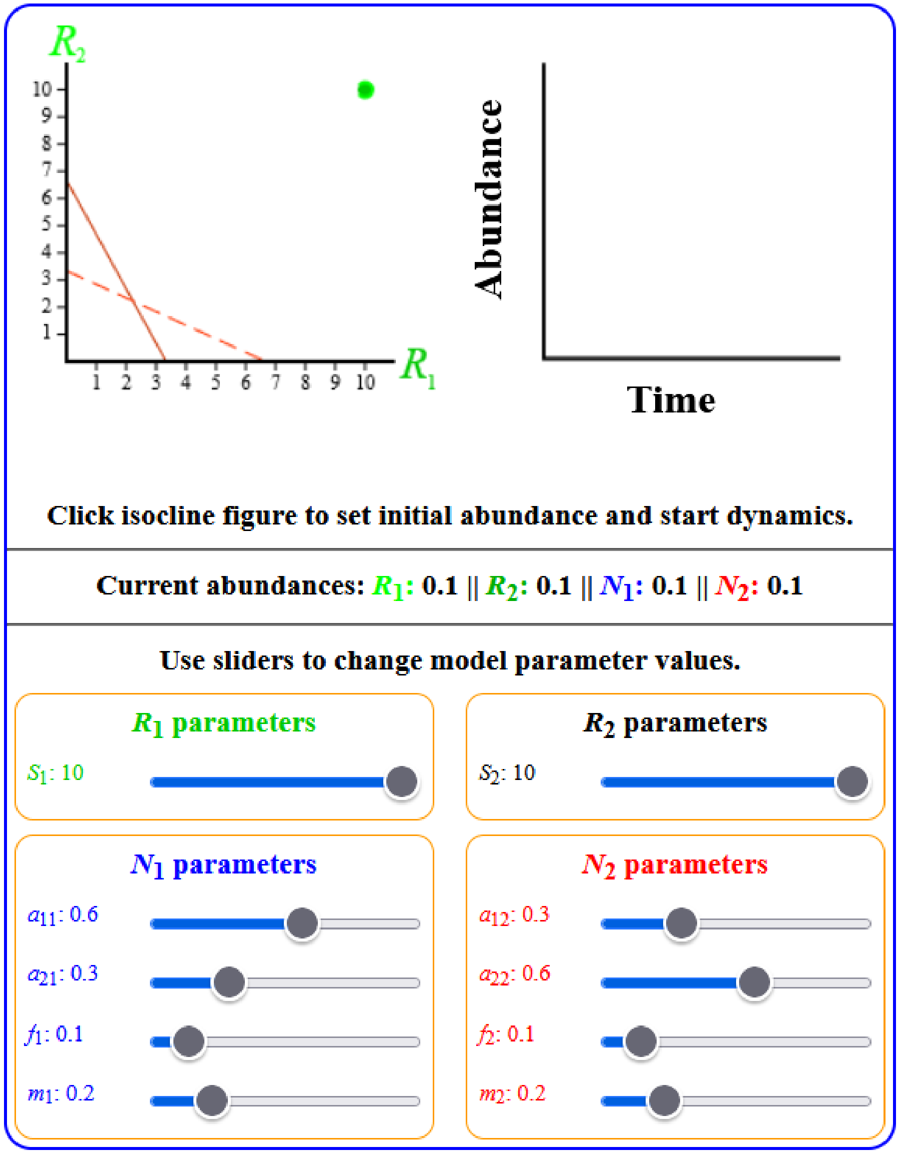
Coexistence of multiple species requires:

1) Heterogeneity in resource supply

2) Species differing in their traits (resource use)

each species consumes proportionally more the resource that is limiting it, i.e., species compete more with themselves (species with higher R* values should consume resources at a higher rate)

-> no upper limit to the number of species that can coexist in a spatially heterogenous habitat https://communityecologybook.org/conres2.html



Tilman's competition for resources - SUMMARY

Population growth is always limited by the resource that is in the short supply (Liebig's law of minimum)

*R** values of one species for each resource are independent of each other (ZNGI)

Outcomes of competition of 2 consumer species limited by 2 resources:

Stable coexistence: each species is limited by a different resource and each species consumes proportionally more the resource that is limiting it
(~ intraspecific competition being stronger than interspecific competition in the Lotka-Volterra competition)

Unstable coexistence (Founder control): each species is limited by a different resource, but each species consumes proportionally more the resource that is limiting the other species.
(~ intraspecific competition being weaker than interspecific competition in the Lotka-Volterra competition)

Dominance control. One species is more limited that the other by both resources, species can never coexist, and the less limited species (with smaller R* for both resources) always wins.
(~ intraspecific competition being weaker in one species but not in the other species in the Lotka-Volterra competition)

