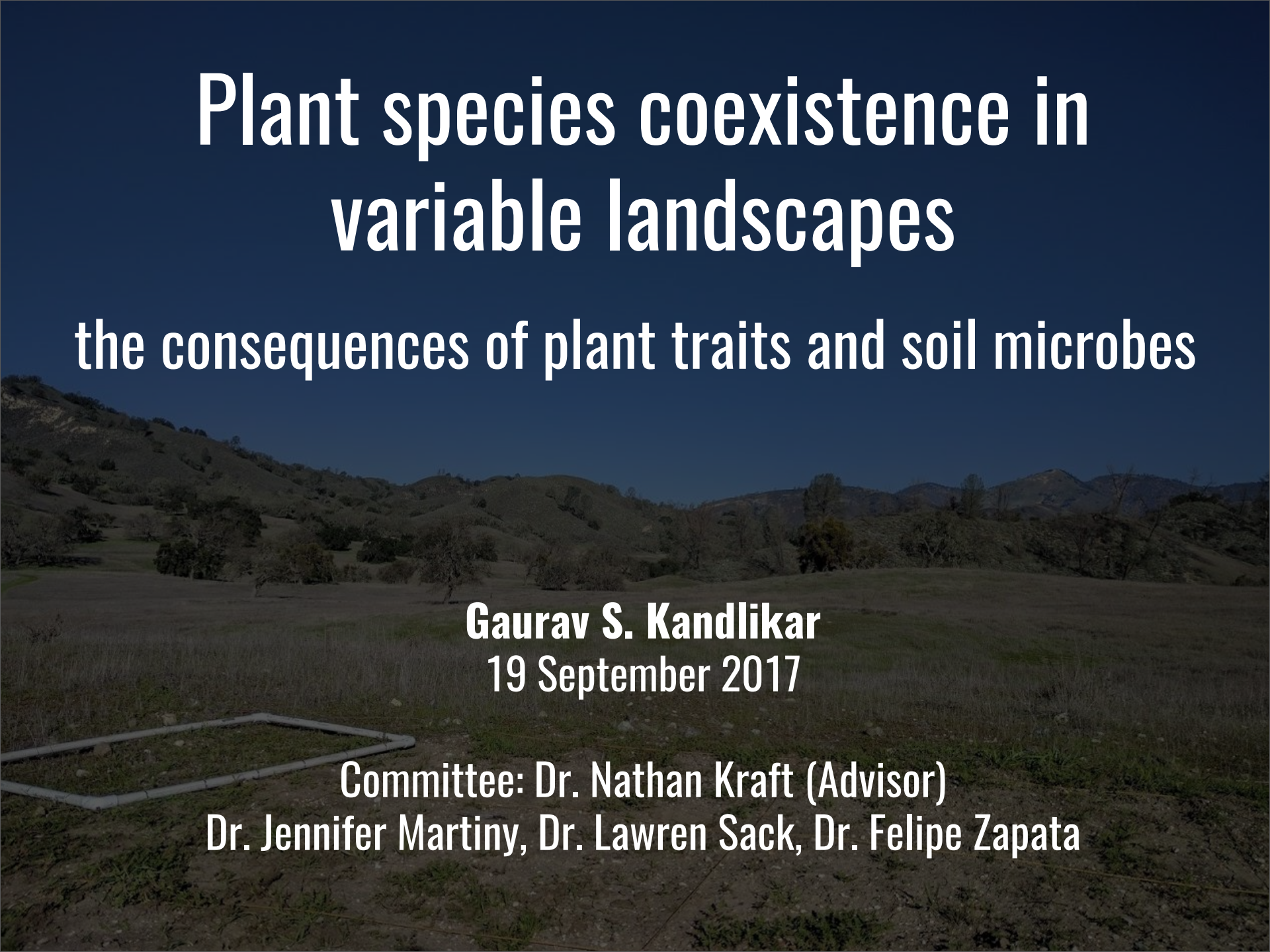
Plant species coexistence in variable landscapes

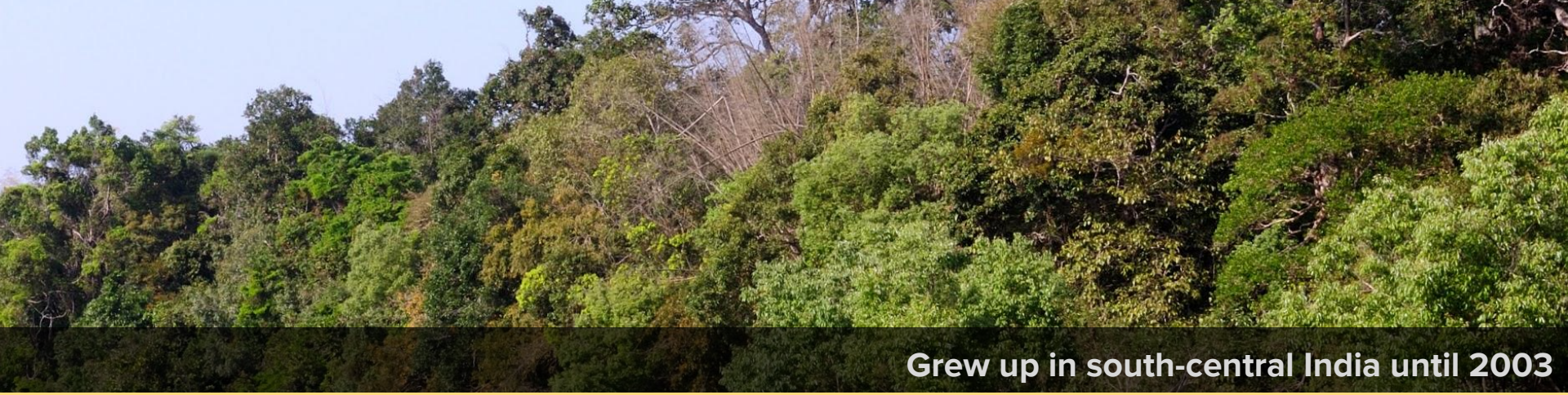
the consequences of plant traits and soil microbes



