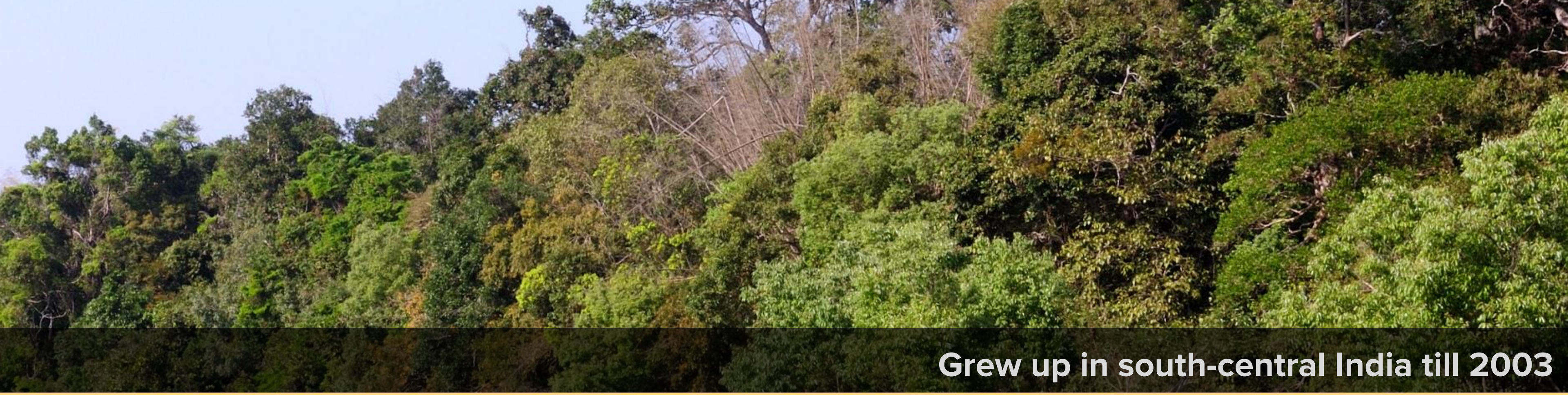
# Plant species coexistence in variable landscapes

## the consequences of plant traits and soil microbes

**Gaurav S. Kandlikar**

19 September 2017

Committee: Dr. Nathan Kraft (Advisor)
Dr. Jennifer Martiny, Dr. Lawren Sack, Dr. Felipe Zapata


Grew up in south-central India till 2003

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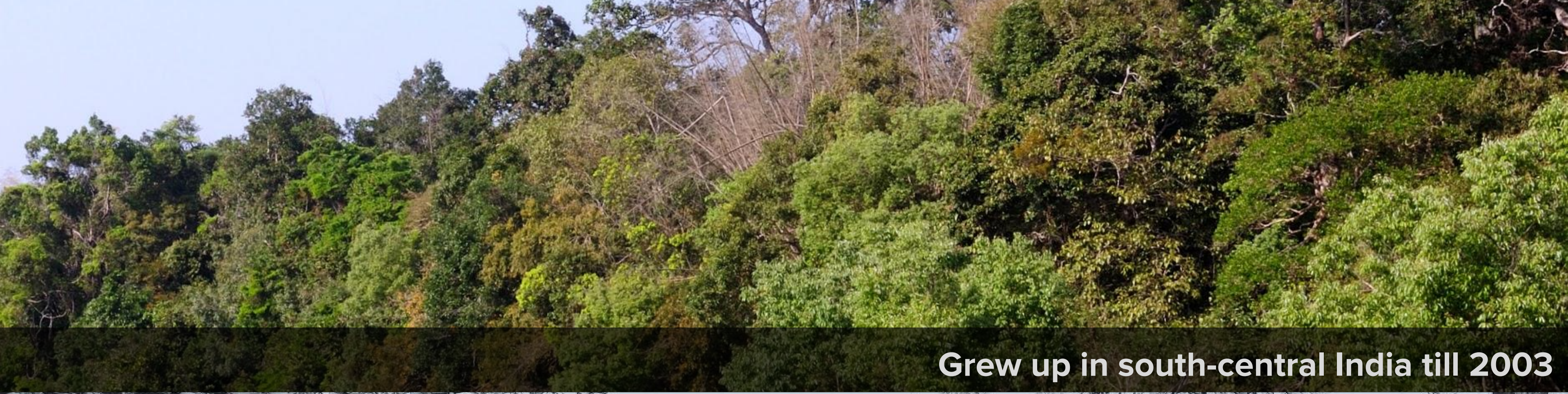
BS in Ecology, Evolution & Behavior/Plant Biology, Univ. Minnesota, 2010-13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M
PhD student w/ Nathan Kraft, Univ. Maryland 2014-15

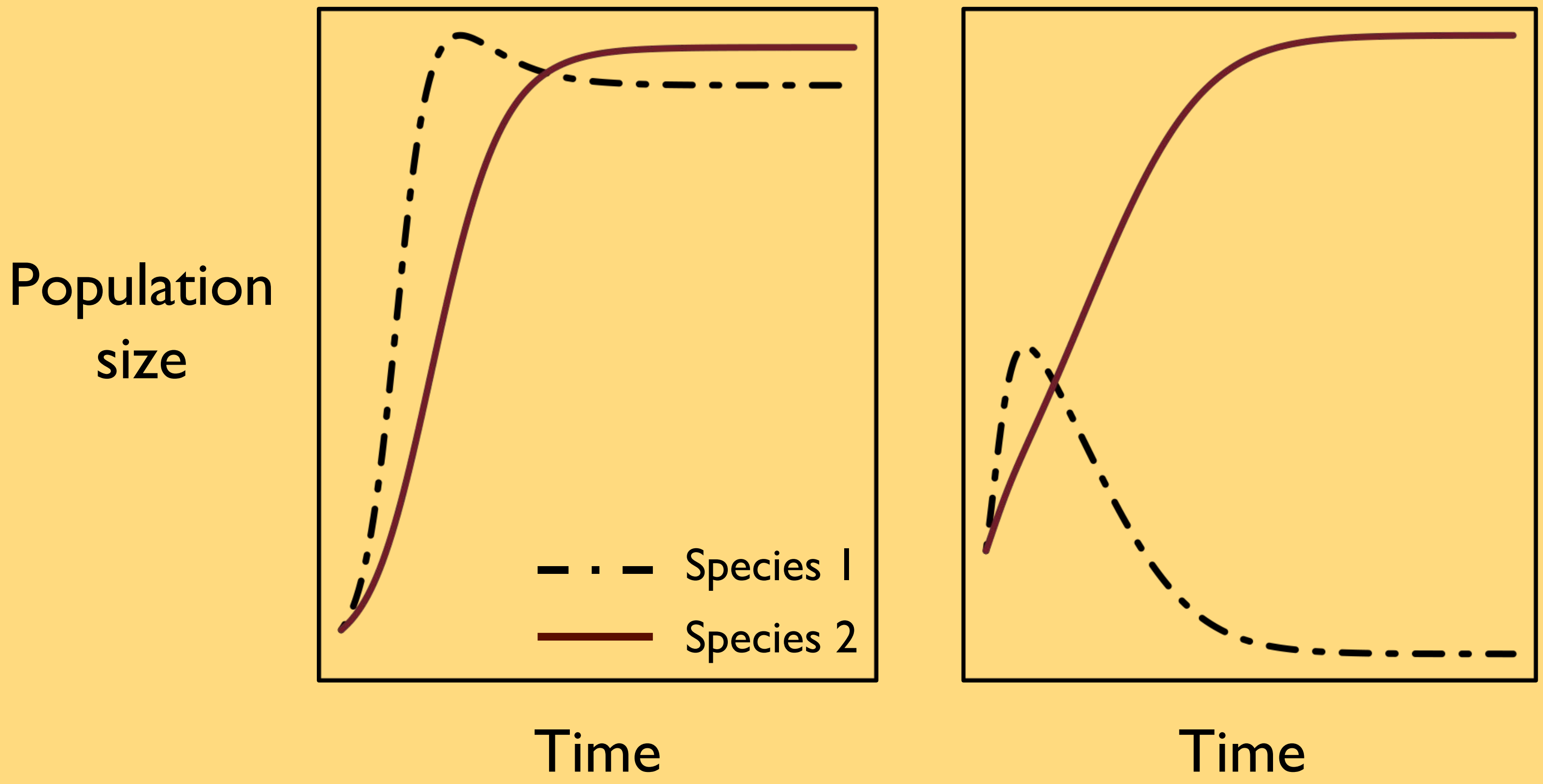

image: https://www.flickr.com/photos/rejik/
Kabani River, Kerala, India


image: https://www.flickr.com/photos/14723335@N05/

**Plant ecologists lack a clear understanding of how some fundamental ecological processes structure communities**

Environmental variation
Interactions between species
Variation between individuals
Feedbacks between plants and soil microbes

# In Lotka-Volterra competition, coexistence is an outcome of interspecific interaction parameters (α)



# Modern coexistence theory frames coexistence as an outcome of two types of differences between species

**Fitness differences**

Confer one species a density-independent competitive advantage

E.g. susceptibility to generalist predator

Promote competitive exclusion

Chesson 2000 AREES

# Modern coexistence theory frames coexistence as an outcome of two types of differences between species

**Fitness differences**

Confer one species a density-independent competitive advantage

E.g. susceptibility to generalist predator

Promote competitive exclusion

**Stabilizing niche differences**

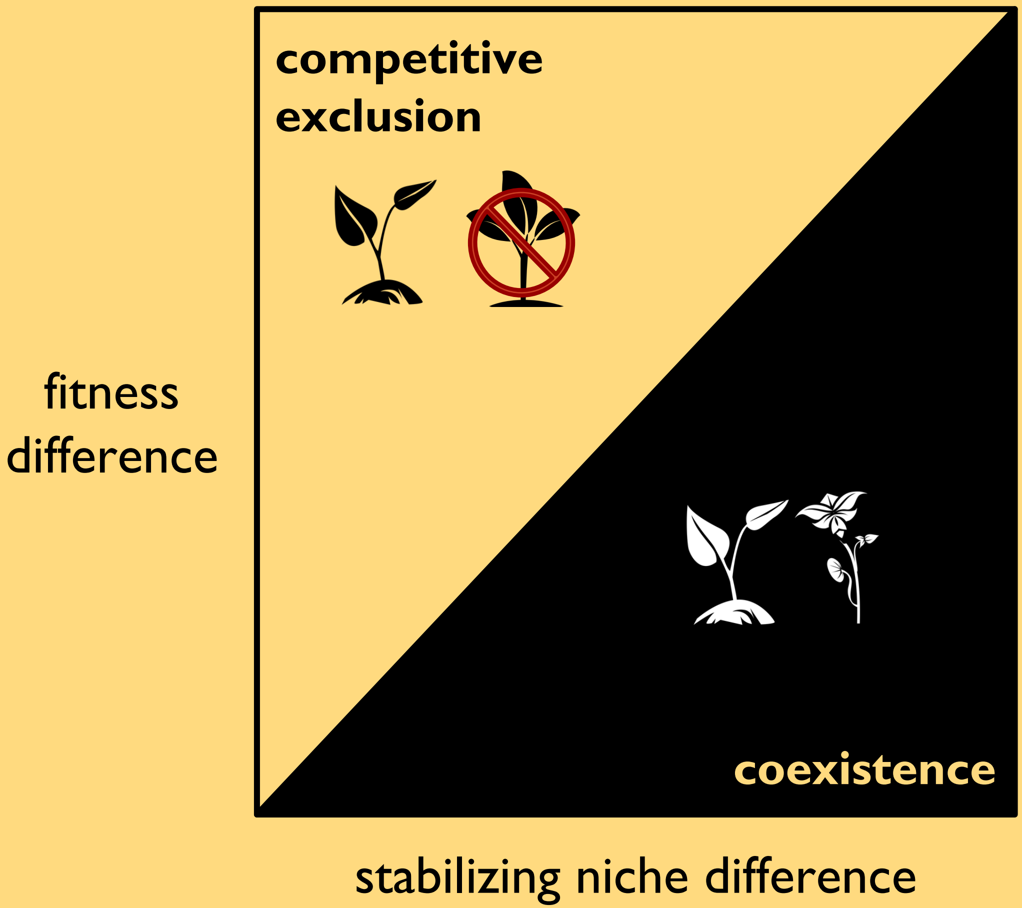
Confer each species a competitive advantage when rare