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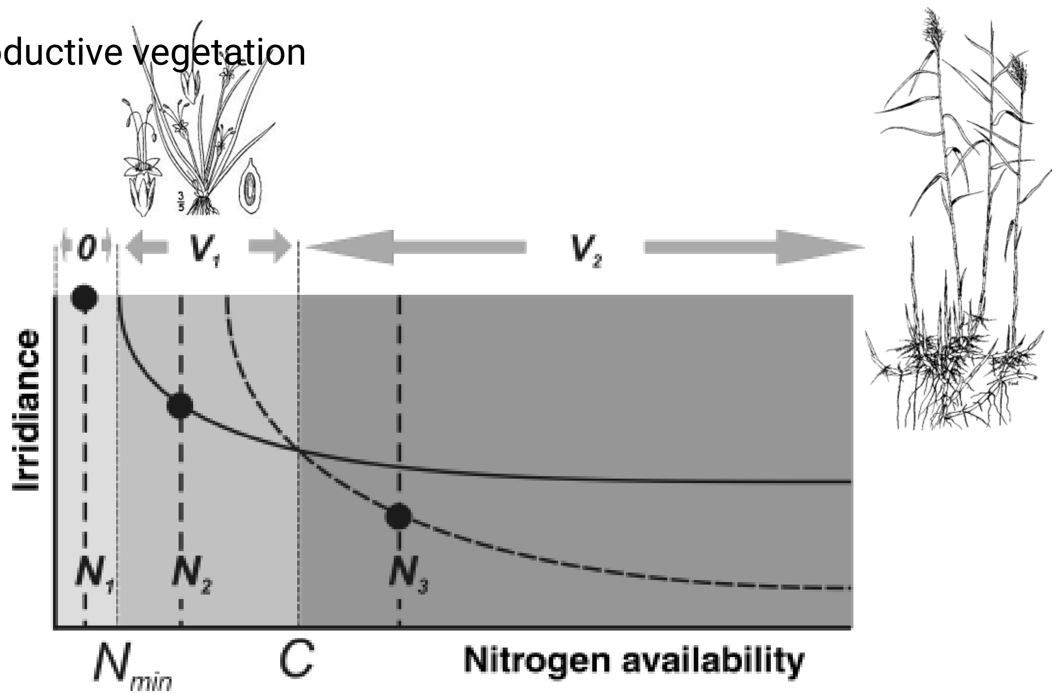
Enhanced nitrogen loss may explain alternative stable states in dune slack succession

Erwin B. Adema, Johan Van de Koppel, Harro A. J. Meijer, Ab P. Grootjans

Low productive vegetation



High productive vegetation

three different nitrogen input levels

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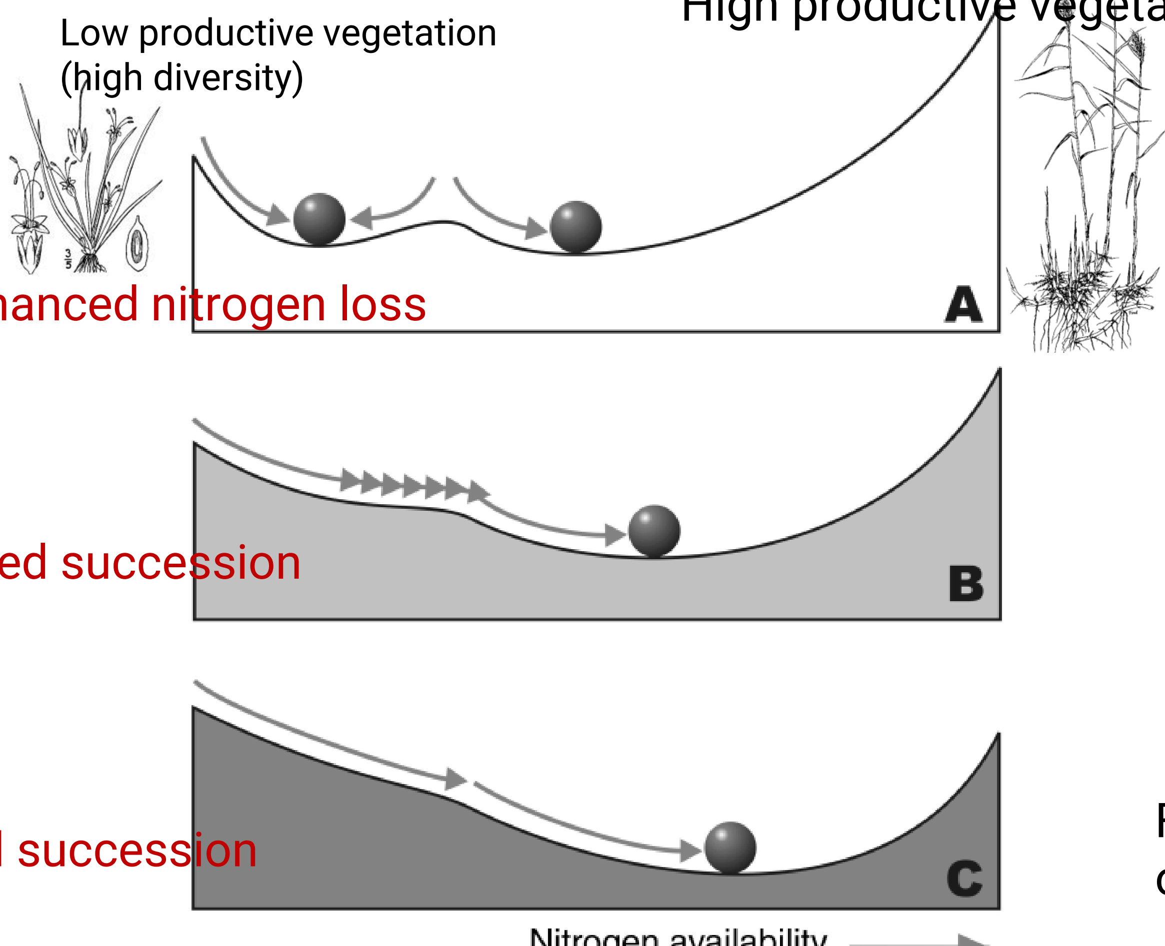

undisturbed conditions
(low N, high water table)