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 until 2003

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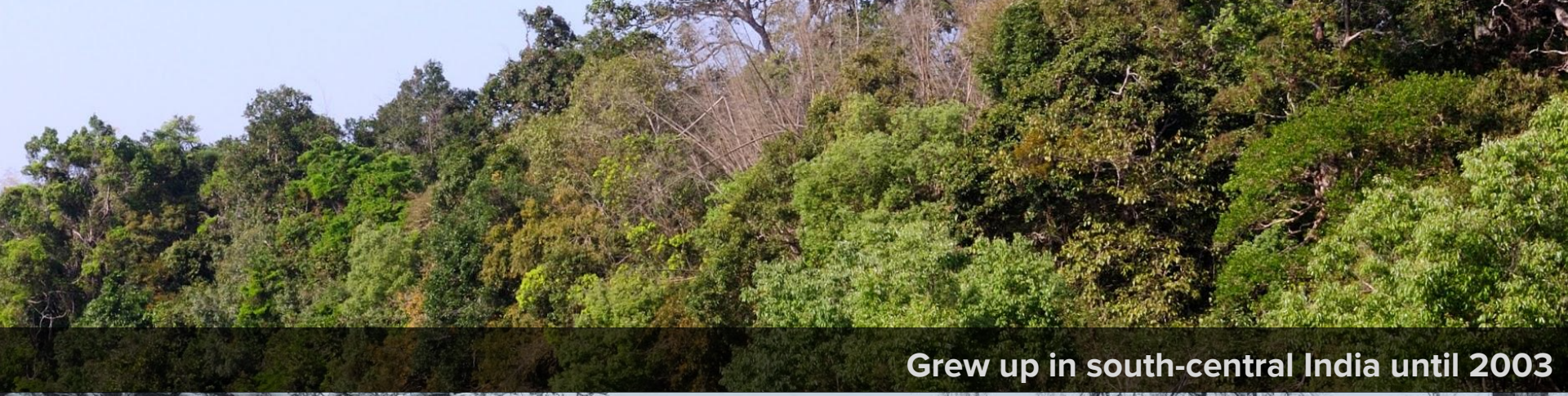
BS in Ecology, Evolution & Behavior/Plant Biology, Univ. Minnesota, 2010-13



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BS in Ecology, Evolution & Behavior/Plant Biology, Univ. Minnesota, 2010-13

PhD student w/ Nathan Kraft, Univ. Maryland 2014-15

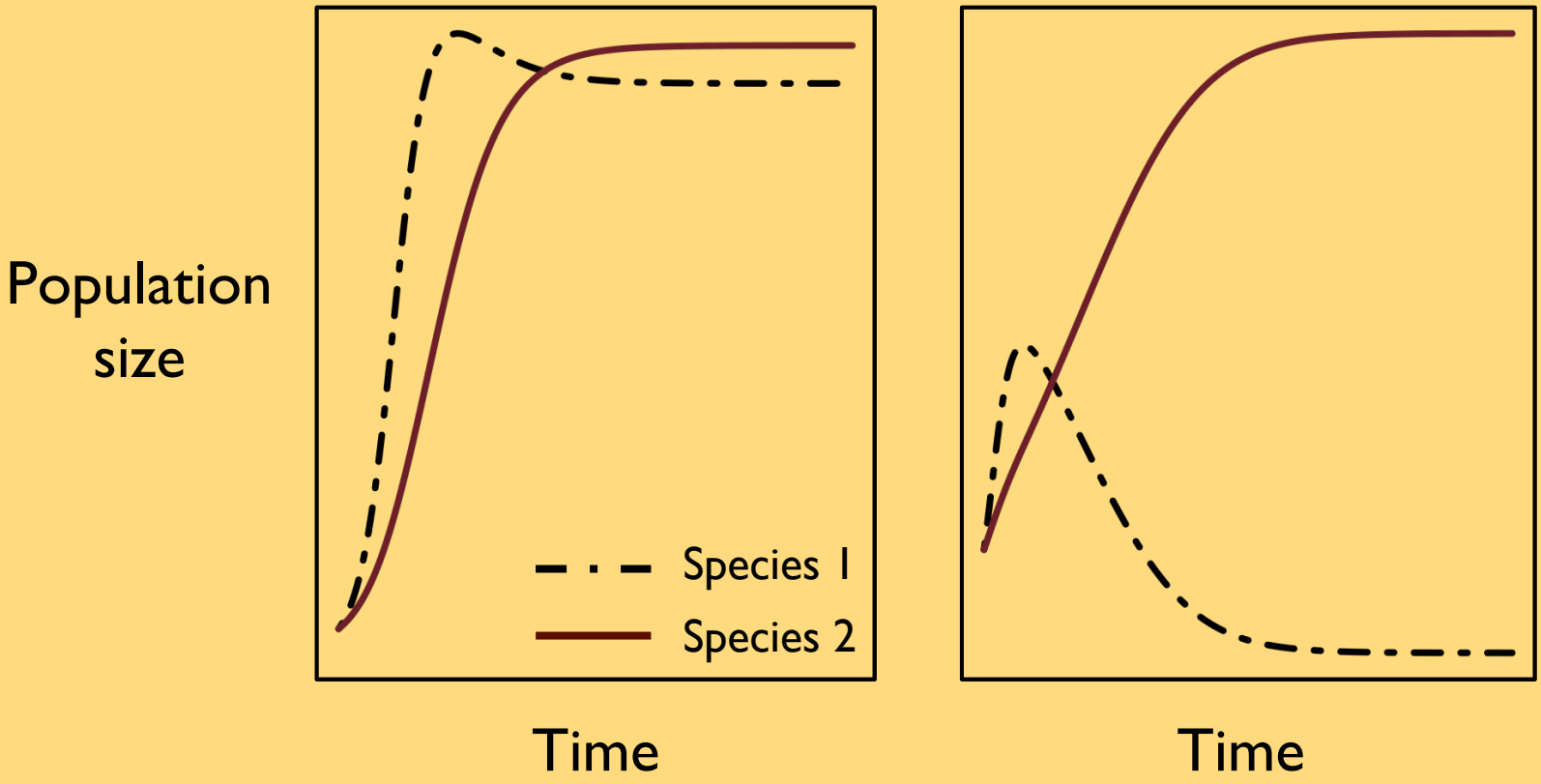
image: https://www.flickr.com/photos/rejik/
Kabani River, Kerala, India