E.g. differences in timing of resource use

Promote coexistence

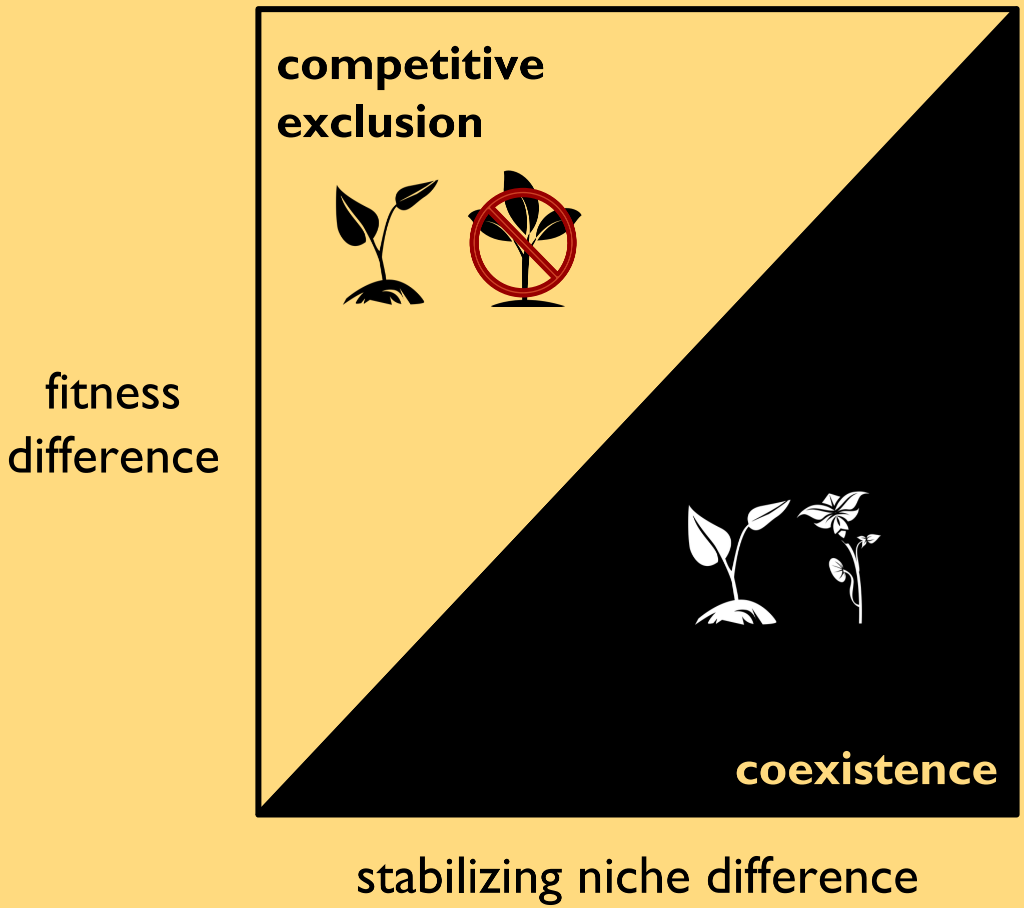
Chesson 2000 AREES

# Species can coexist when stabilizing niche differences overcome fitness differences



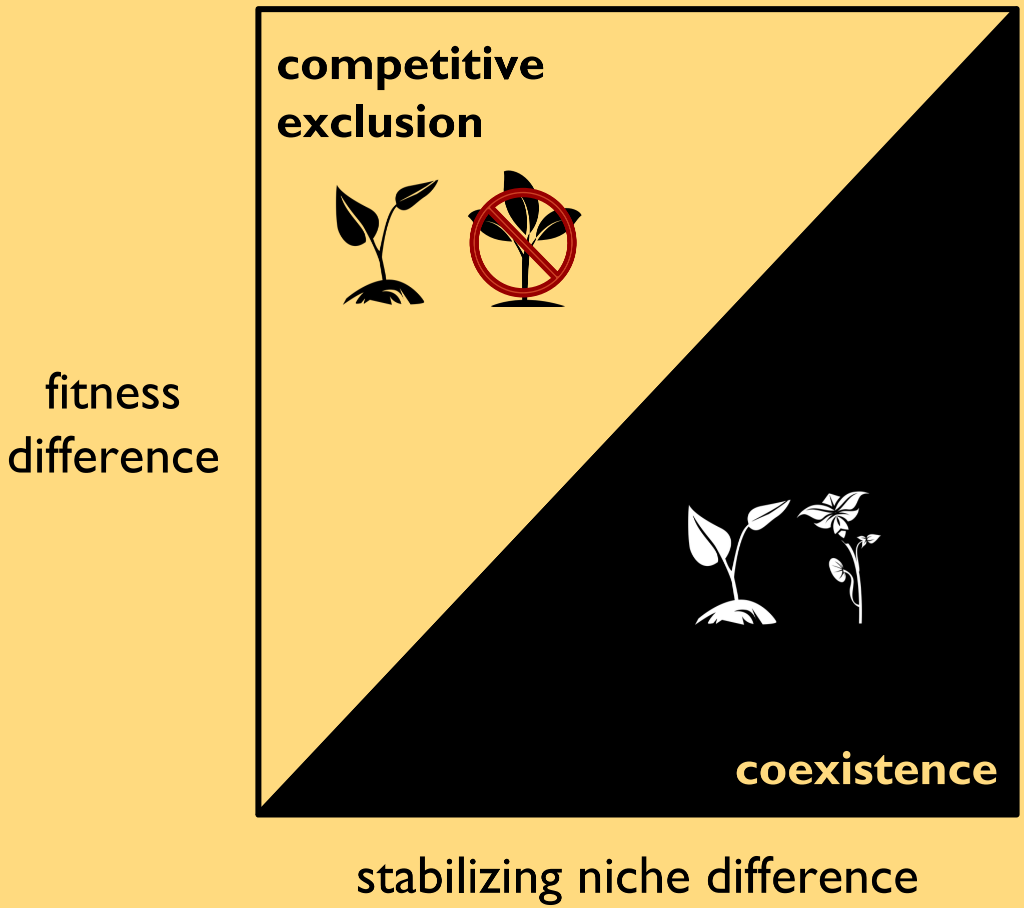

Adler et al. 2007 Ecol. Letters

# What determines the magnitude of fitness and niche differences?




Adler et al. 2013 Ecol. Letters

# What determines the magnitude of fitness and niche differences?

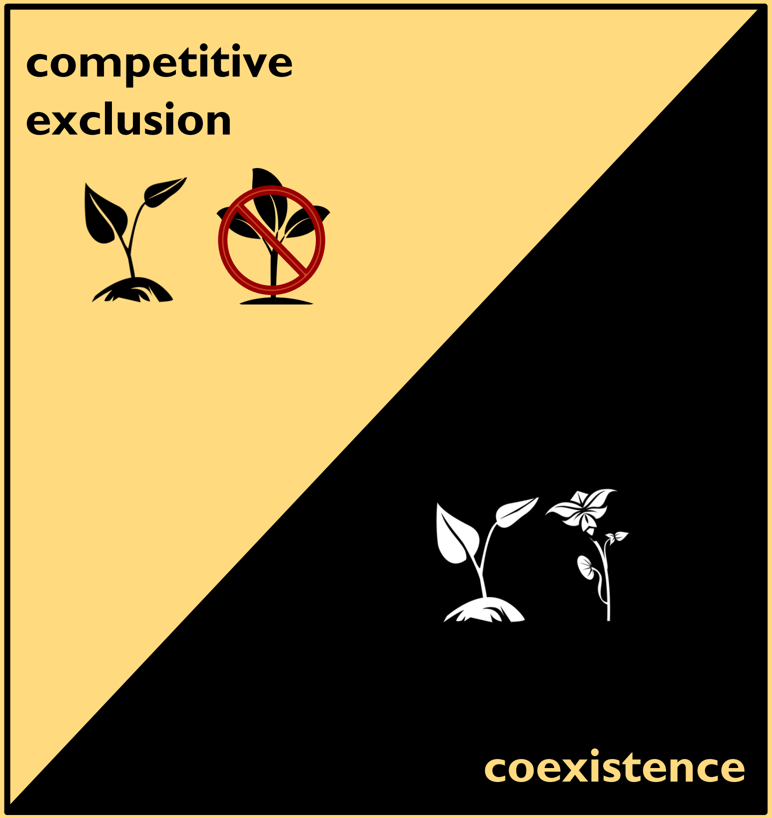



Species ecological strategies

Adler et al. 2013 Ecol. Letters

# What determines the magnitude of fitness and niche differences?

fitness difference




stabilizing niche difference

Species ecological strategies

Intra-specific variation in functional traits

Turcotte & Levine 2016 TREE

# What determines the magnitude of fitness and niche differences?

fitness difference


stabilizing niche difference

Species ecological strategies

Intra-specific variation in functional traits

Plant interactions with soil microbial communities

Chesson & Kuang 2008 Nature; Bever et al. 2015 AREES

# Dissertation Questions

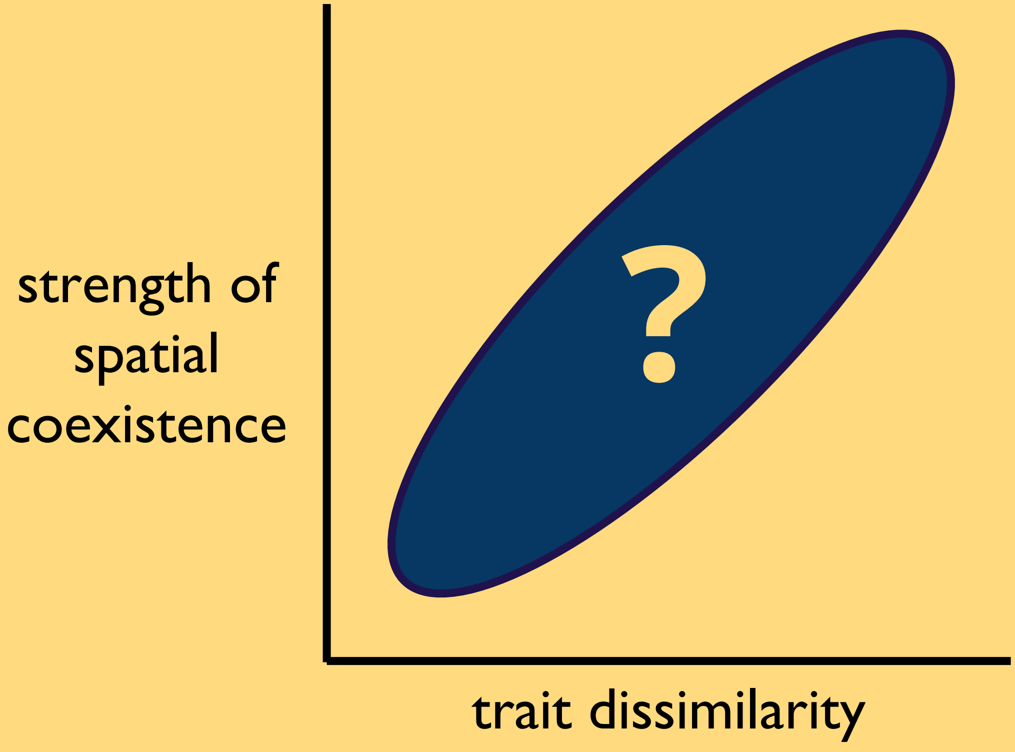
1. How do differences in species functional traits relate to spatial drivers of coexistence?

2. How does intra-specific trait variation influence the outcome of competitive interactions?

3. How can we jointly consider the consequences of resource competition and plant-microbe interactions in a unified framework?

# Chapter 1

How do functional traits shape plant demographic responses to heterogeneous environments?



# Spatial environmental variation can promote coexistence of species with decoupled environmental responses

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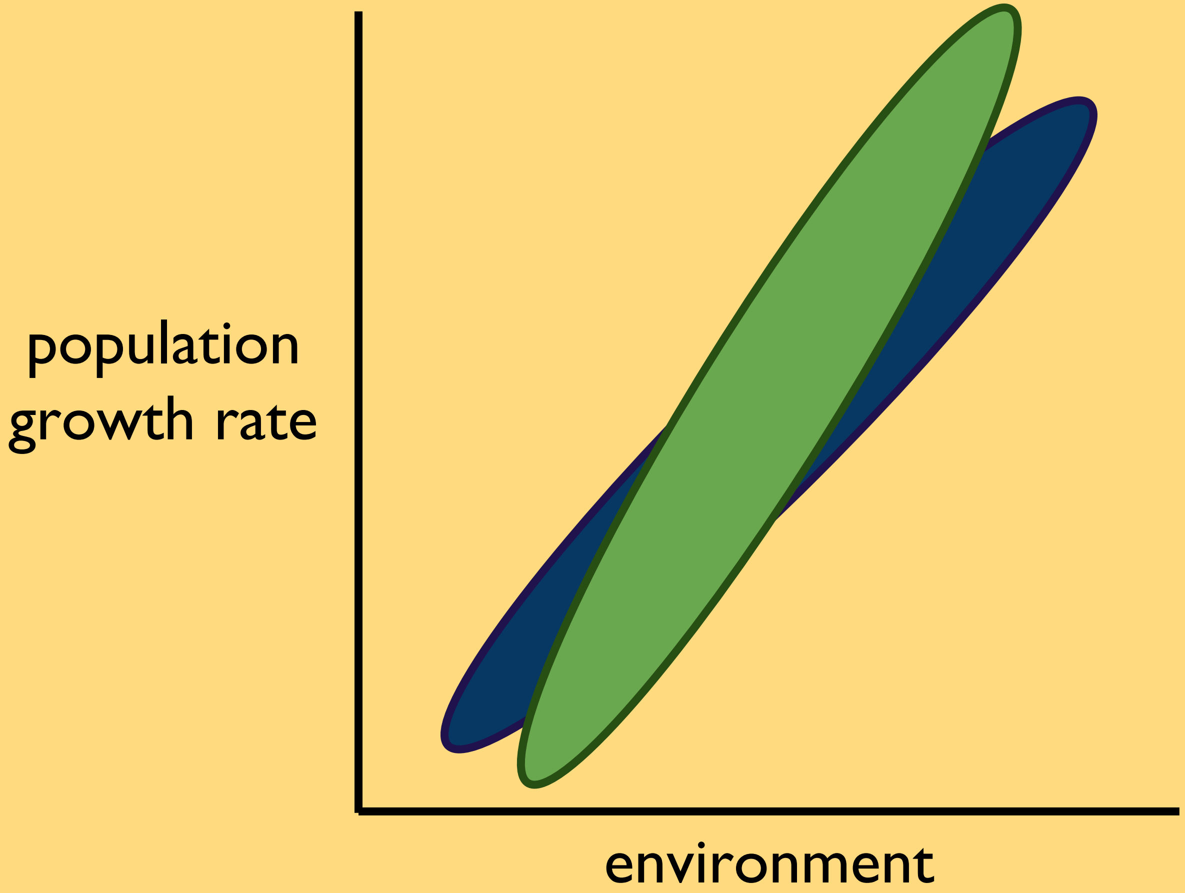
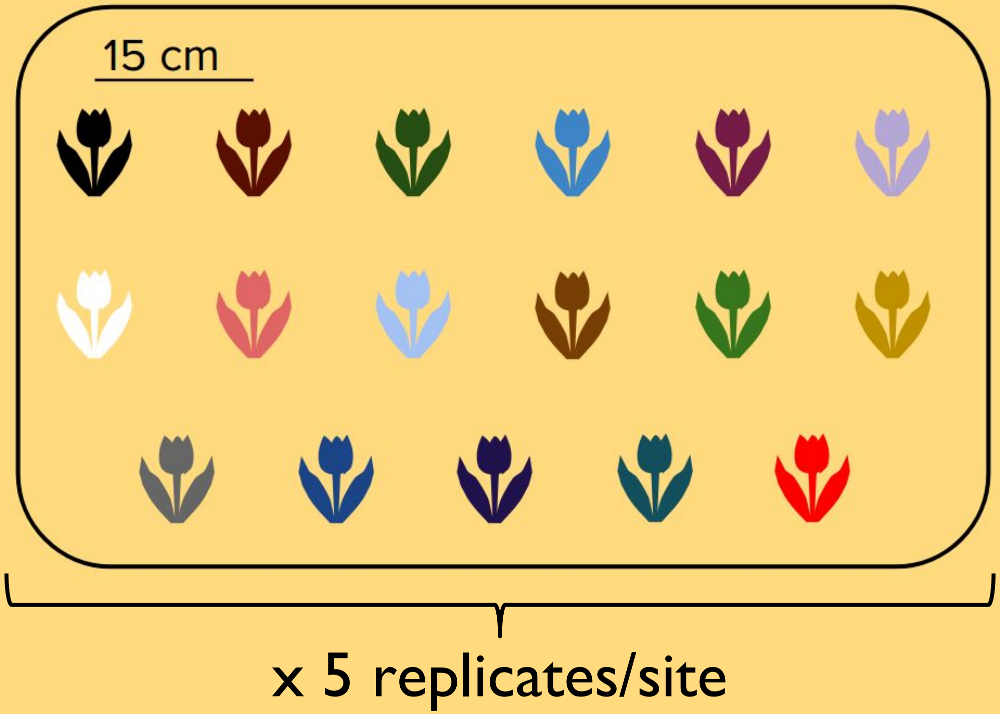


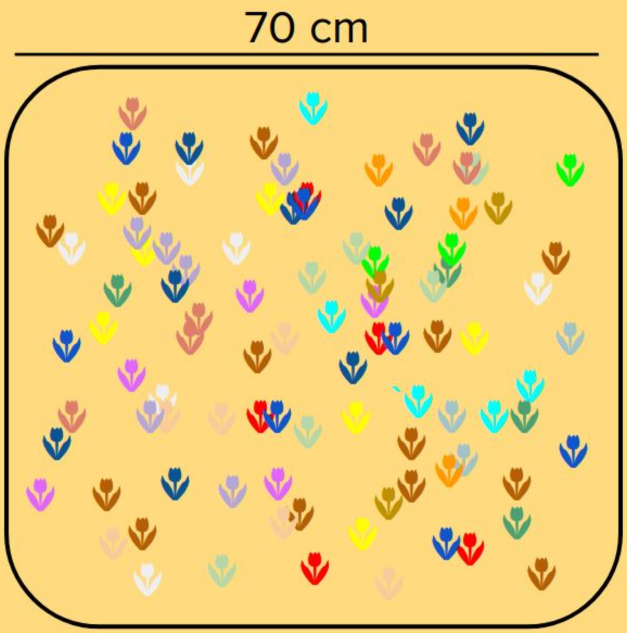
# Spatial environmental variation can promote coexistence of species with decoupled environmental responses

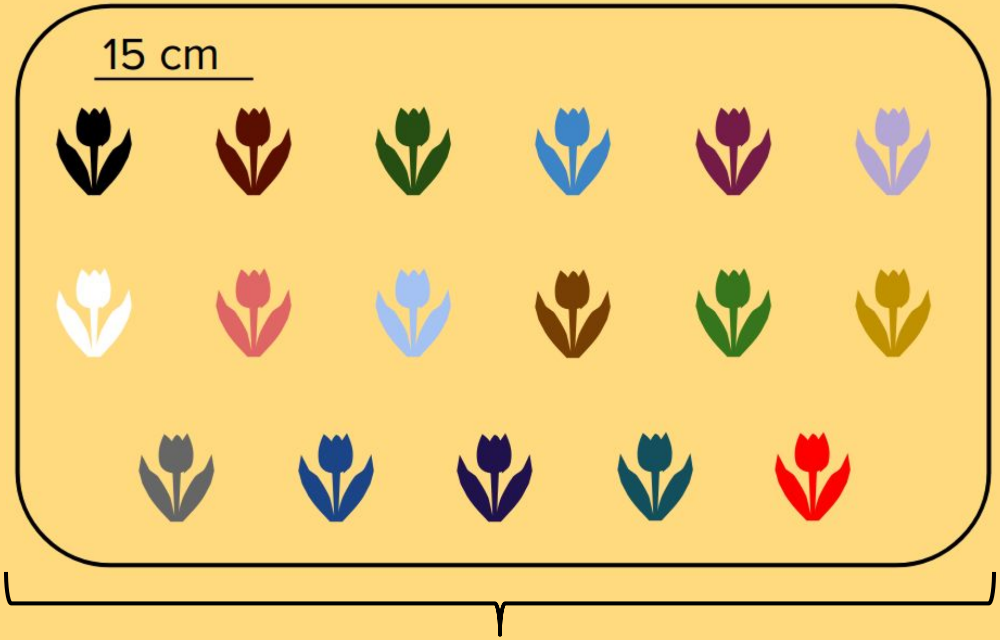
# Chapter questions

1. Which environmental factors drive variation in species responses to spatial heterogeneity?

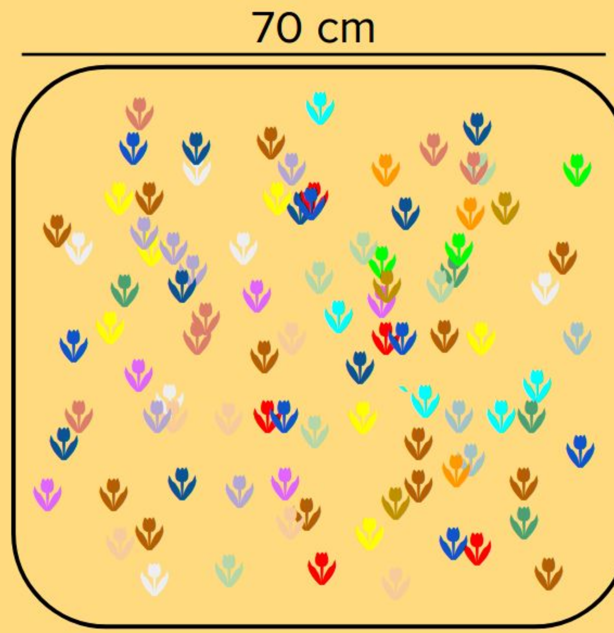
2. Which functional traits mediate species responses to the environmental drivers?