Increasing N deposition

Further increase in N
or decrease in water table

Tilman's competition for resources - PROBLEMS

- Holds only if the competition for resource is symetrical (resource exploitation is proportional to individual biomass), but this is often not the case (e.g. plants competing for light)

- Only a limited evidence for this mechanism explaining species coexistence in natural communities

Neutral theory: demographic stochasticity and dispersal limitation can be more important than functional differences among species for generating community patterns (Hubbell 2005)

Species similarities, not differences, explain the high diversity of many natural communities

Why is competitive exclusion is rarely observed in nature?

Niche mechanisms
Intraspecific > interspecific competition

Resource partitioning (Tilman)

Differential responses to spatial and temporal environmental variation (storage effect, Chesson)

Species–specific natural enemies (Janzen, Connell)

Non-niche mechanisms
equal opportunities for all species to succeed

Neutral theory (Hubbel)

Phenotype similarity (Chesson)

Disturbances (Chesson, Fox)

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⇨ **Modern Coexistence Theory**

Modern Coexistence Theory

Niche mechanisms alone cannot ensure stable coexistence

Niche and neutral processes are not mutually exclusive but complementary

Peter Chesson

Modern Coexistence Theory

commentary

TREE vol. 6, no. 1, January 1991

A Need for Niches?

Peter Chesson

Annu. Rev. Ecol. Syst. 2000. 31:343–66

Mechanisms of Maintenance of Species Diversity

Peter Chesson

The Roles of Harsh and Fluctuating Conditions in the Dynamics of Ecological Communities

Peter Chesson, Nancy Huntly

American Naturalist, Volume 150, Issue 5 (Nov., 1997), 519-553.

vol. 166, no. 4 The American Naturalist October 2005

E-Article

Examining the Relative Importance of Spatial and Nonspatial Coexistence Mechanisms

Robin E. Snyder,[1,*] Elizabeth T. Borer,[2,†] and Peter Chesson[3,‡]

Modern Coexistence Theory

Niche mechanisms alone cannot ensure stable coexistence

Niche and neutral processes are not mutually exclusive but complementary

Peter Chesson

species coexistence is facilitated by

1. **stabilizing mechanisms** (reduce niche overlap and lead to niche differenciation, species limiting themselves more than they limit others)

2. **equalizing mechanisms** (reducing fitness differences among species, balance species' competitive abilities)

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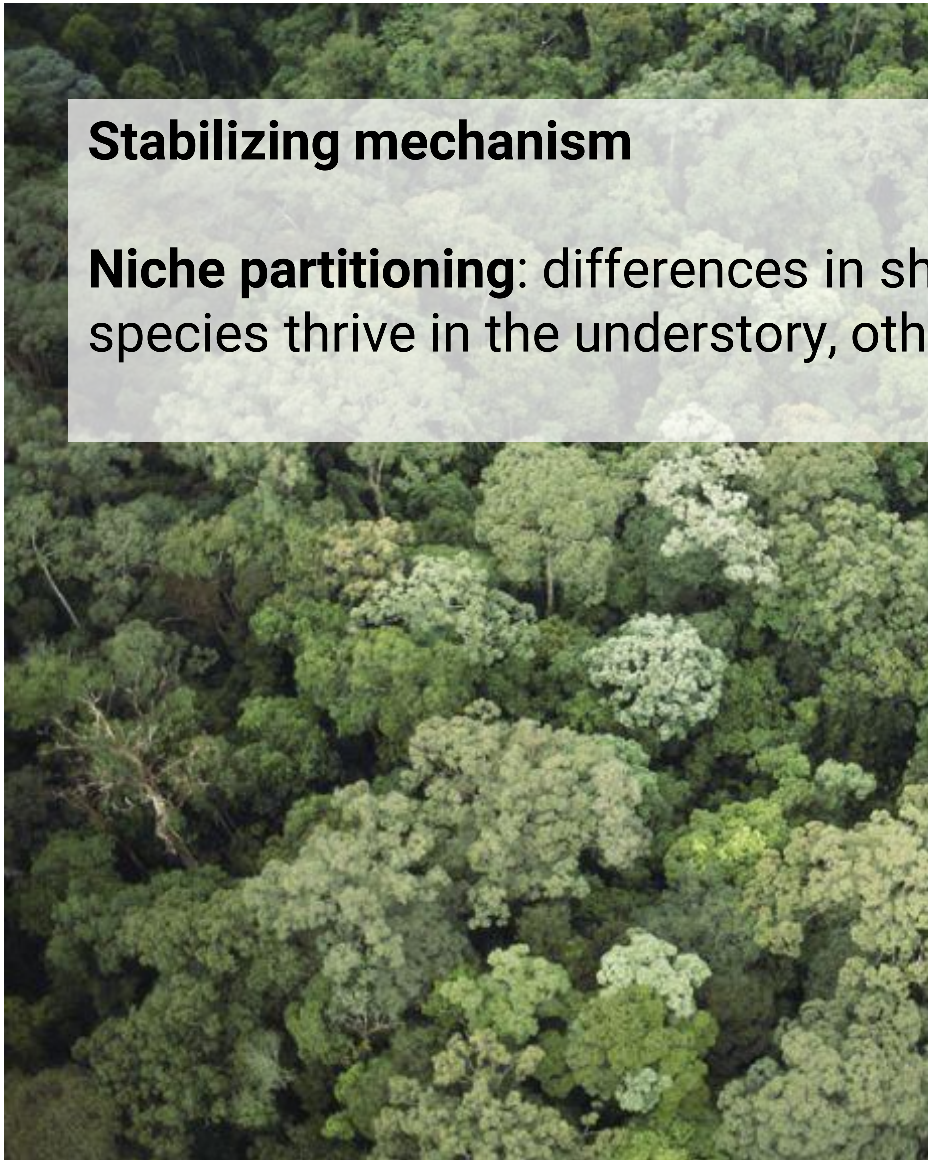
1. **stabilizing mechanisms** (reduce niche overlap and lead to niche differenciation, species limiting themselves more than they limit others)