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

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

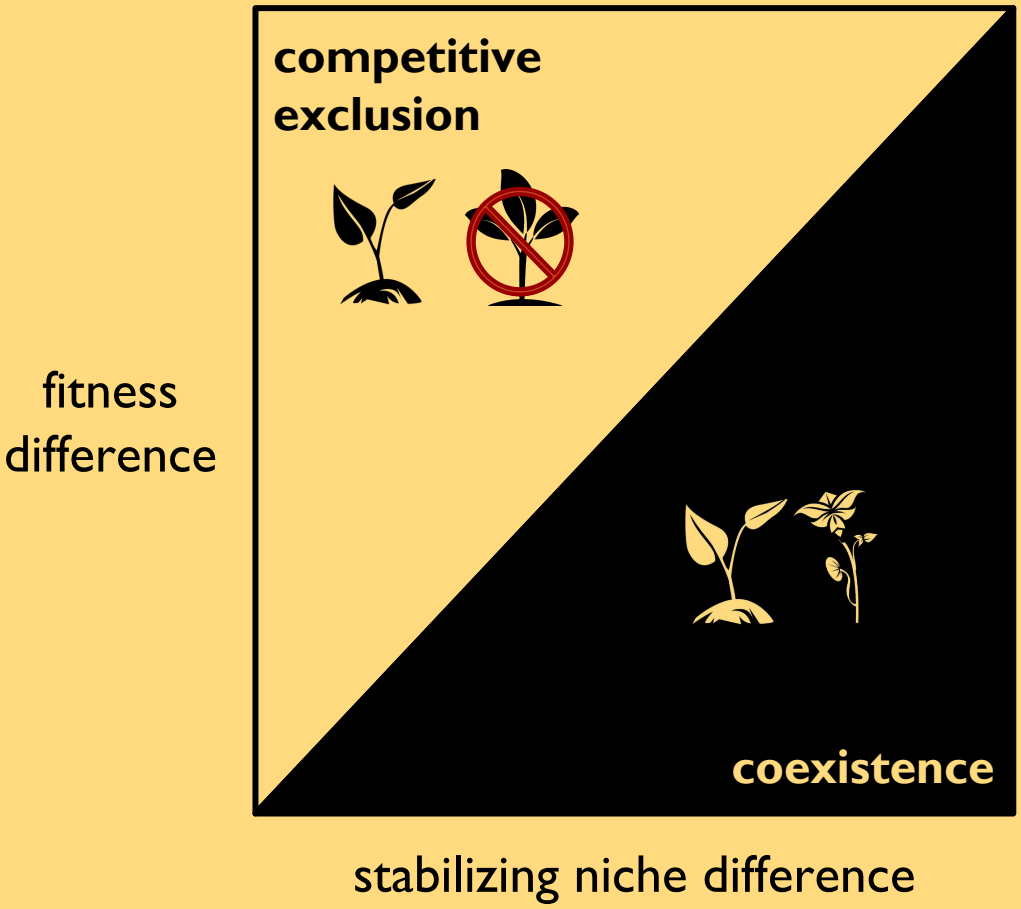
Stabilizing niche differences

Confer each species a competitive advantage when rare

E.g. differences in timing of resource use

Promote coexistence

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?

fitness difference

stabilizing niche difference

Adler et al. 2013 Ecol. Letters

What determines the magnitude of fitness and niche differences?

fitness difference

stabilizing niche difference

Species ecological strategies

Adler et al. 2013 Ecol. Letters

What determines the magnitude of fitness and niche differences?

fitness difference

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Species ecological strategies

Intra-specific variation in functional traits

Turcotte & Levine 2016 TREE

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

Dissertation Questions

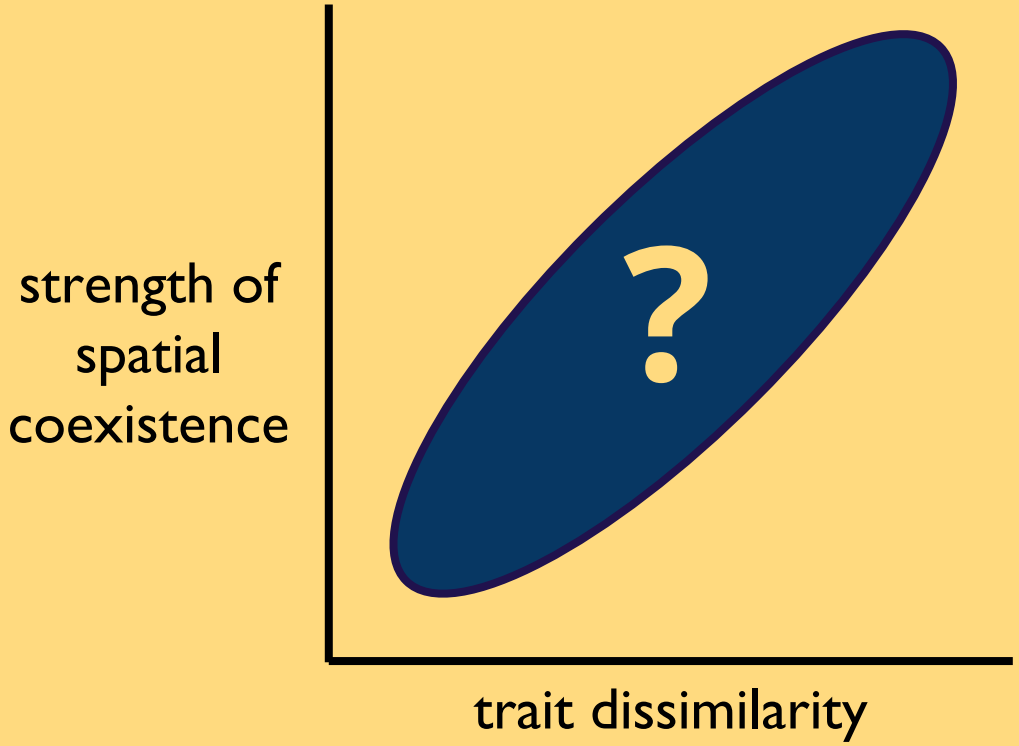
Ch. 1. How do differences in species functional traits relate to spatial drivers of coexistence?