15 cm
x 5 replicates/site


70 cm

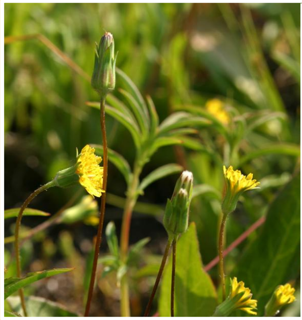



x 5 replicates/site




$$\frac{N_{t+1,j,x}}{N_{t,j,x}} = \overbrace{(1-g_{j,x}) * s_j}^{seedbank\ survival} + \frac{\overbrace{g_{j,x} * \lambda_{j,x}}^{\substack{germiation\ rate\ \& \\ per-germinant\ fecundity}}}{\underbrace{1 + r_{j,x} * \eta_x}_{\substack{sensitivity\ to\ competitors\ \& \\ number\ of\ competitors\ faced}}}$$

# chapter 1 background


*Uropappus lindleyi*


*Centaurea melitensis*


*Chaenactis glabriuscula*


*Lasthenia californica*


*Hemizonia congesta*


*Micropus californicus*


*Amsinckia menziesii*


*Clarkia purpurea*


*Clarkia bottae*


*Euphorbia peplus*


*Medicago polymorpha*


*Acmispon wrangelianus*


*Bromus madritensis*

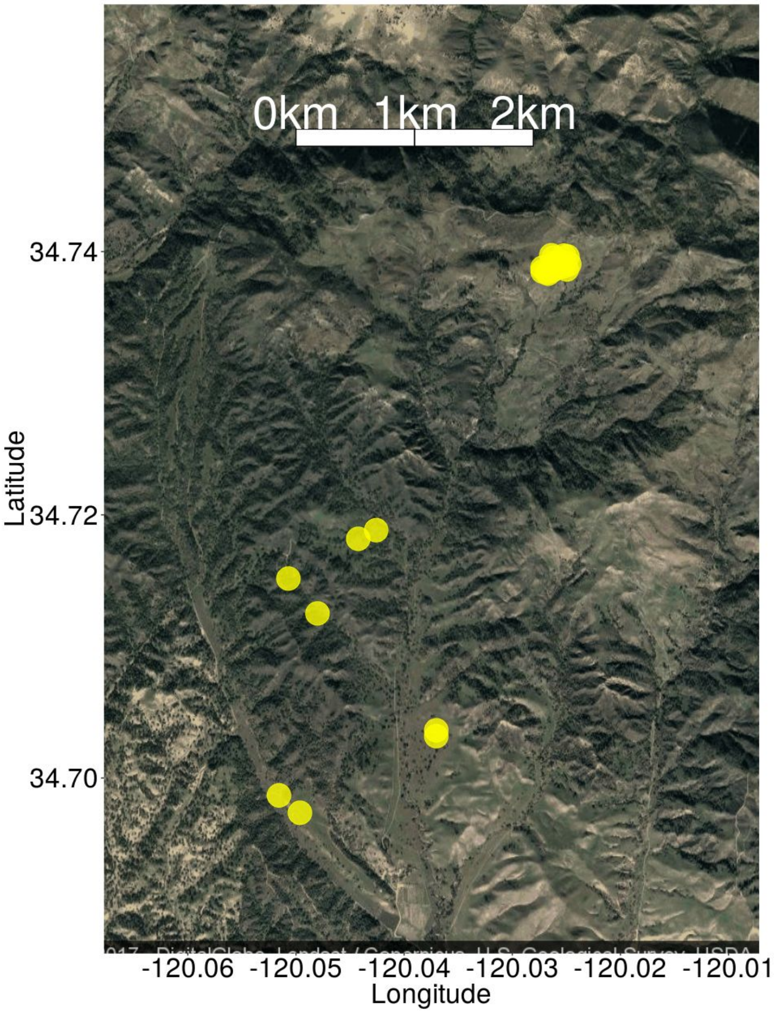

*Hordeum murinum*


*Vulpia microstachys*


*Salvia columbariae*


*Plantago erecta*

*Images from CalPhotos (http://calphotos.berkeley.edu/)*


0km 1km 2km
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34.72
34.70
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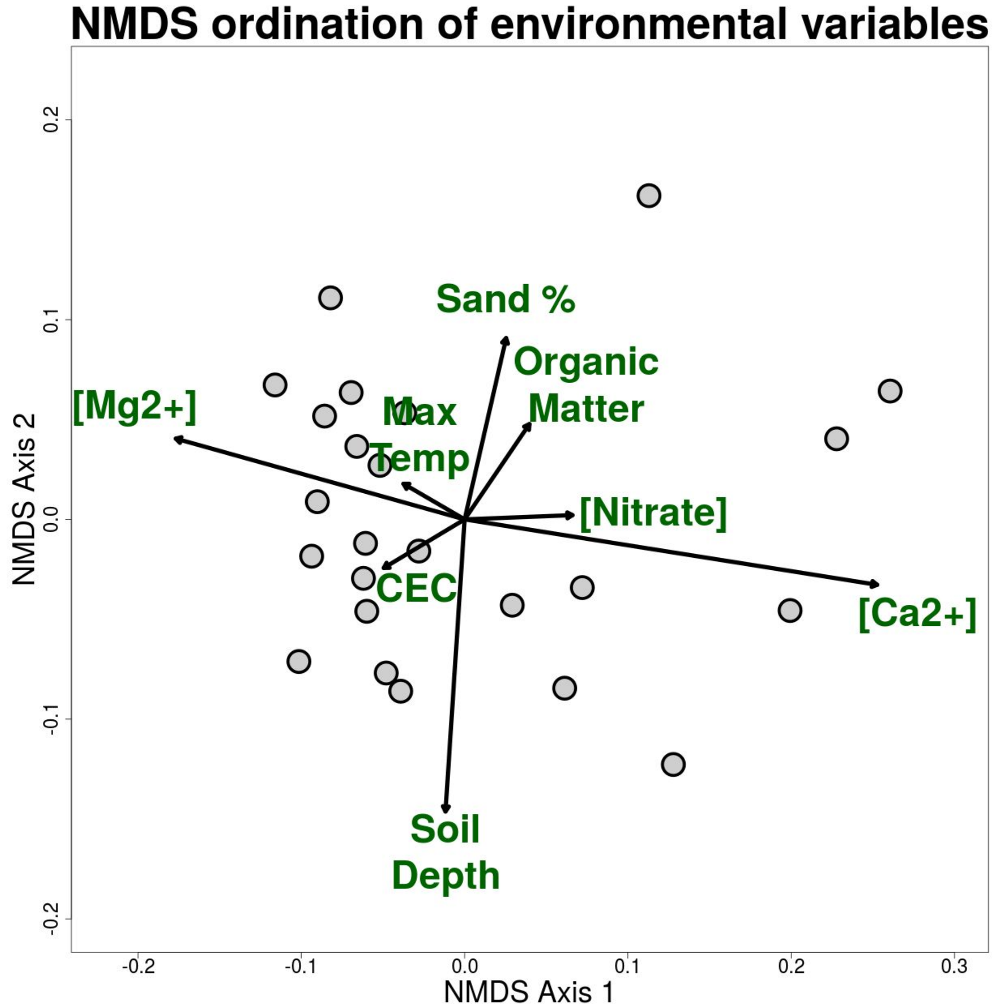
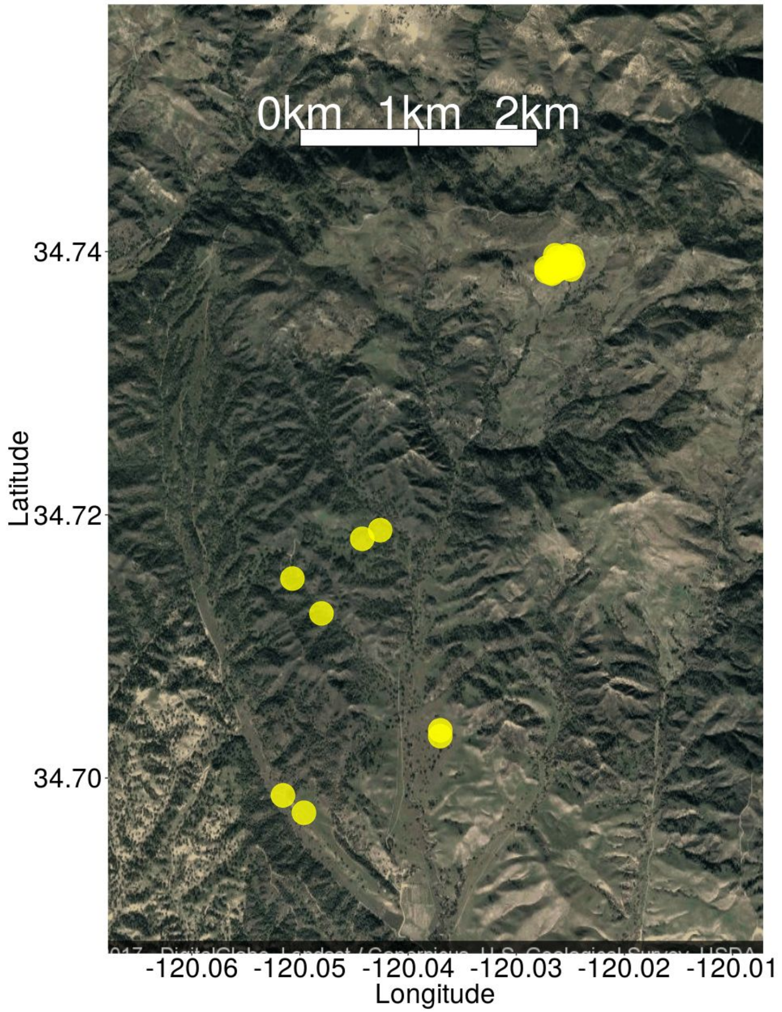
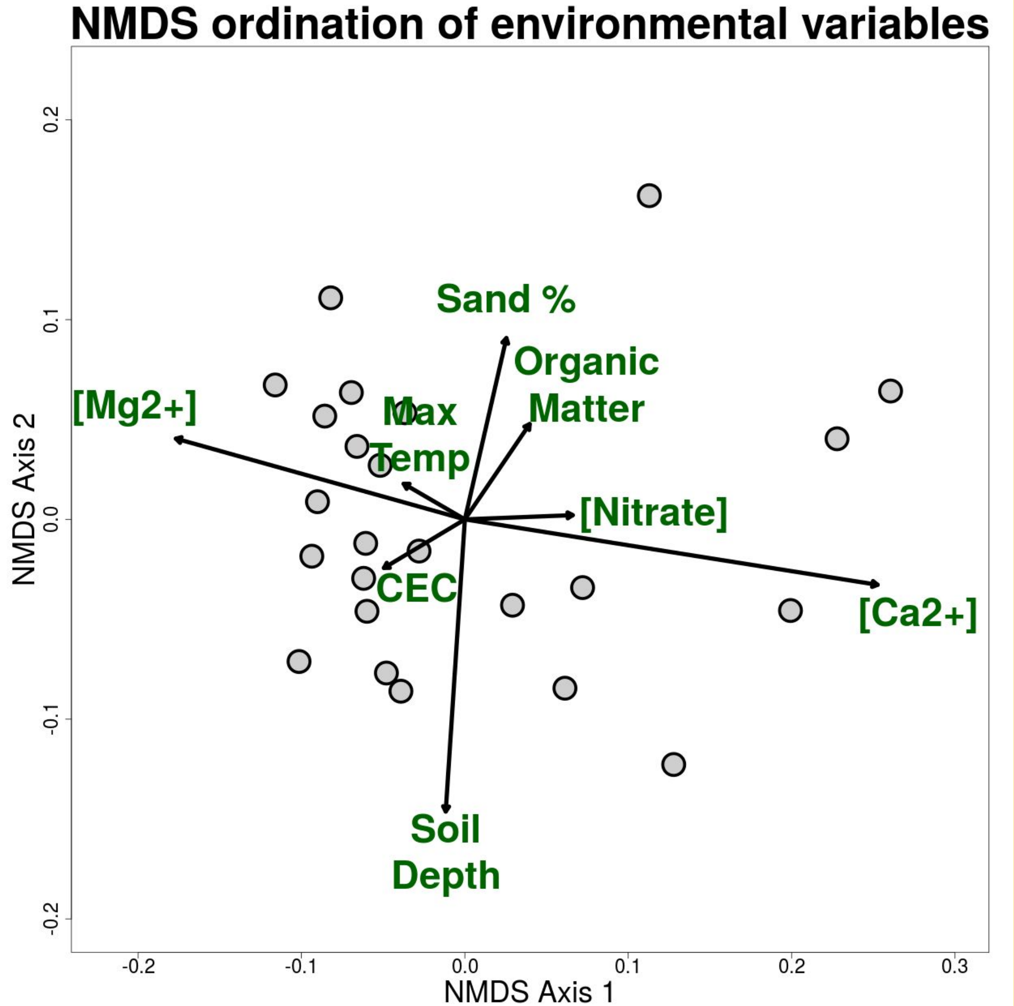
Longitude


NMDS ordination of environmental variables
Sand %
Organic Matter
[Mg2+]
Max Temp
[Nitrate]
CEC
[Ca2+]
Soil Depth
NMDS Axis 2
0.2
0.1
0.0
-0.1
-0.2
-0.2 -0.1 0.0 0.1 0.2 0.3
NMDS Axis 1