2. **equalizing mechanisms** (reducing fitness differences among species, balance species' competitive abilities)

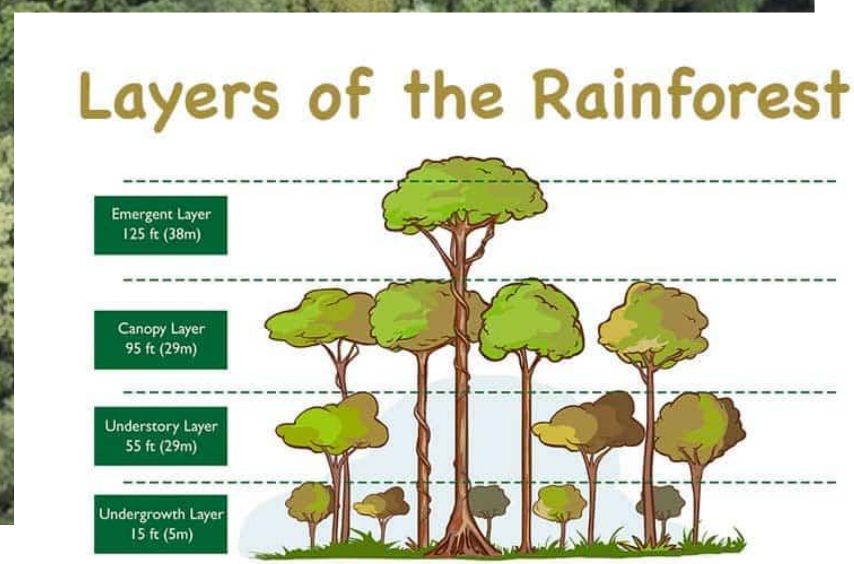
They cannot lead to stable coexistence in the long run, but increase the time span over which one species can outcompete other one

Modern Coexistence Theory



Stabilizing mechanism

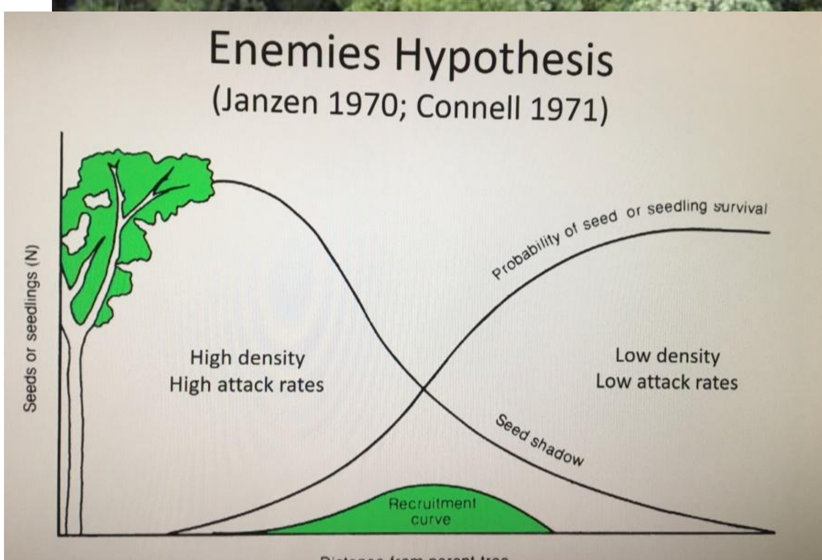
Niche partitioning: differences in shade tolerance (some species thrive in the understory, others prefer the canopy)