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

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

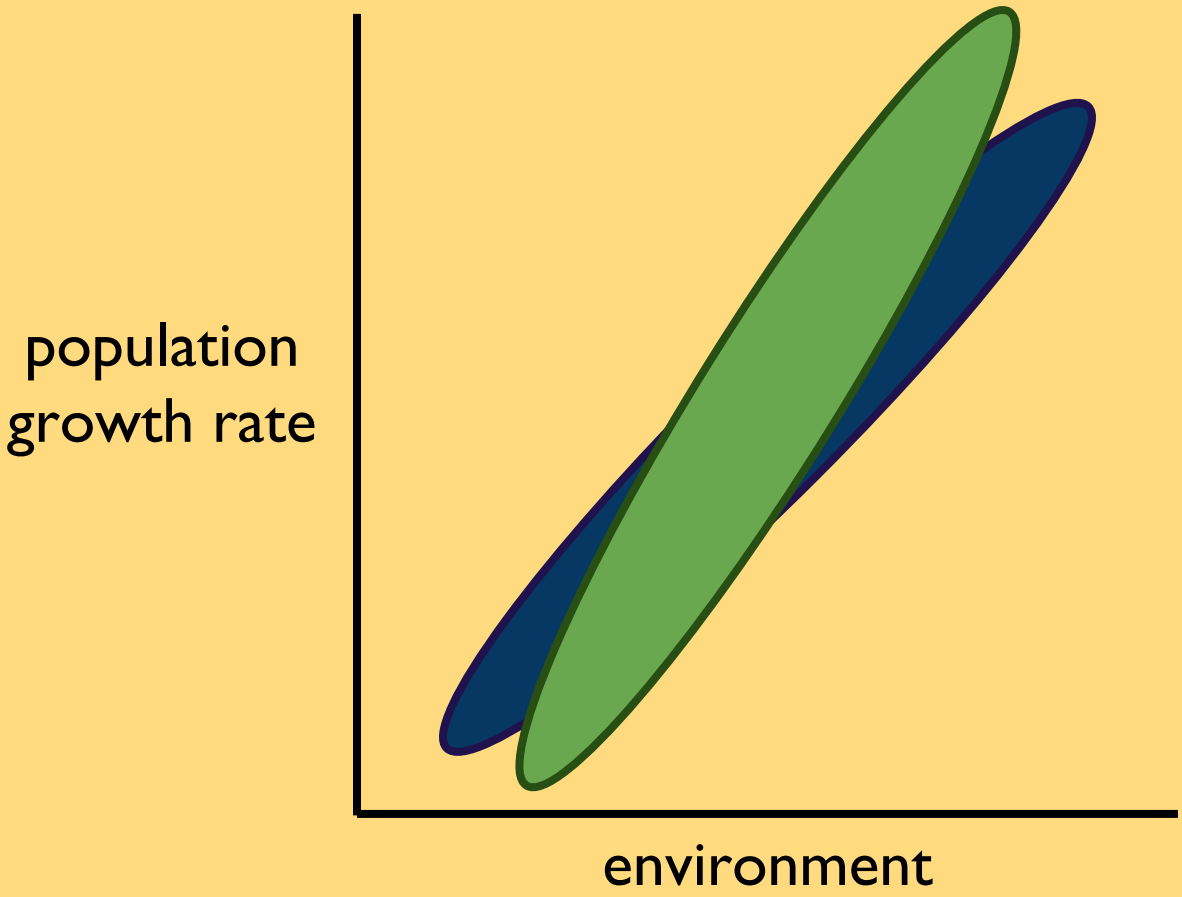
Chapter 1

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

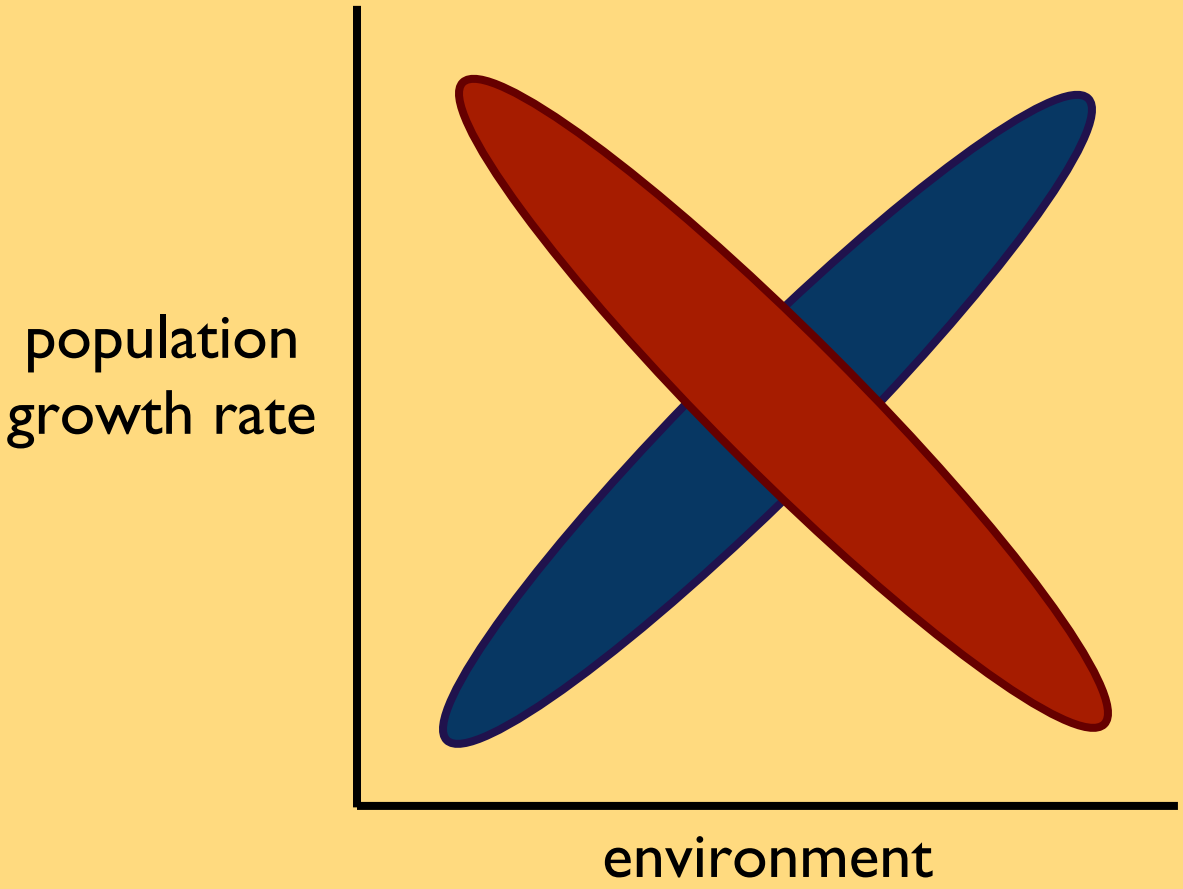


Spatial environmental variation can promote coexistence of species with decoupled demographic responses

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



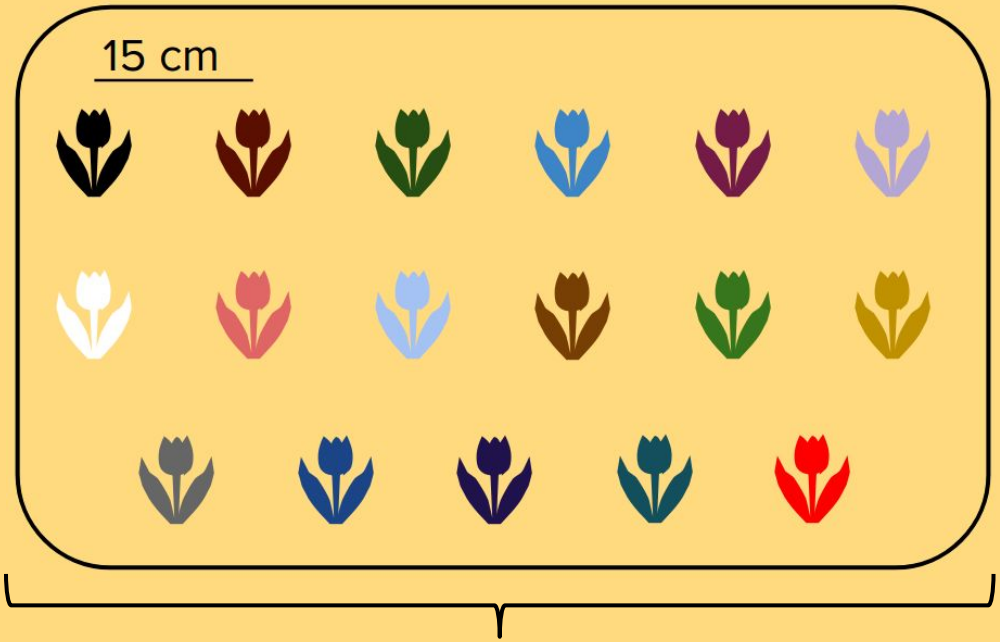
Spatial environmental variation can promote coexistence of species with decoupled demographic responses