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+
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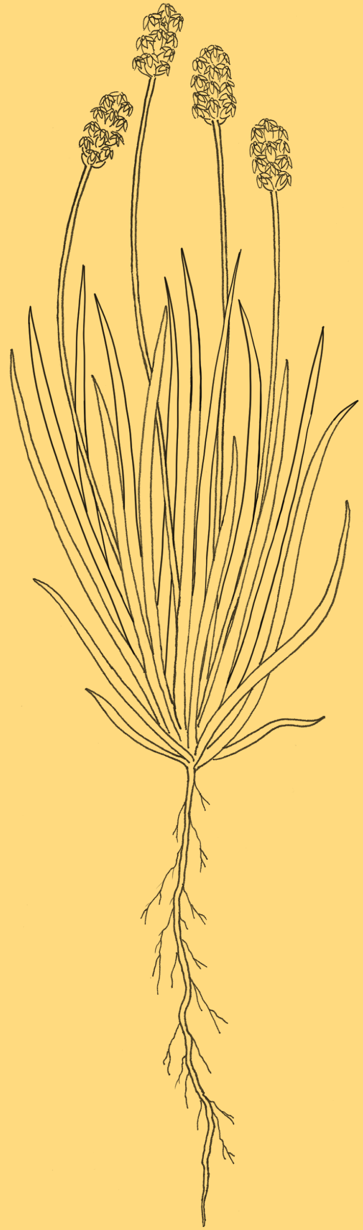
```

**Leaves**
Leaf size
Specific leaf area
Leaf dry matter content
$\delta\ C^{13}$ (Integrated WUE)
Leaf N concentration

*Leaf osmotic potential*

**Roots**
Specific root length
Rooting depth

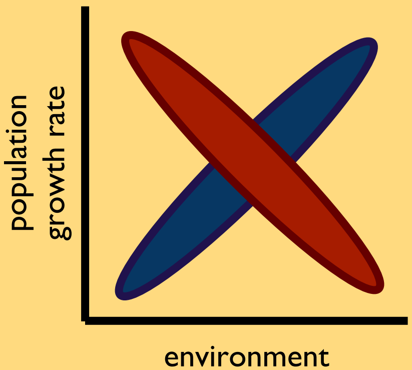


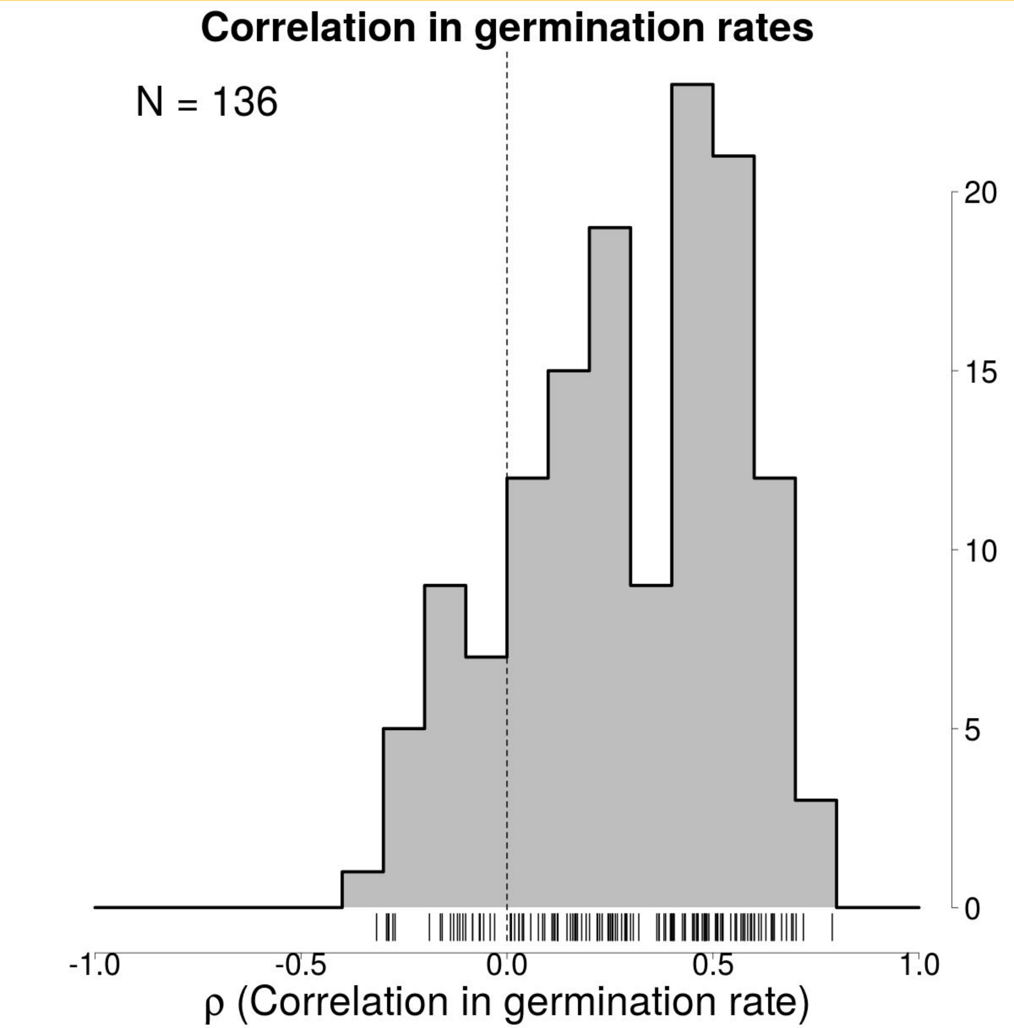
**Reproduction**
Seed mass
Fruiting phenology

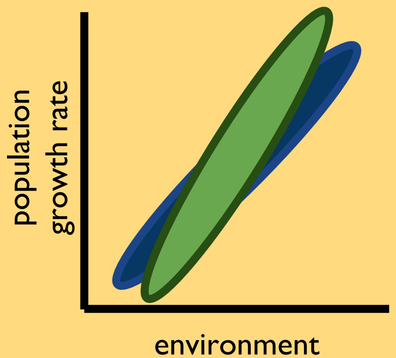
**Whole-plant**
Maximum height
Canopy shape index

Illustration of *Plantago erecta* by Joanna Shih (UCLA)

# Species pairs tend to have distinct demographic responses to environmental gradients



$$p_{i,j} \sim \overbrace{a_0}^{species\ effect} + \underbrace{a_1 z_j}_{trait\ effect} + \overbrace{b_0 x_i}^{environment\ effect} + \underbrace{b_1 z_j x_i}_{interaction} + \overbrace{\epsilon_{\alpha j} + \epsilon_{\beta i} + \gamma_i}^{error\ terms}$$

Jamil et al. 2012 J. Veg. Sci

# Q1: Which environmental factors drive variation in species responses to spatial heterogeneity?

$$p_{i,j} \sim \overbrace{a_0}^{species\ effect} + \underbrace{a_1 z_j}_{trait\ effect} + \boxed{\overbrace{b_0 x_i}^{environment\ effect}} + \underbrace{b_1 z_j x_i}_{interaction} + \overbrace{\epsilon_{\alpha j} + \epsilon_{\beta i} + \gamma_i}^{error\ terms}$$

Jamil et al. 2012 J. Veg. Sci

# Q2: Which functional traits mediate species responses to the environmental drivers?

$$p_{i,j} \sim \overbrace{a_0}^{species\ effect} + \underbrace{a_1 z_j}_{trait\ effect} + \overbrace{b_0 x_i}^{environment\ effect} + \boxed{\underbrace{b_1 z_j x_i}_{interaction}} + \overbrace{\epsilon_{\alpha j} + \epsilon_{\beta i} + \gamma_i}^{error\ terms}$$

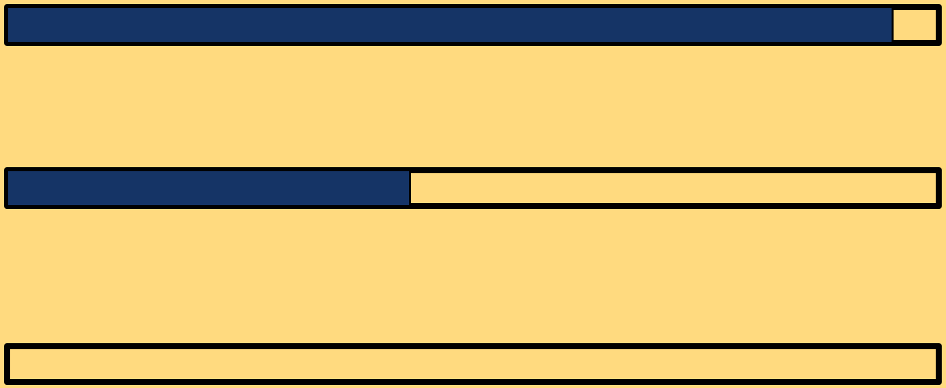
Jamil et al. 2012 J. Veg. Sci

# chapter I timeline

**Data collection**

**Analyses**

**Writeup**



## Projected timeline

Finish analysis of soil microbe sequence data: October 2017
Run GLMM models: October - November 2017
Start writing ms: November - December 2017