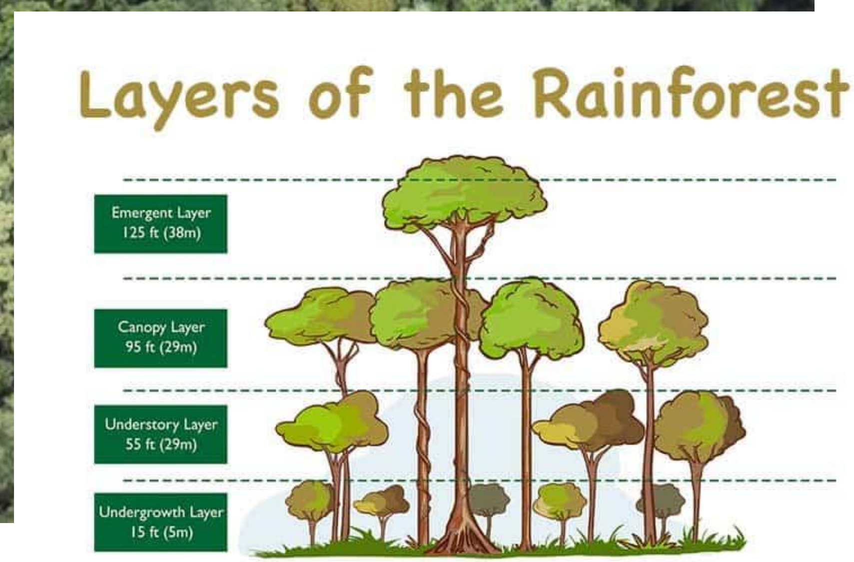


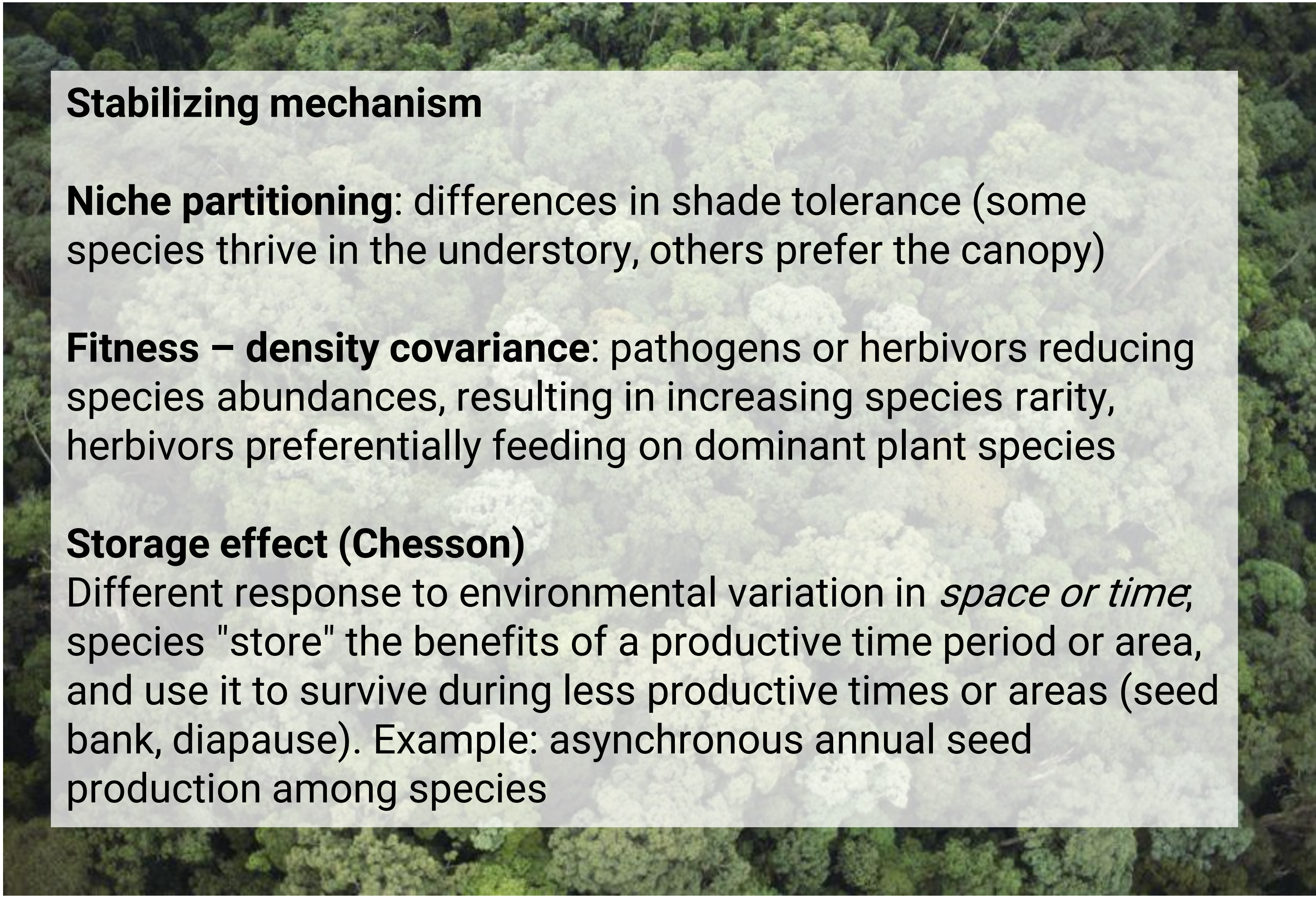
Stabilizing mechanism

Niche partitioning: differences in shade tolerance (some species thrive in the understory, others prefer the canopy)

Fitness – density covariance: pathogens or herbivors reducing species abundances, resulting in increasing species rarity, herbivors preferentially feeding on dominant plant species







Stabilizing mechanism

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Storage effect (Chesson)
Different response to environmental variation in *space or time*; species "store" the benefits of a productive time period or area, and use it to survive during less productive times or areas (seed bank, diapause). Example: asynchronous annual seed production among species

Storage effect (Chesson)

Three conditions for species coexistence:

1) Covariance between environment and competition intensity

2) species-specific environmental responses (differences in species response to the same environment)