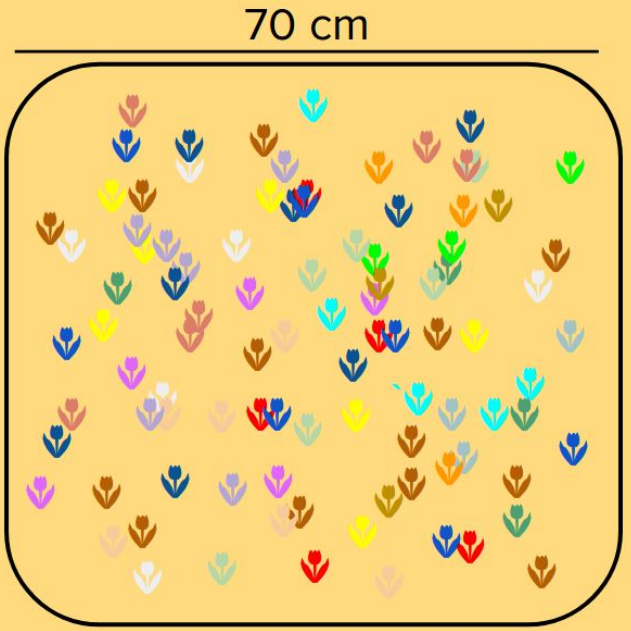
Chapter questions

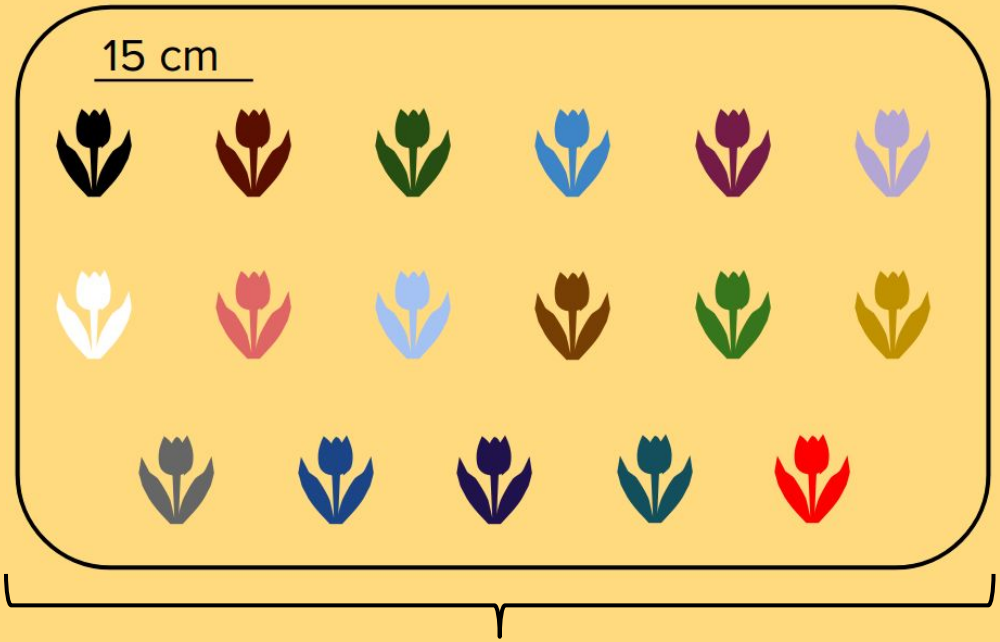
1. Which environmental factors drive variation in species responses to spatial heterogeneity?

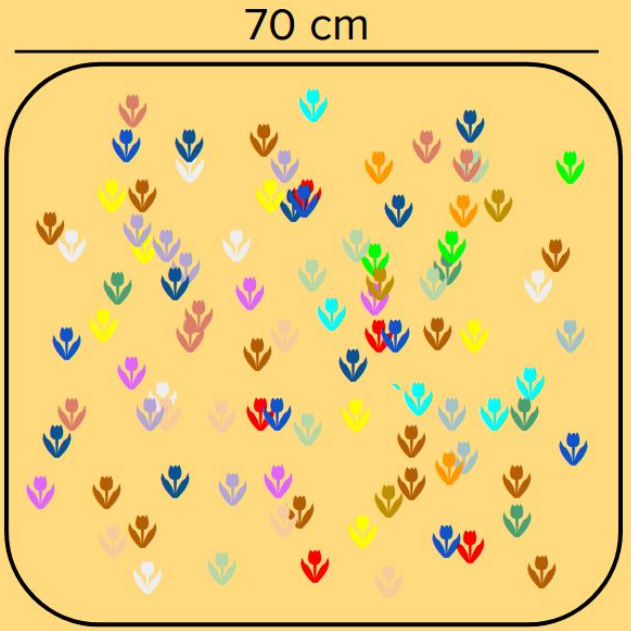
2. Which functional traits mediate species responses to the environmental drivers?