Collect leaf osmotic potential on grasses: March/April 2018
Finish writing ms: March-May 2018
**Submit MS: May 2018**

**Plant ecologists lack a clear understanding of how some fundamental ecological processes structure communities**

**Environmental variation**

**Interactions between species**

Variation between individuals

Feedbacks between plants and soil microbes

# Chapter 2

What is the nature of intra-specific trait variation and how does it influence species coexistence?

Individuals can vary substantially in their functional traits.

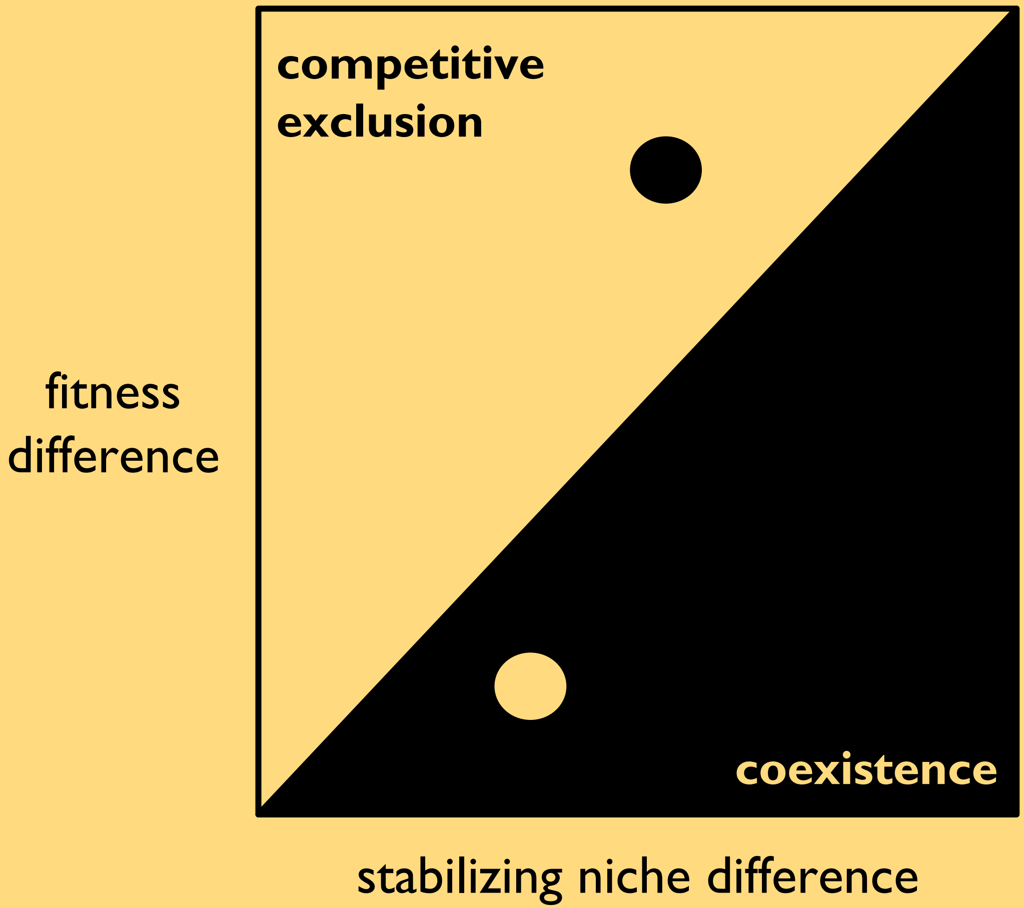
Siefert et al. 2015 Ecol. Letters

Individuals can vary substantially in their functional traits.

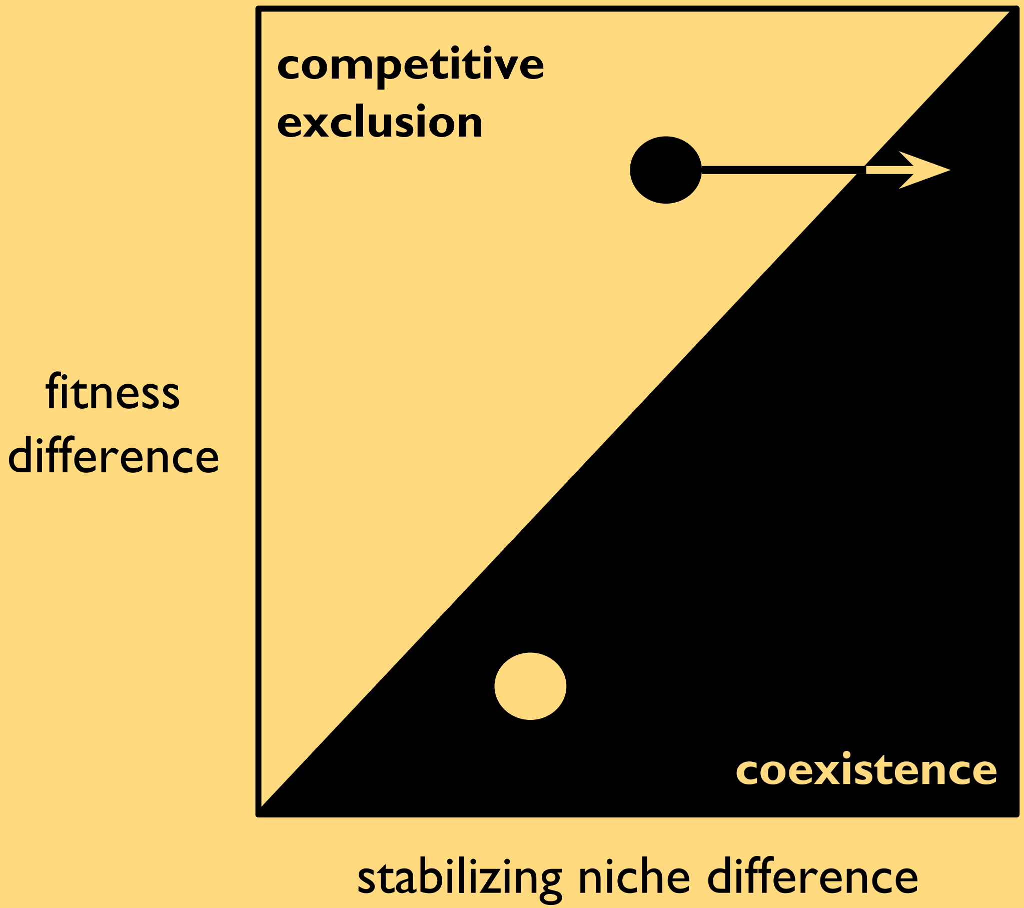
The consequences of such intra-specific trait variation (ITV) on coexistence and community structure remain murky.

Violle et al. 2012 TREE; Turcotte & Levine 2016 TREE

# ITV may promote or destabilize coexistence

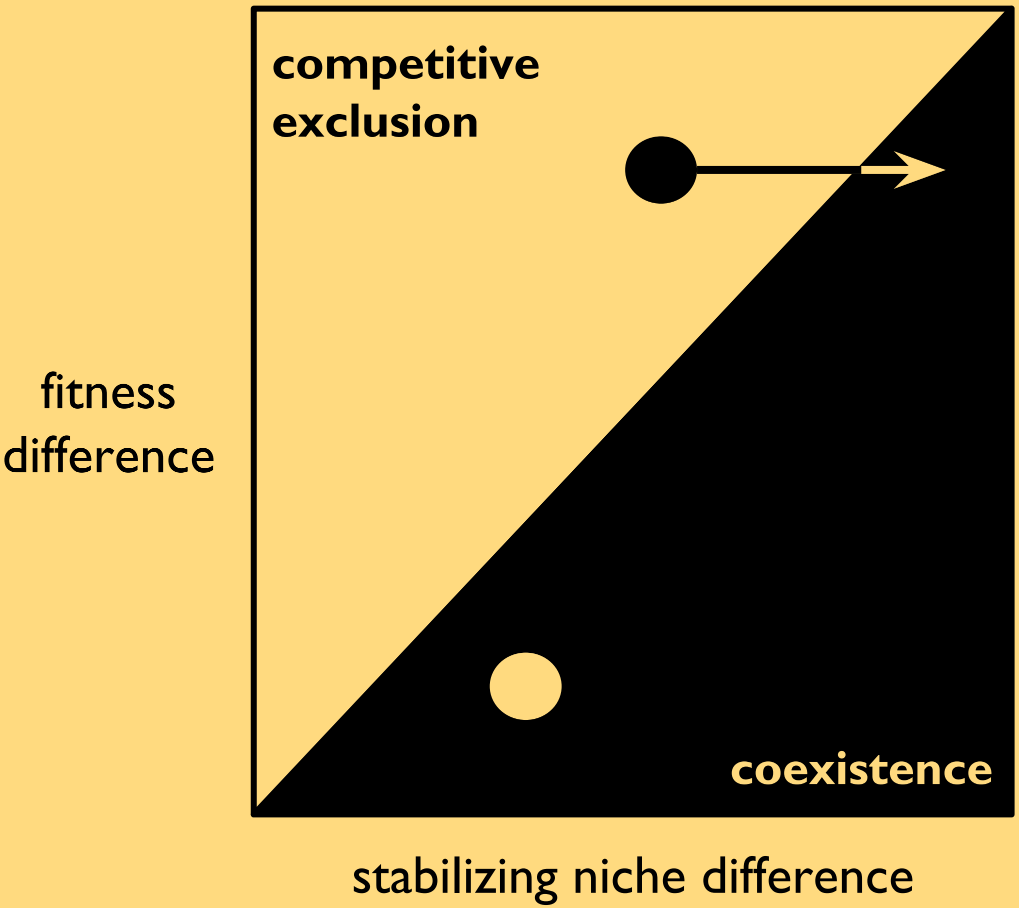


# ITV may promote or destabilize coexistence




Clark 2010 Science

# ITV may promote or destabilize coexistence

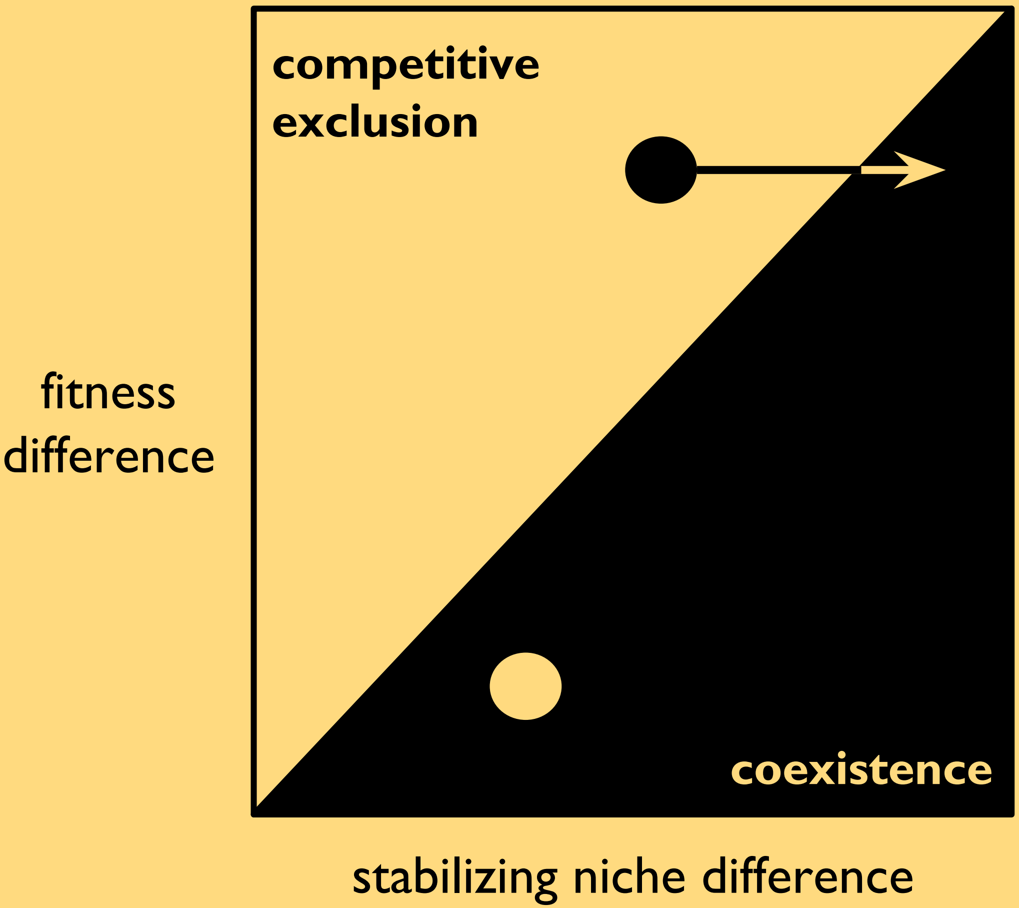



Growing without competitors

***low stabilizing niche differences***

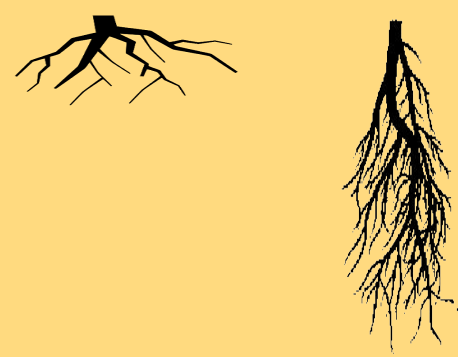
Clark 2010 Science

# ITV may promote or destabilize coexistence



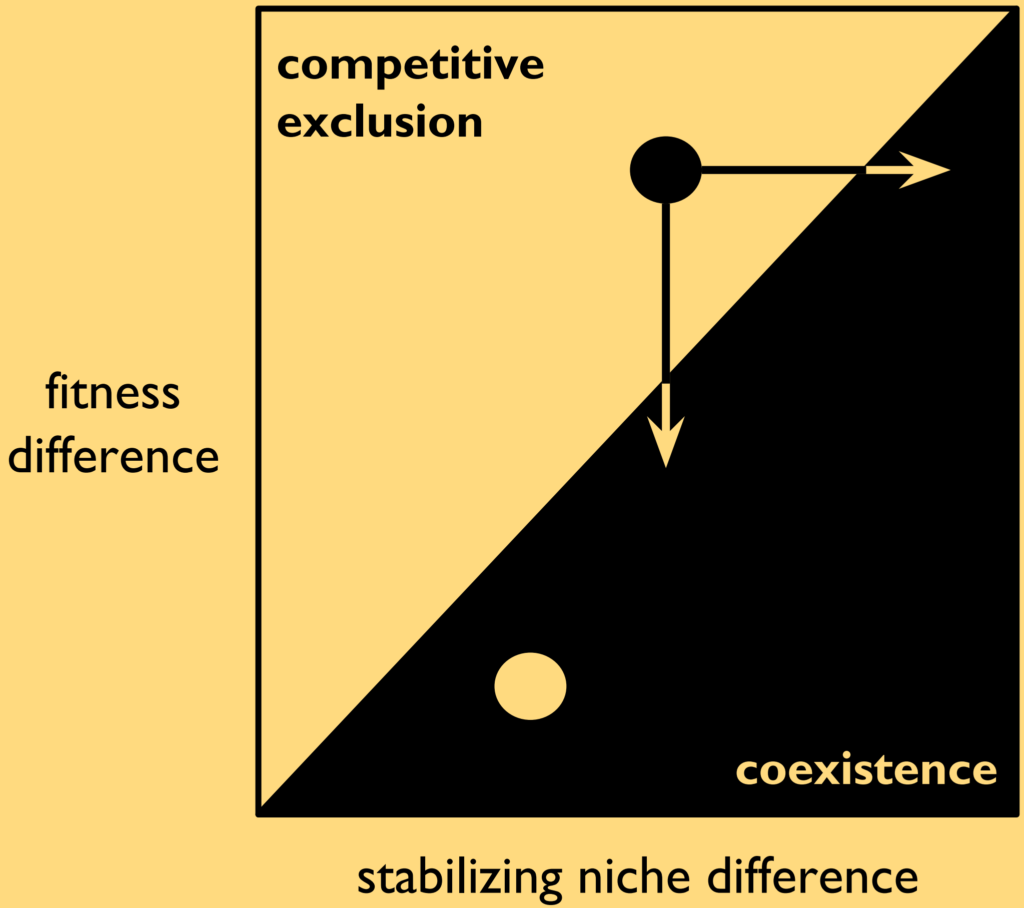

Growing without competitors
***low stabilizing niche differences***

Growing in competition
***high stabilizing niche differences***



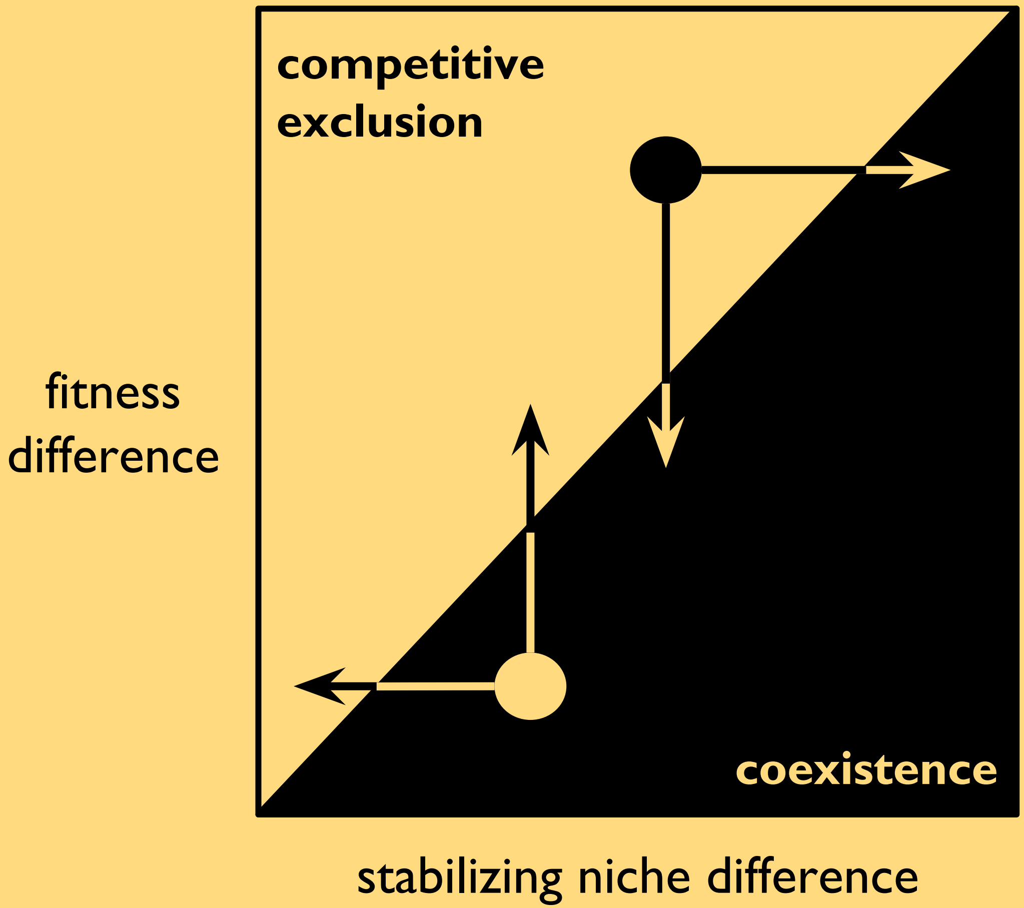
Clark 2010 Science

# ITV may promote or destabilize coexistence




Fridley et al. 2007 J. Ecology

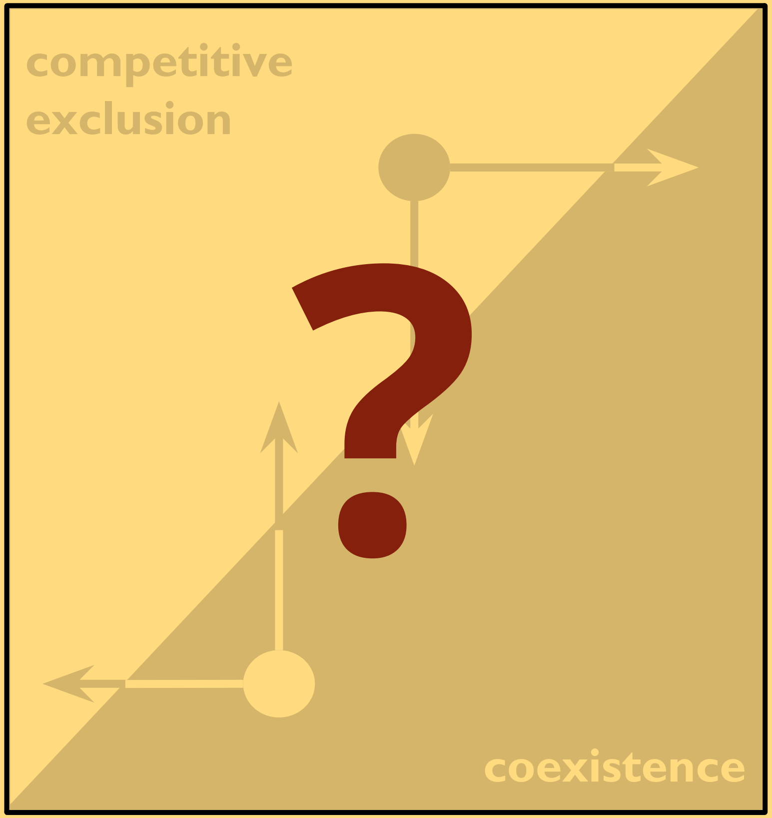
# ITV may promote or destabilize coexistence




Hart et al. 2016 Ecology Letters

# ITV may promote or destabilize coexistence

fitness difference




stabilizing niche difference

## Outstanding questions

Are there species-specific shifts of functional traits in response environmental variation?

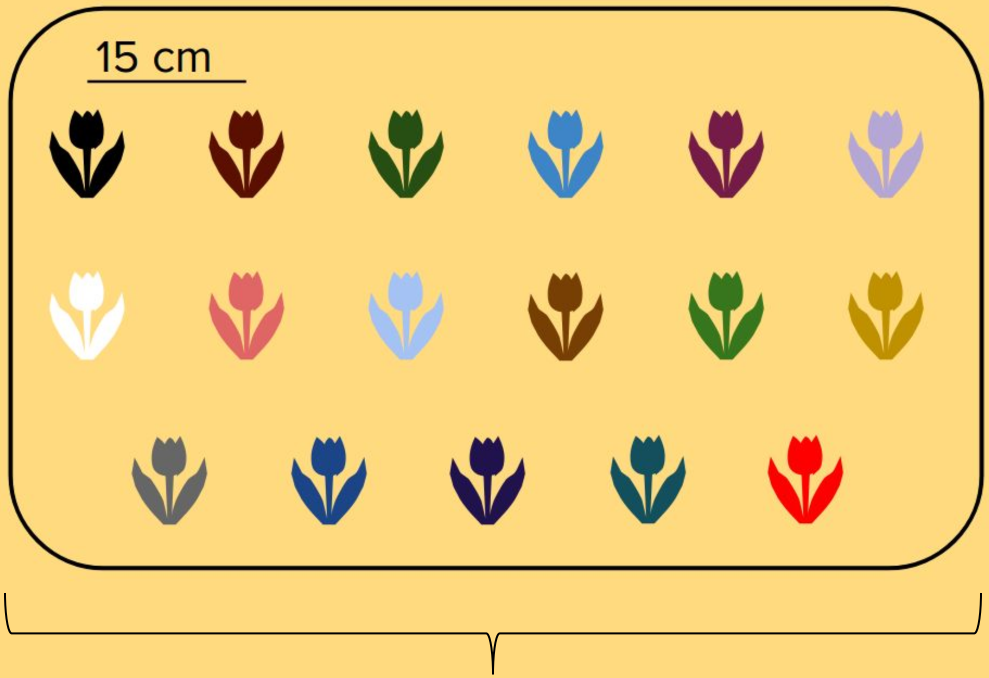
Can observed ITV change the outcome of competition?