3) Buffered population growth (the ability of a population to diminish the impact of competition under worsening environment)

Desert annual plants

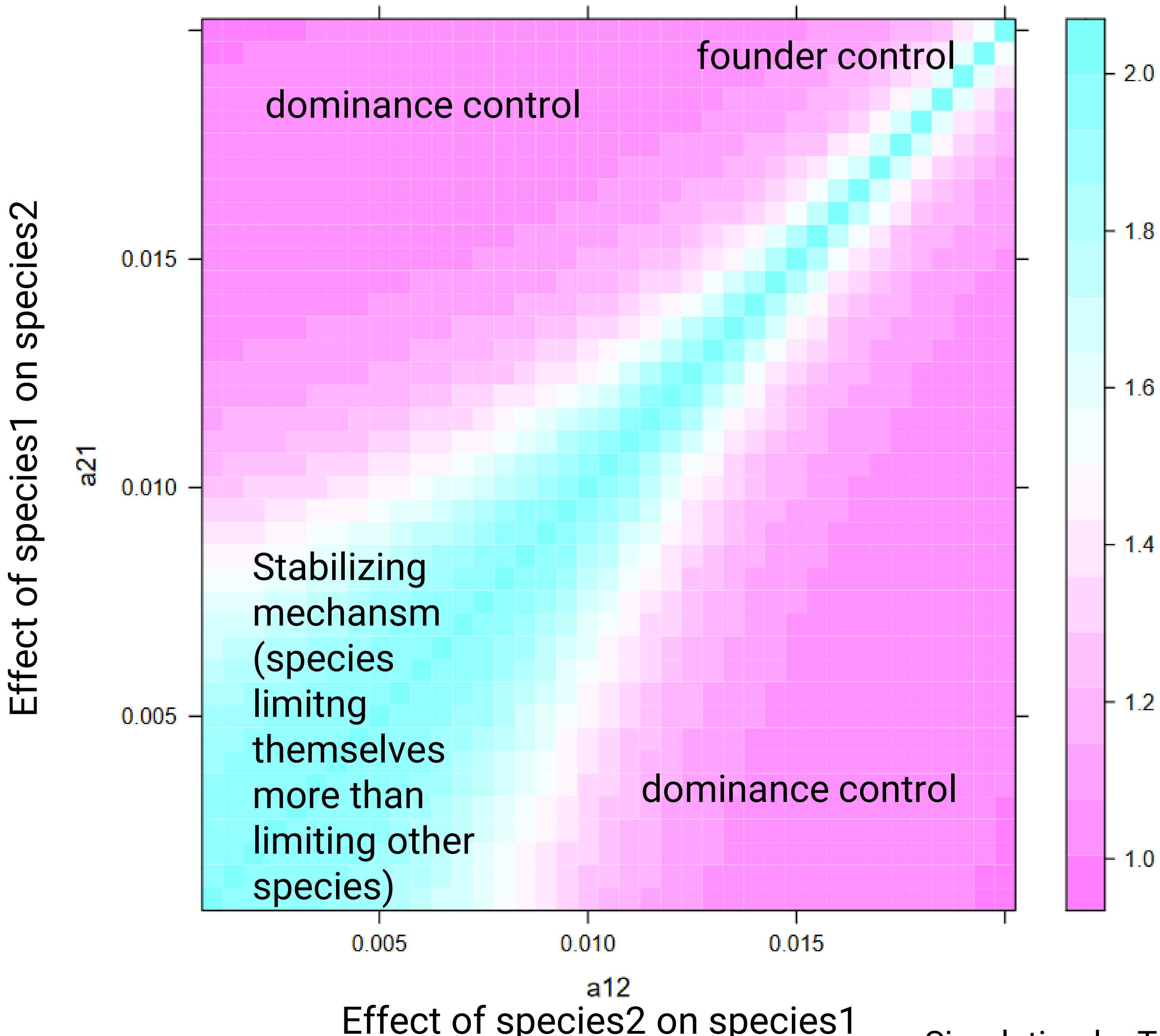
Modern Coexistence Theory

Equalizing mechanism

Anything that reduces fitness of all species equally

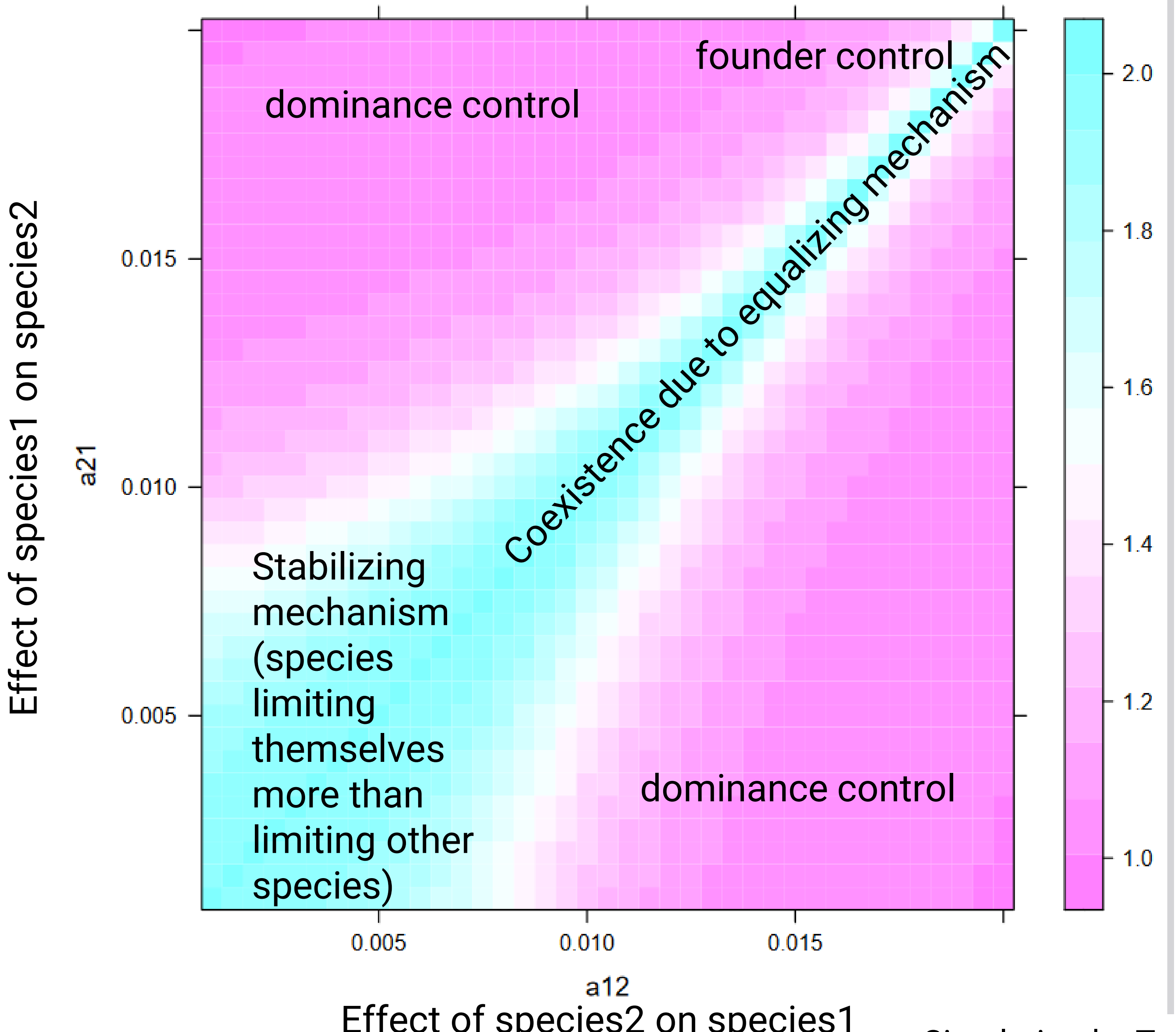
Disturbances or **harsh environment** reducing growth rates of all species

EQUALIZING MECHANISM IN LOTKA-VOLTERRA SYSTEM



Simulation by Tomas Herben

EQUALIZING MECHANISM IN LOTKA-VOLTERRA SYSTEM



Simulation by Tomas Herben

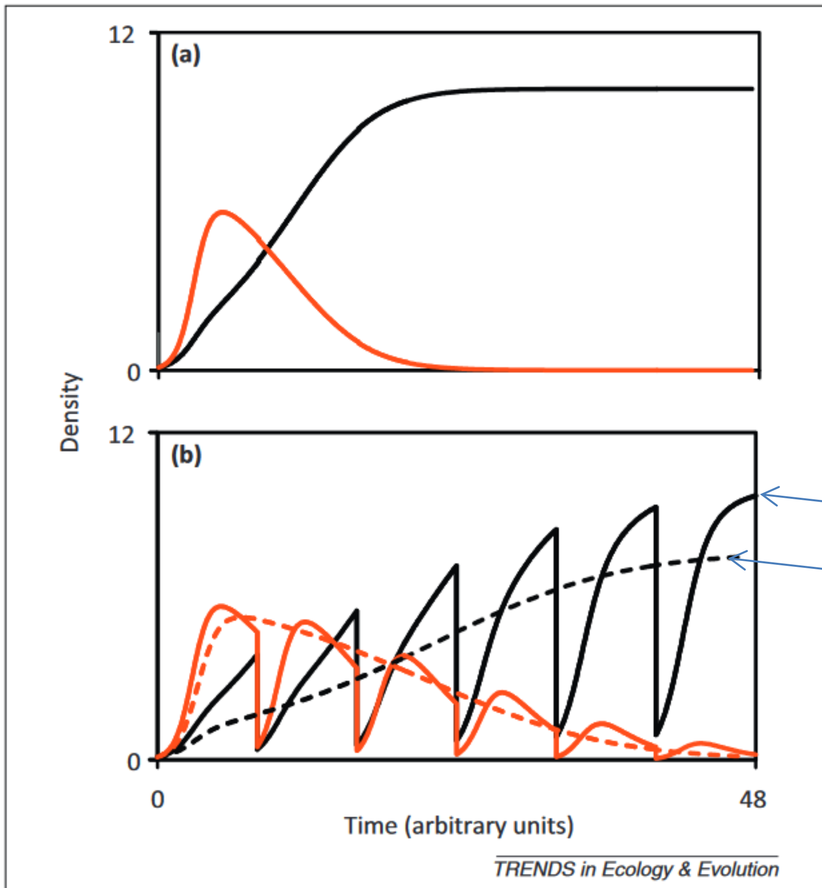
Opinion

CASE STUDIES

Cell PRESS

The intermediate disturbance hypothesis should be abandoned

Jeremy W. Fox



Disturbances slow exclusion by increasing average mortality rate, NOT by interupting competitive exclusion - **equalizing effect**

dN/dt with periodic disturbance

density-independent mortality rate

Opinion

CASE STUDIES

Cell PRESS

The intermediate disturbance hypothesis should be abandoned

Jeremy W. Fox

Disturbances can be **stabilizing** when they preferentially reduce the dominant species (harvest of the superior competitor, herbivors affecting the dominant), so that rare species can increase in abundances