x 5 replicates/site







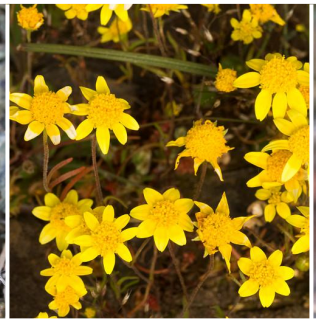
x 5 replicates/site

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


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

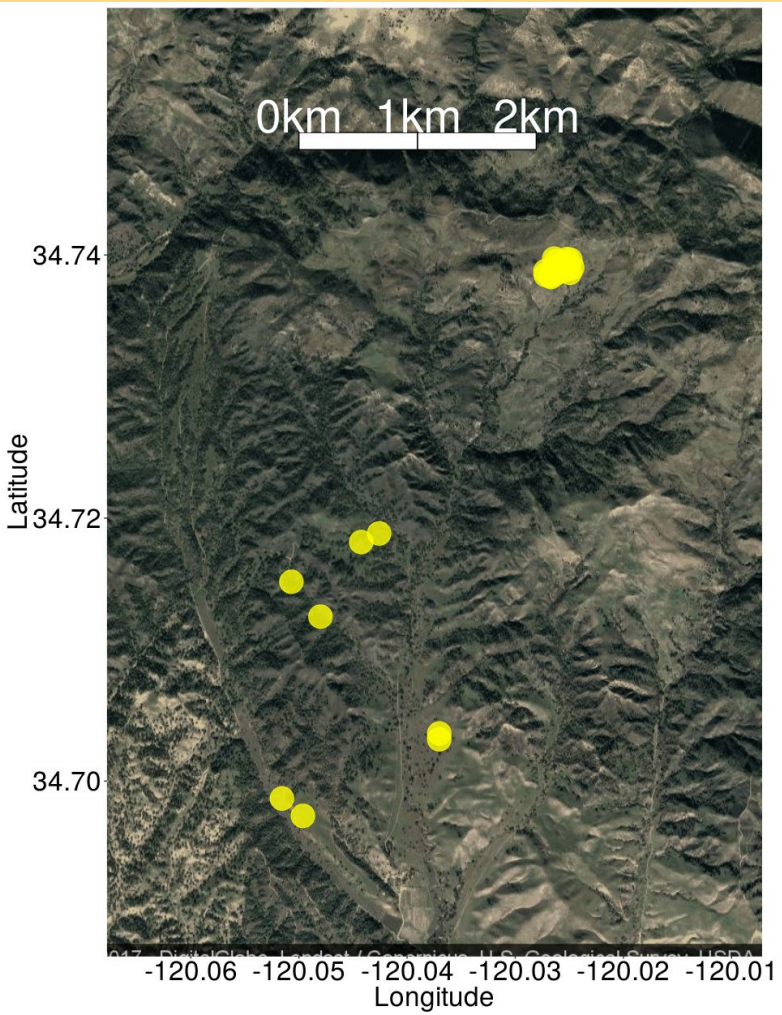

Hordeum murinum


Vulpia microstachys


Salvia columbariae


Plantago erecta