# Chapter questions

1. What is the structure of trait variation across an environmental gradient?

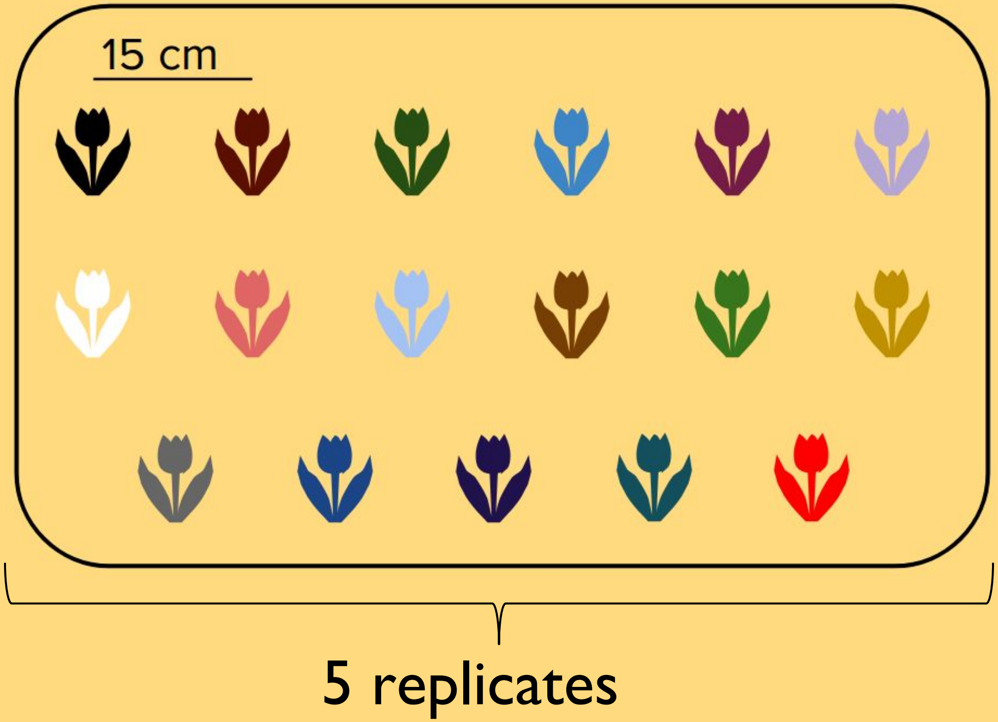
2. Do species shift their ecological strategies in competition, and how might this influence the outcome of competition?

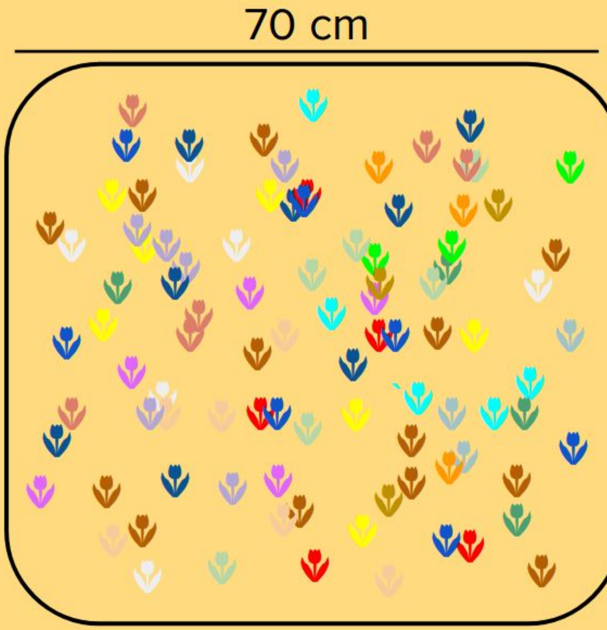
# At 24 sites, plants were grown with a very low density of competitors



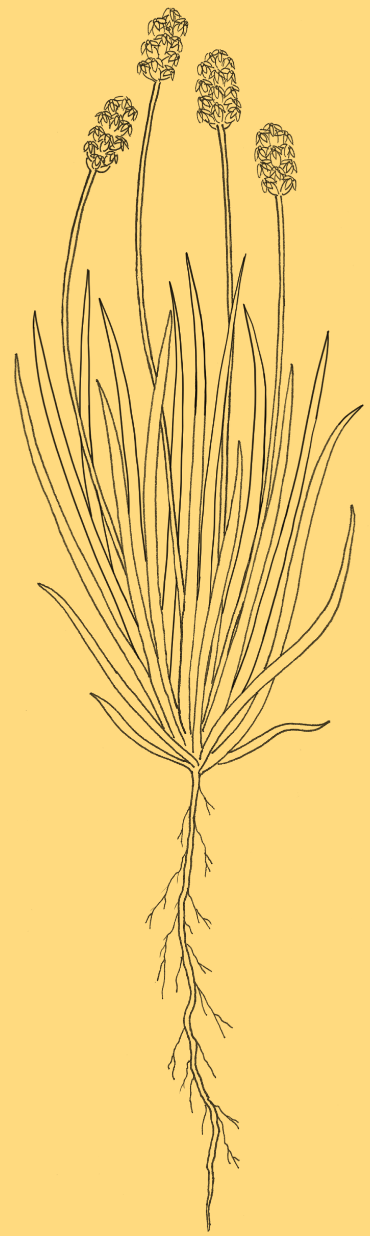

5 replicates/site at 24 sites

# At one site, plants were grown with and without competitors



**Leaves**
Leaf size
Specific leaf area
Leaf dry matter content



**Roots**
Specific root length

**Whole-plant**
Canopy shape index
Height

Illustration of *Plantago erecta* by Joanna Shih (UCLA)

Q1: What is the structure of trait variation across an environmental gradient?

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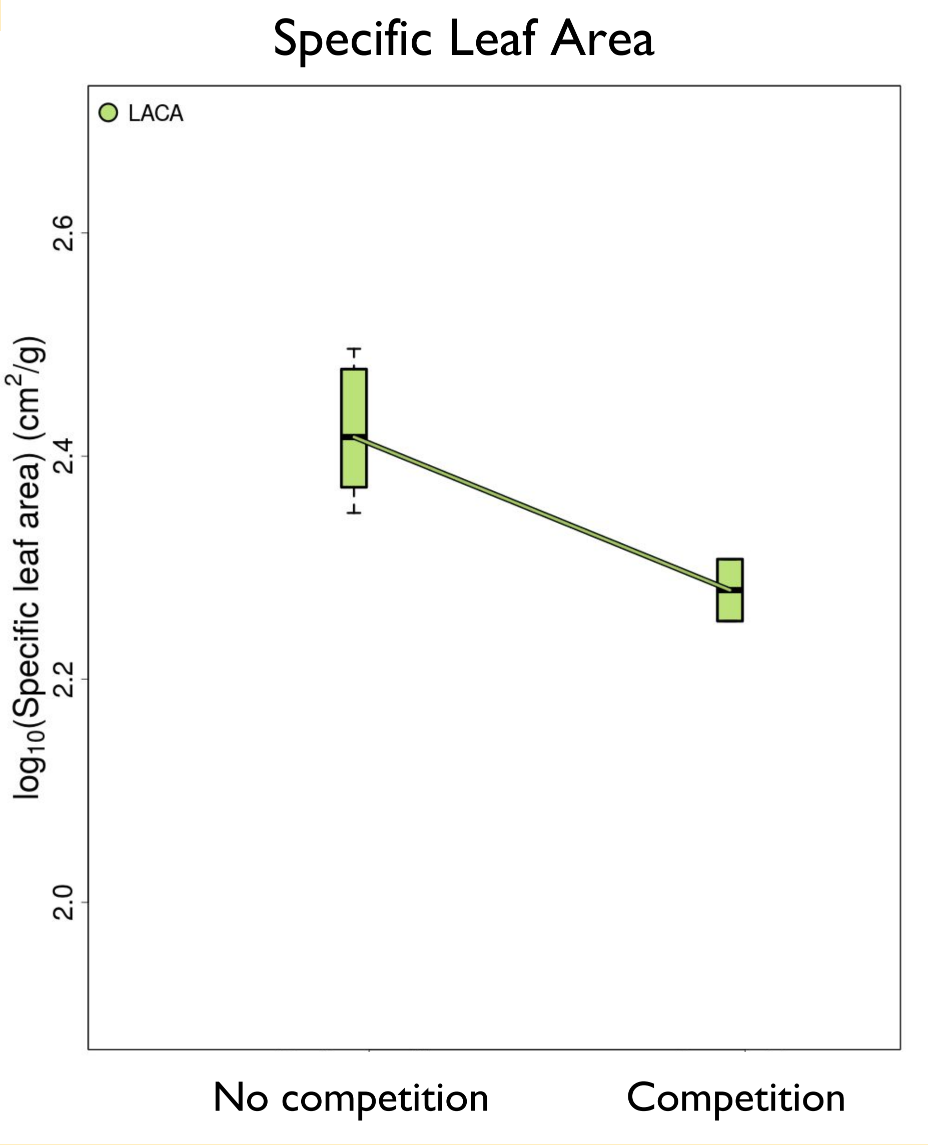
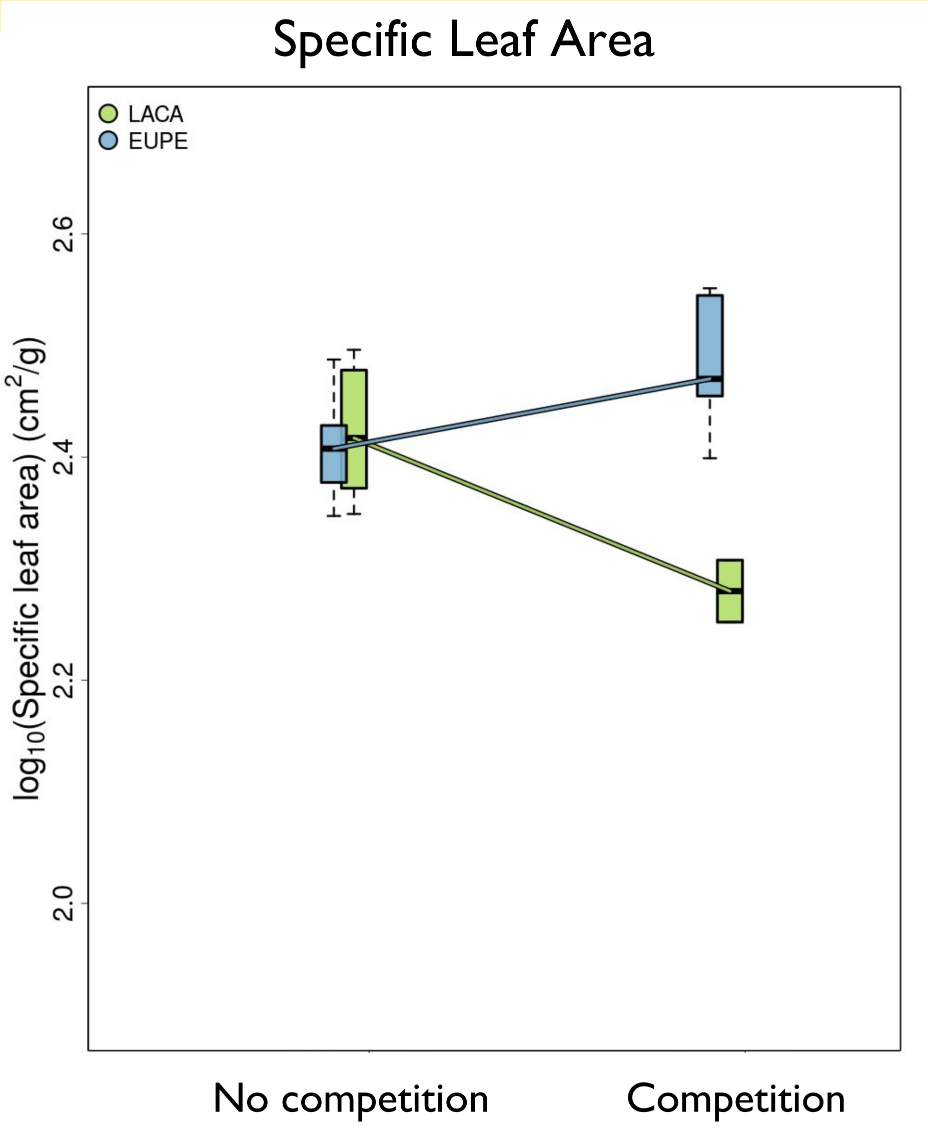
$$trait_{i,j} \sim \overbrace{a}^{\text{trait mean}} + \underbrace{b_0 x_i}_{\text{species effect}} + \overbrace{c_0 z_j}^{\text{environment effect}} + \underbrace{c_1 x_i z_j}_{\text{interaction}} + \overbrace{\epsilon_{\alpha j} + \epsilon_{\beta i} + \gamma_i}^{\text{error terms}}$$

Q2: Do species shift their ecological strategies in competition, and how might this influence the outcome of competition?

# Trait changes in response to competition are species-specific



# Trait changes in response to competition are species-specific



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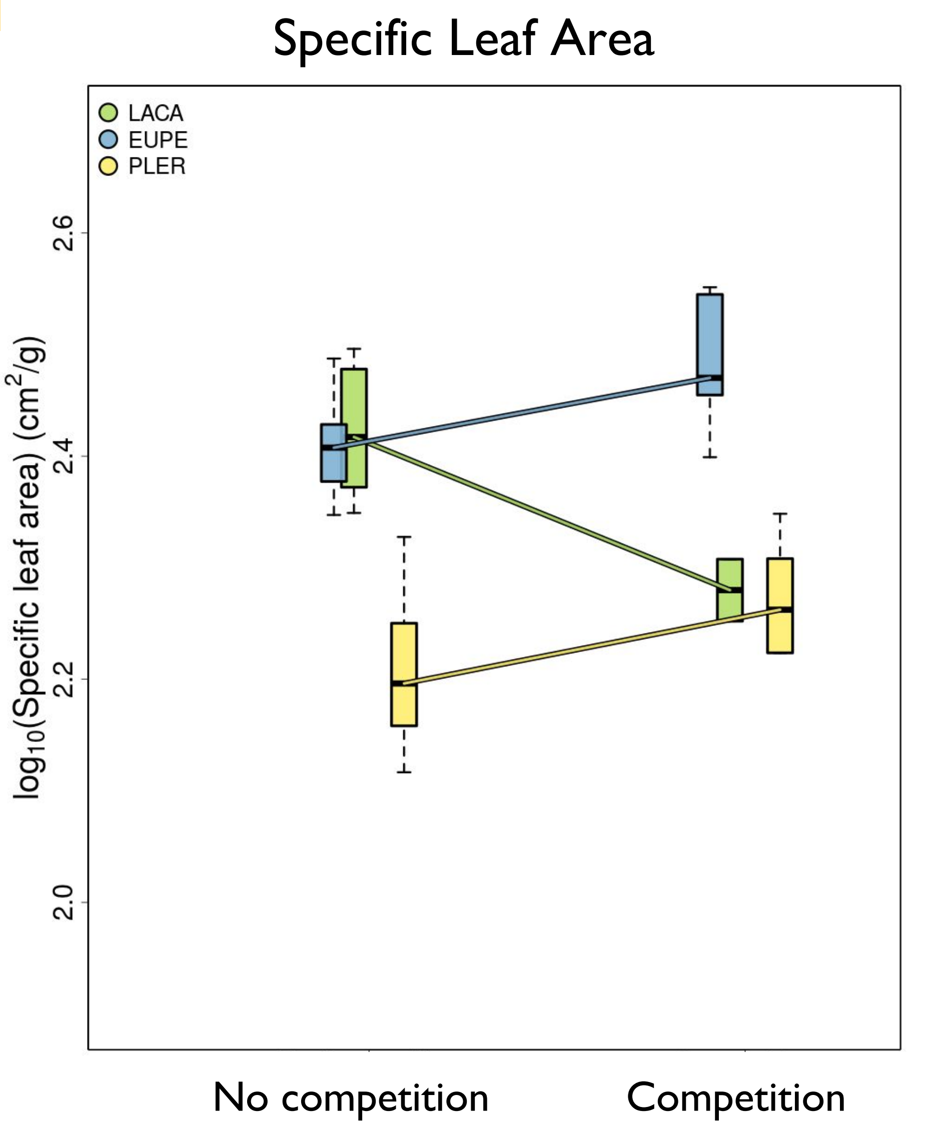

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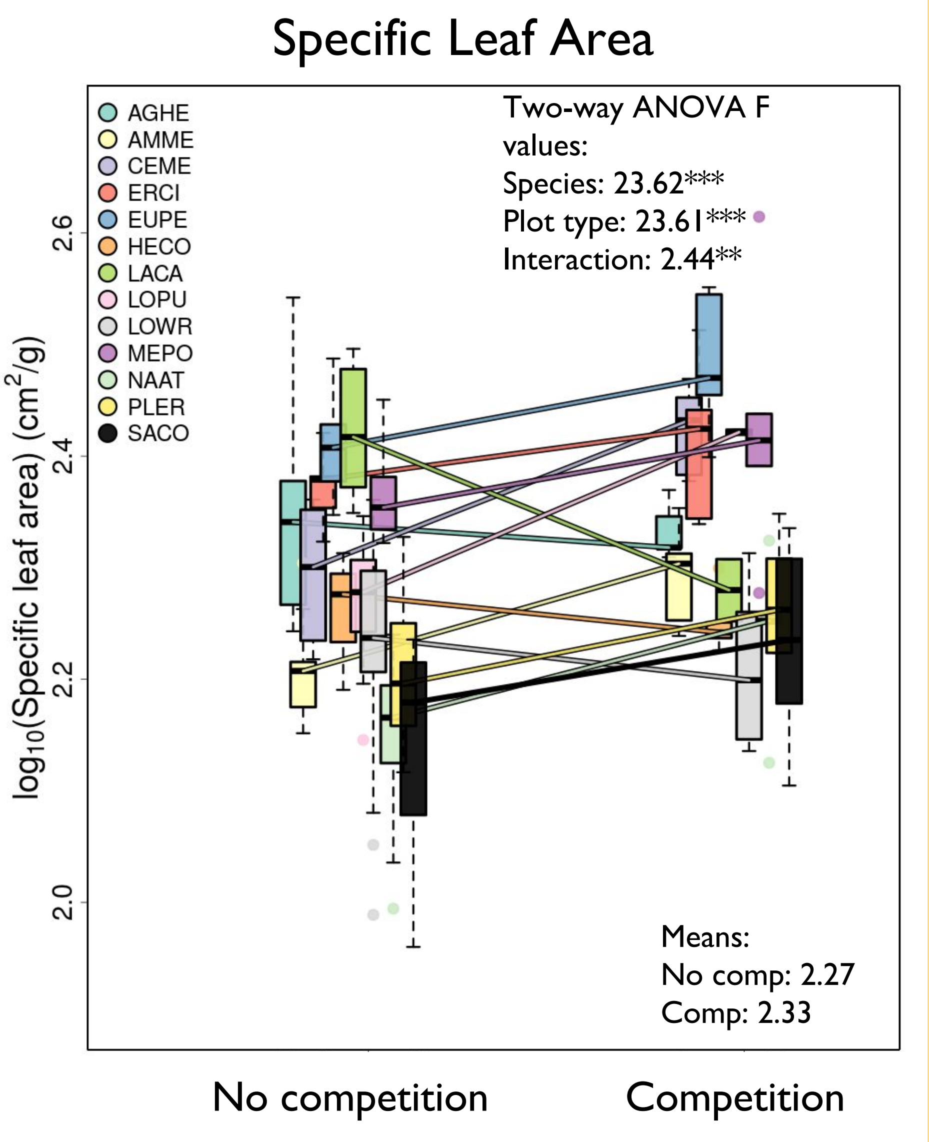

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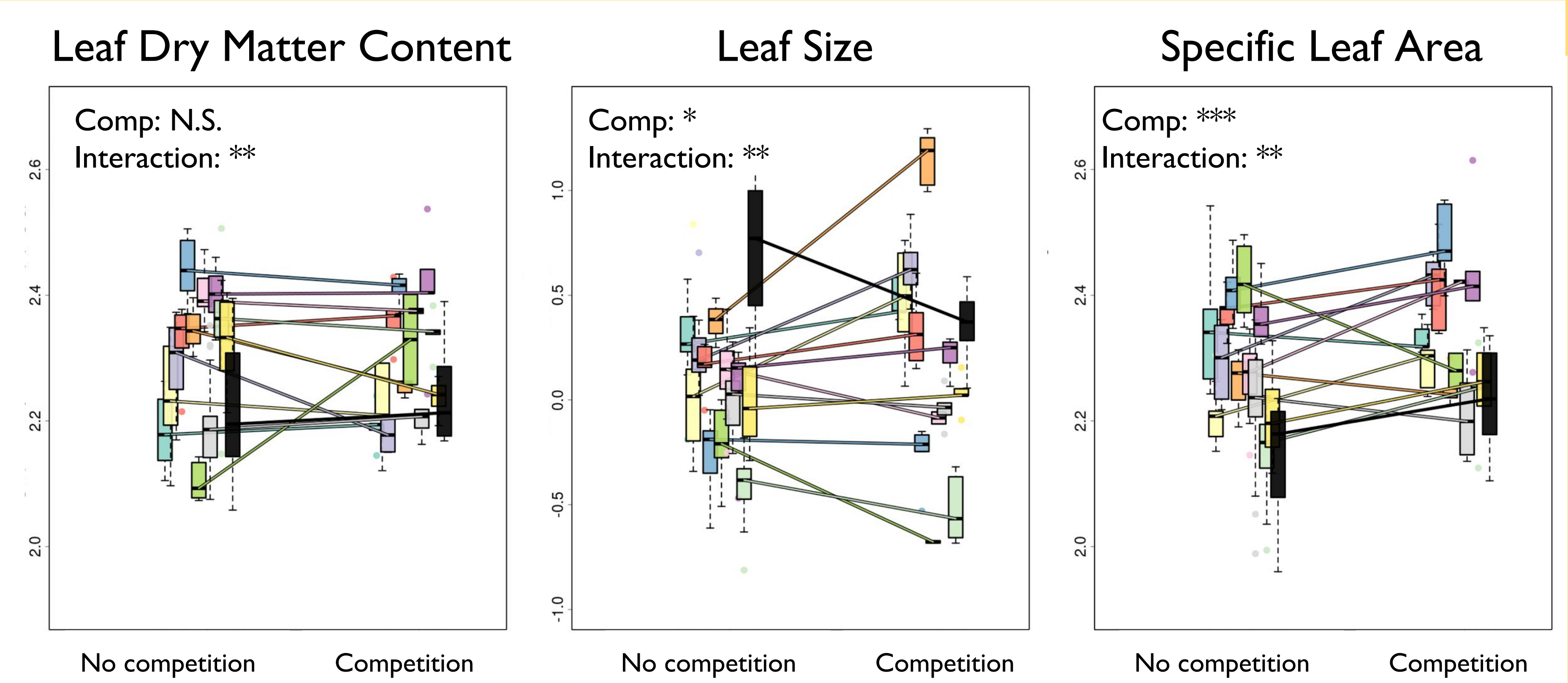
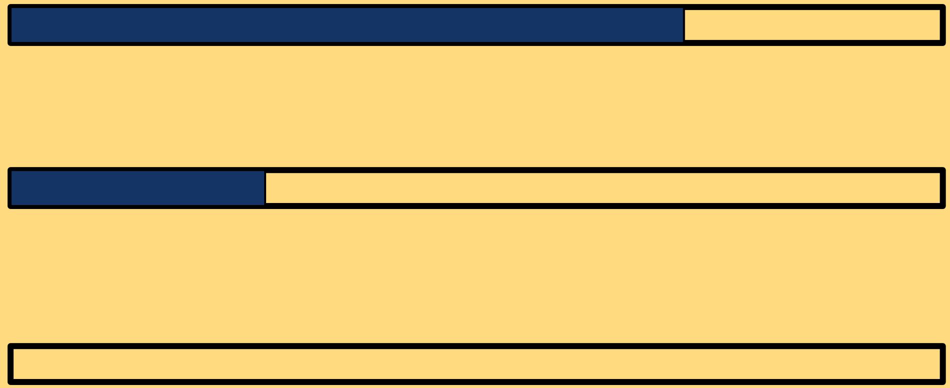


**Data collection**

**Analyses**

**Writeup**



**Projected timeline**

Process fine root samples for SRL: October-November 2018
Collect trait data in conspecific/heterospecific background: March-May 2018
Conduct analyses: September-December 2018
Write MS: January-April 2019