CASE STUDIES

ECOLOGY LETTERS

Full Access

A niche for neutrality

Peter B. Adler, Janneke HilleRisLambers, Jonathan M. Levine

First published: 08 January 2007 | https://doi.org/10.1111/j.1461-0248.2006.00996.x | Citations: 771

Does the diversity in natural communities result from strong stabilizing mechanisms (niches) or weak stabilization operating on species of similar fitness (neutrality)?

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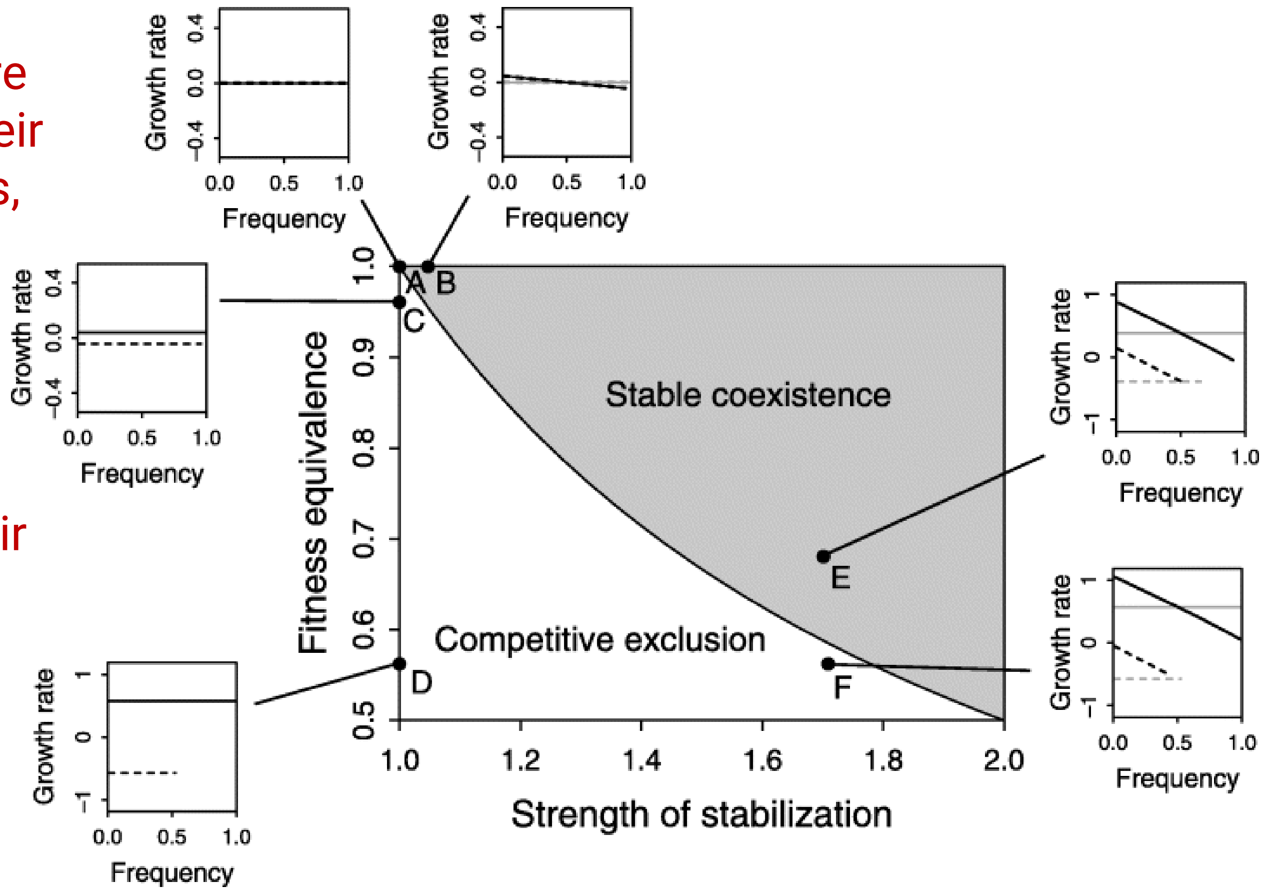
If species are similar in their growth rates, even small niche differences (stabilizing force) can stabilize their coexistence



Large niche differences are needed if differences in growth rates are high

CASE STUDIES

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These two forces interact:
If species are similar in their growth rates, even small niche differences (stabilizing force) can stabilize their coexistence. In contrast, large niche differences are needed if differences in growth rates are high.

SUMMARY

Species coexistence is possible if:

Intraspecific competition > Interspecific competition (species increase when rare and decline when common**)**

Species are limited by different resources (Intra>Inter)

Species are different in their niches OR similar in their fitness; these two forces interact