Images from CalPhotos (http://calphotos.berkeley.edu/)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34.72
34.70
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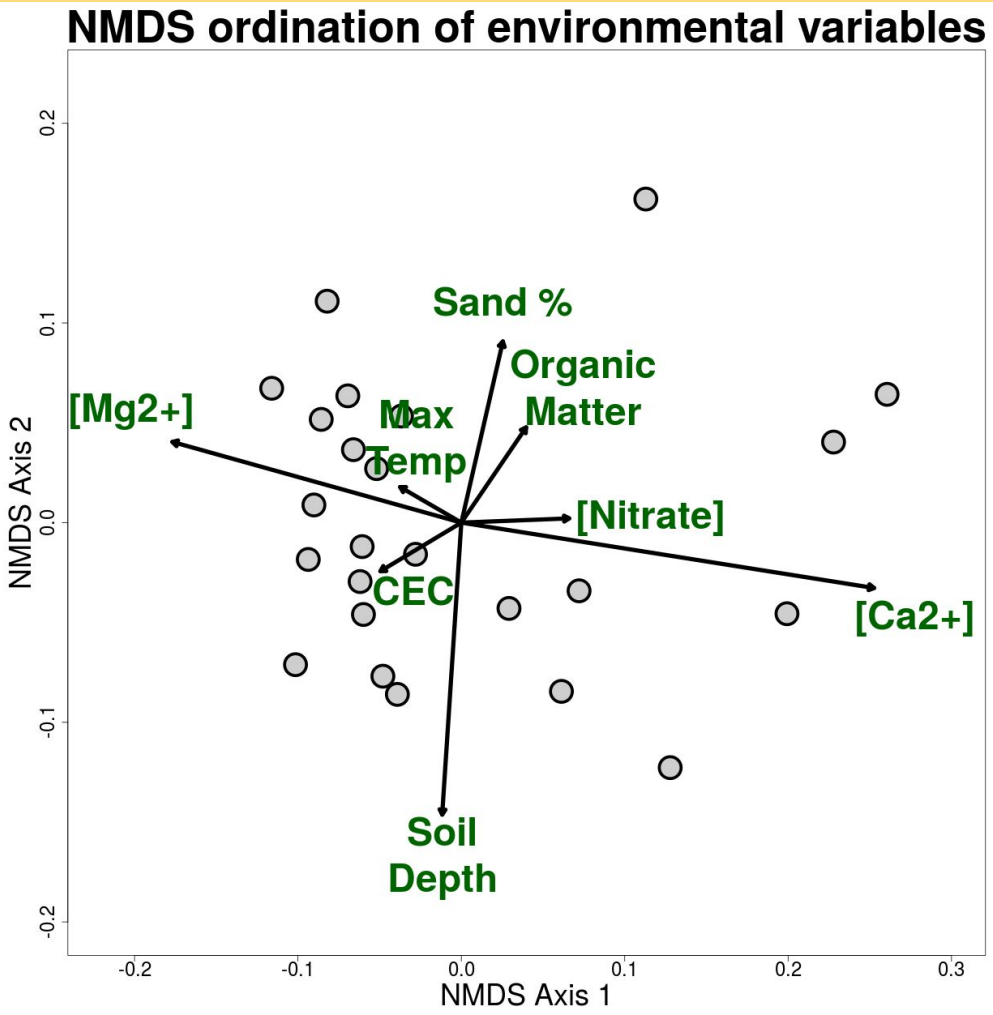
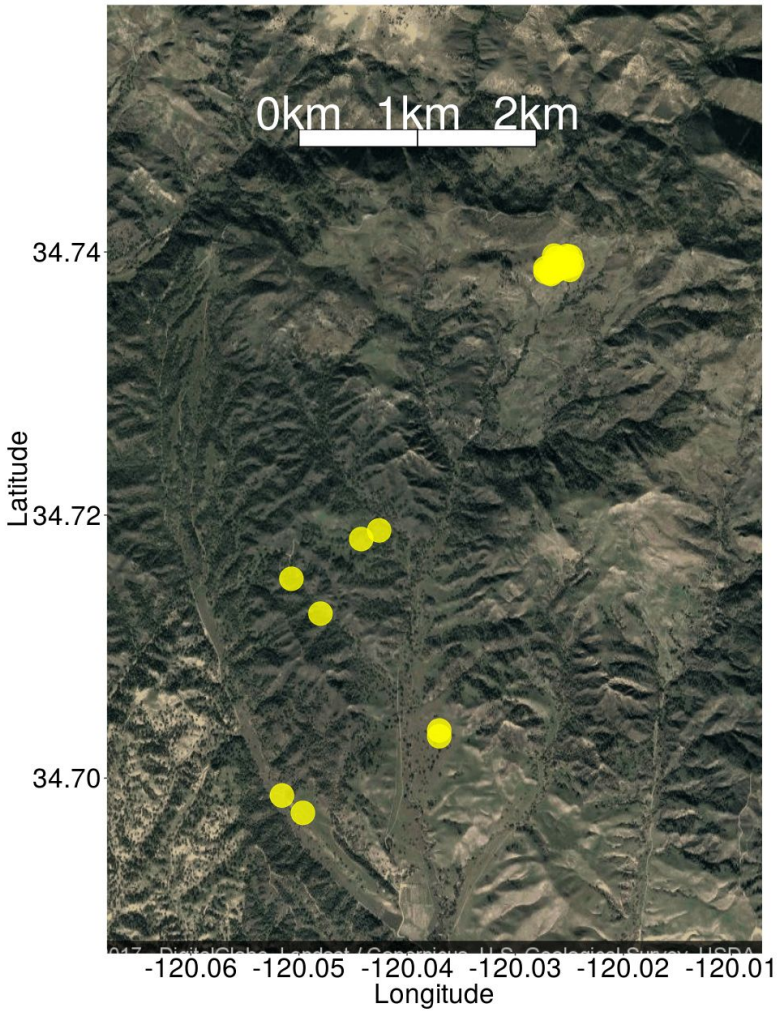
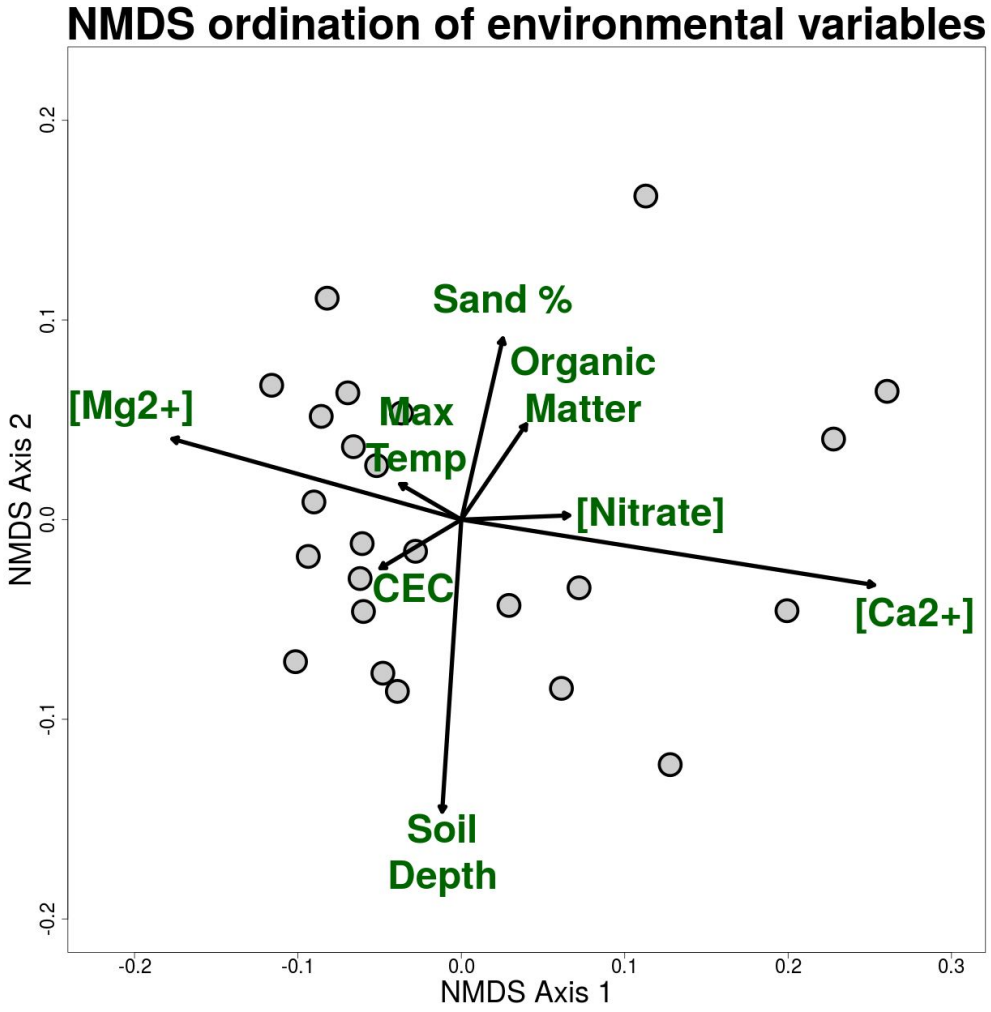
-120.06 -120.05 -120.04 -120.03 -120.02 -120.01
Longitude