**Submit MS: Summer 2019**

**Plant ecologists lack a clear understanding of how some fundamental ecological processes structure communities**

Environmental variation

Interactions between species

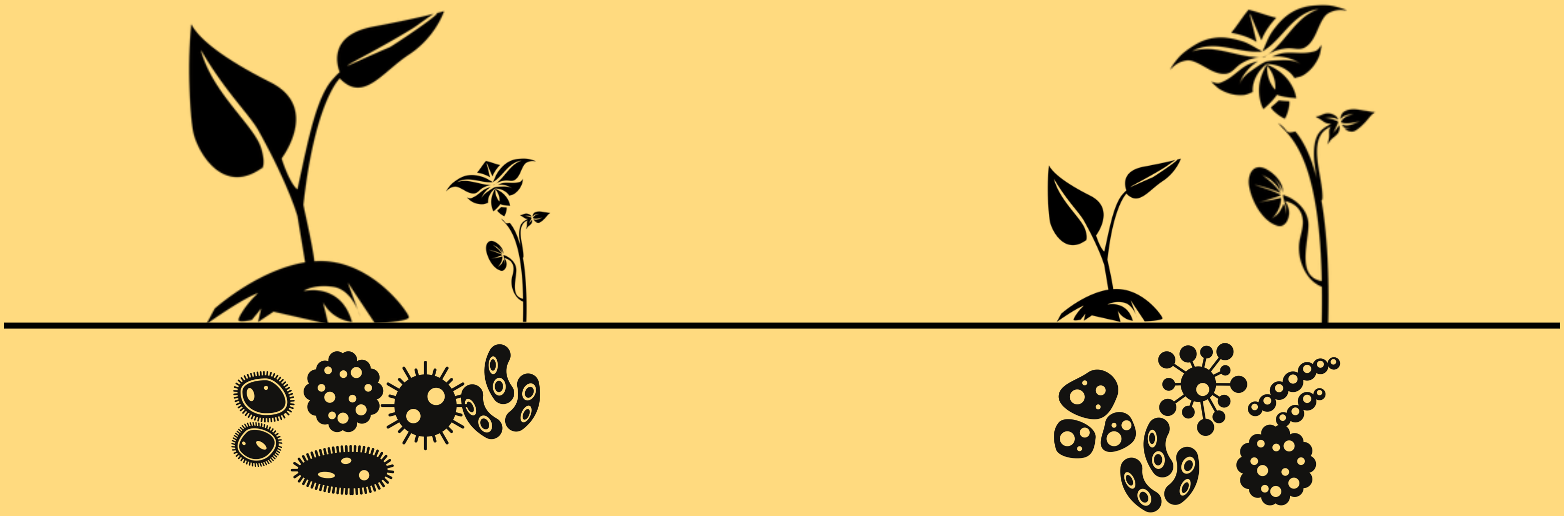
**Variation between individuals**

Feedbacks between plants and soil microbes

# Chapter 3

How can we jointly consider the consequences of resource competition and plant-microbe interactions in a unified framework?

Microbes are ubiquitous and varied, and they can have dramatic impacts on plant community structure.



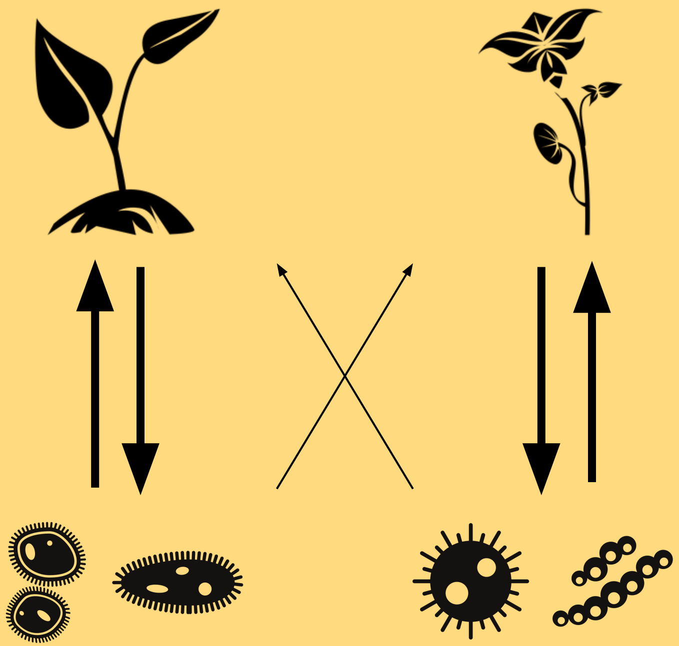
Van der Putten et al. 1993 Nature; Redman 2002 Science; Mangan et al. 2010 Nature

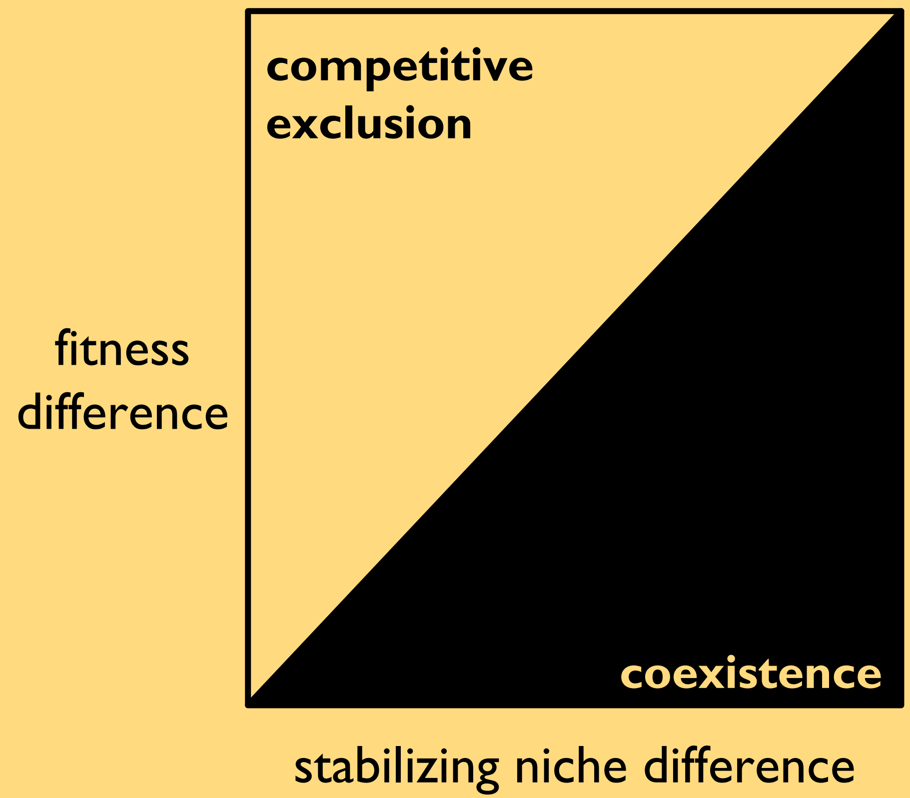
# Plant-soil feedbacks can promote plant species coexistence

Bever et al. 1997 J Ecology

# What is the relative importance of PSFs and competition to plant coexistence?

Smith-Ramesh & Reynolds 2017 J. Veg. Sci; Van Der Putten et al. 2016 Func. Ecol.




competitive
exclusion
coexistence
fitness
difference
stabilizing niche difference

# Chesson & Kuang (2008) model the dynamics of focal species, resources, and natural enemies

$$\frac{1}{N_j}\frac{dN_j}{dT} = \overbrace{\sum_l c_{jl} v_l R_l}^{\substack{growth\ due\ to\\ resource\ uptake}} - \overbrace{\sum_m a_{jm} P_m}^{\substack{loss\ to\\ natural\ enemy}} - \overbrace{\mu_j}^{\substack{maintenance\\ cost}}$$

$$\frac{1}{R_l}\frac{dR_l}{dT} = \overbrace{r_l(1-\alpha_l R_l)}^{\substack{resource\\ replacement}} - \overbrace{\sum_j N_j C_{jl}}^{\substack{consumption\ by\\ focal\ species}}$$

$$\frac{1}{P_m}\frac{dP_m}{dT} = \overbrace{r_m(1-\alpha_m P_m)}^{\substack{intrinsic\ growth\\ rate}} + \overbrace{\sum_j W a_{jm} P_m}^{\substack{growth\ due\\ to\ consumption}}$$

Chesson & Kuang (2008) Nature

# Species interactions with nutrients and enemies both influence niche and fitness differences.

Niche difference = $$1 - \frac{\boxed{\Sigma_l \frac{C_{jl}V_l C_{kl}}{r_l^R \alpha_I^R}} + \boxed{\Sigma_m \frac{a_{jm} w a_{km}}{r_m^P \alpha_m^P}}}{\sqrt{\left(\boxed{\Sigma_l \frac{c_{jl}^2 v_l}{r_l^R \alpha_l^R}} + \boxed{\Sigma_l \frac{a_{jm}^2 w}{r_m^P \alpha_m^P}}\right)\left(\boxed{\Sigma_l \frac{c_{kl}^2 v_l}{r_l^R \alpha_l^R}} + \boxed{\Sigma_l \frac{a_{km}^2 w}{r_m^P \alpha_m^P}}\right)}}$$

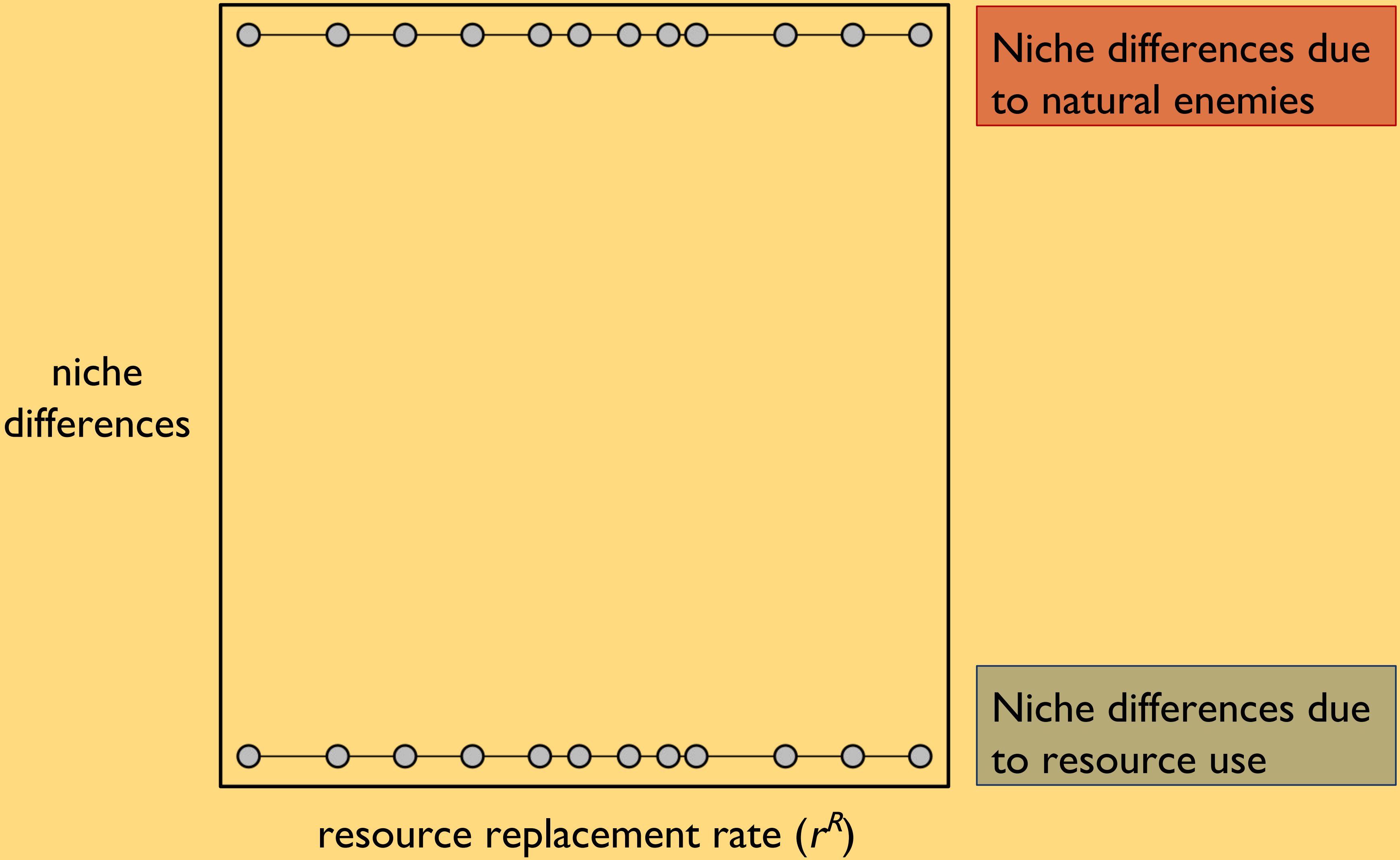
Species fitness = $$\frac{\boxed{\sum_l \frac{C_{jl} v_l}{\alpha_l^R}} - \boxed{\sum_m \frac{a_{jm}}{\alpha_m^P}} - \mu_j}{\sqrt{\left(\boxed{\sum_l \frac{c_{jl}^2 v_l}{r_l^R \alpha_l^R}} + \boxed{\sum_m \frac{a_{jm}^2 w}{r_m^P \alpha_m^P}}\right)}}$$

Due to natural enemies

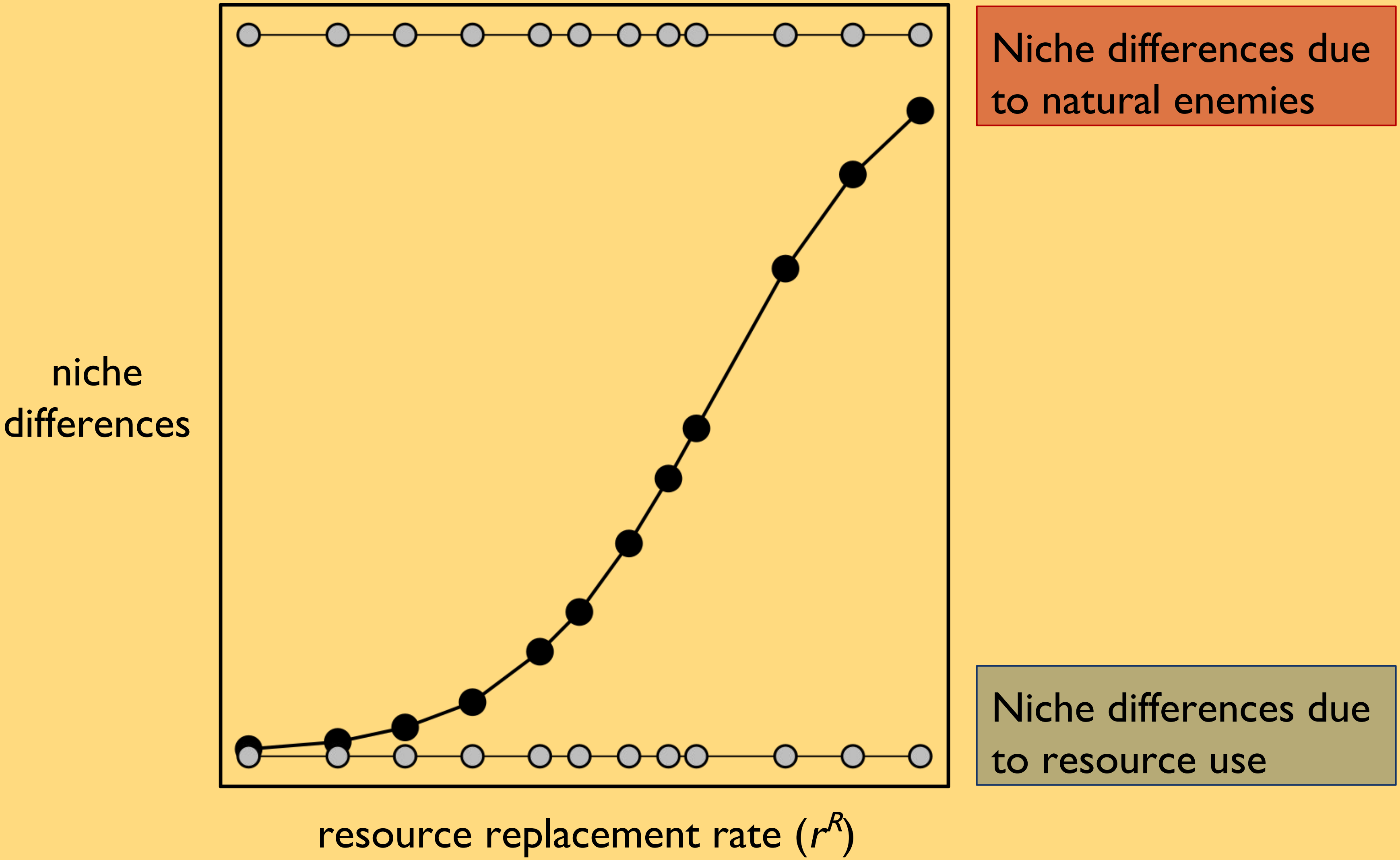
Due to resource use

Chesson & Kuang (2008) Nature

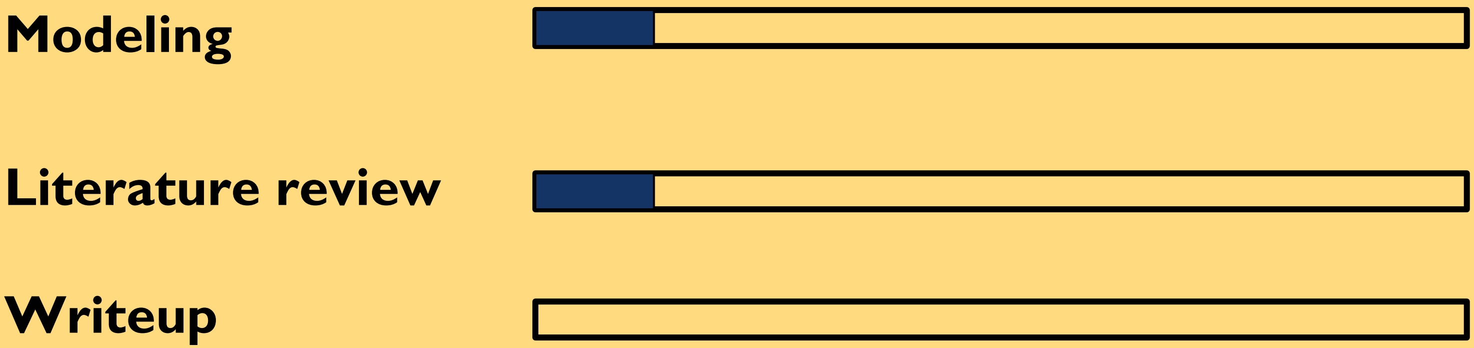
# This frameworks allows investigation of how resource and enemy interactions jointly influence plant species coexistence



# This frameworks allows investigation of how resource and enemy interactions jointly influence plant species coexistence



# chapter 3 timeline




**Projected timeline**

Analyze model across parameter space: September 2017-May 2018
Review of PSF literature: September 2017-May 2018
Conduct greenhouse experiment informed by model: Fall 2018
Start writing MS: May 2018
Submit MS: May 2019

**Plant ecologists lack a clear understanding of how some fundamental ecological processes structure communities**

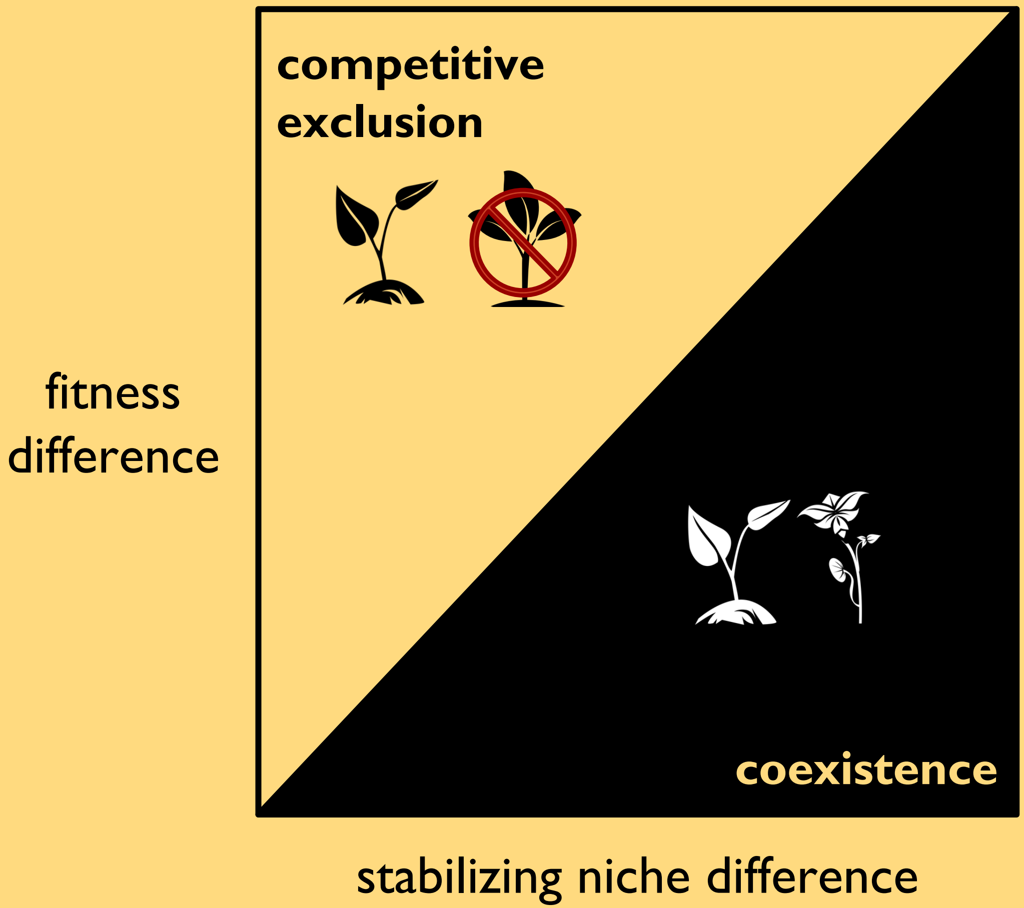
Environmental variation

Interactions between species

Variation between individuals

**Feedbacks between plants and soil microbes**

# What determines the magnitude of fitness and niche differences?




Species ecological strategies

Intra-specific variation in functional traits

Plant interactions with soil microbial communities

Chesson & Kuang 2008 Nature; Bever et al. 2015 AREES

Investigating the role of ecological processes using functional traits and through the lens of modern coexistence theory can help us advance towards a more **theoretically justified and predictive community ecology**

image: https://www.flickr.com/photos/rejik/
Kabani River, Kerala, India

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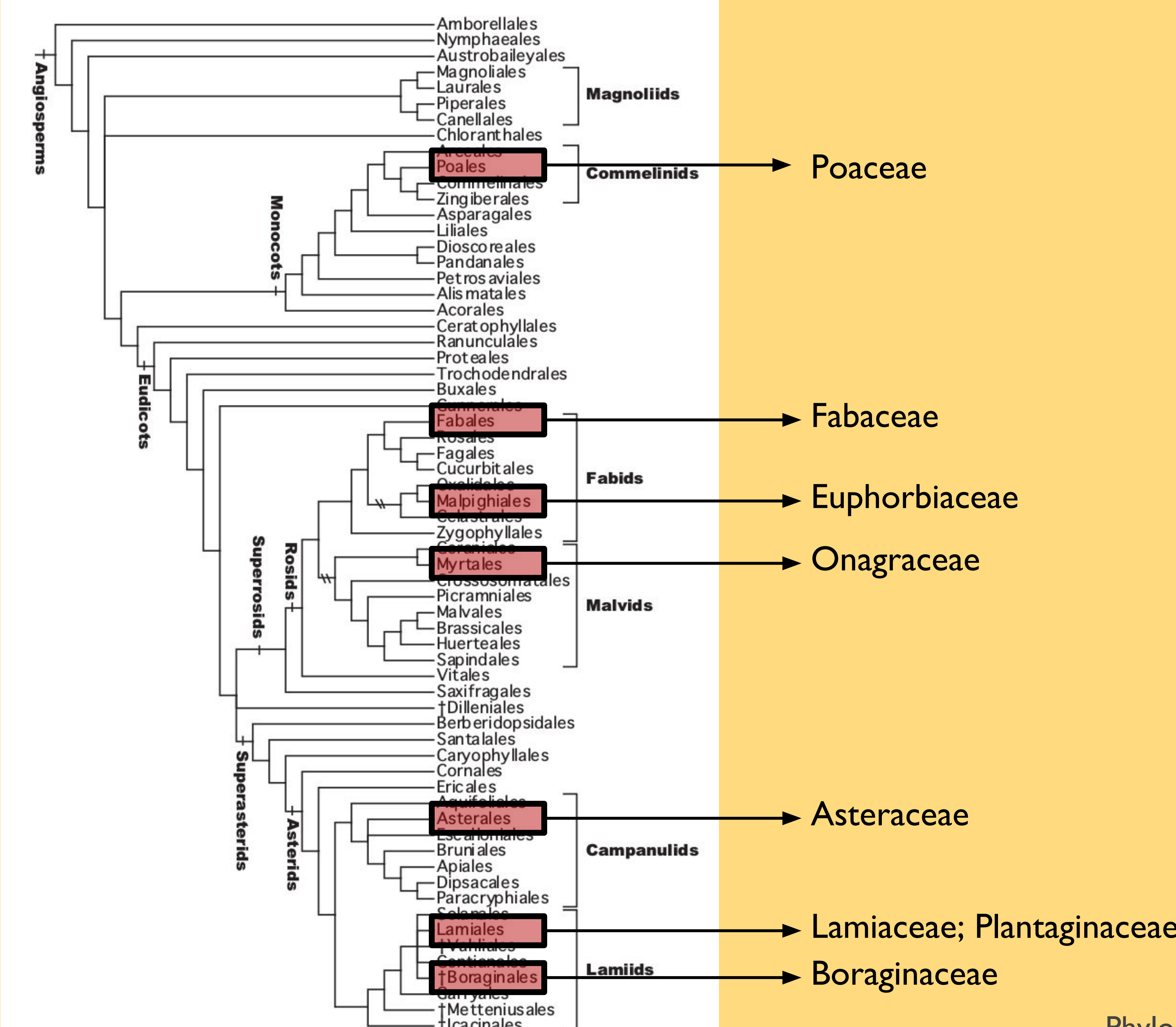


Phylogeny: APG IV