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



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+
9CCCCGGGGGGGGGGGGGFGAAGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGG
@753_2016_S83_L001:132:000000000-AYYCC:1:1101:20240:1570 1:N:0:TAGCGCTC+AAGGCTAT
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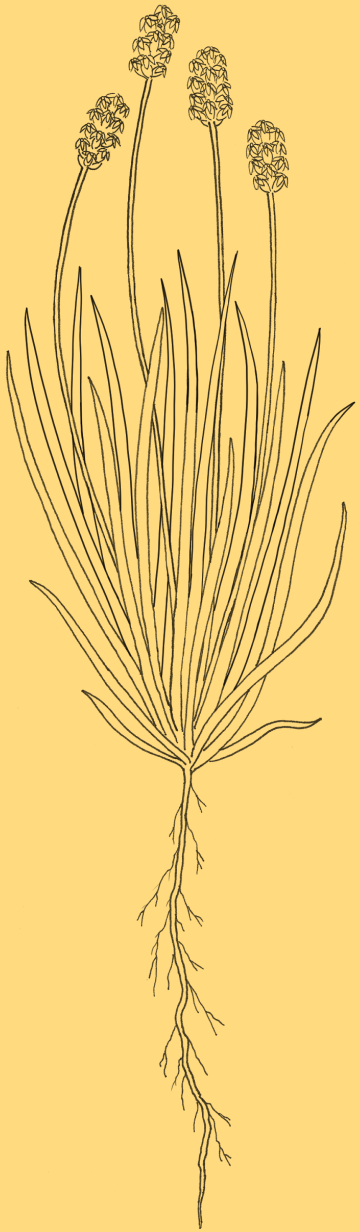
```

Leaves
Leaf size
Specific leaf area
Leaf dry matter content
δC^{13} (Integrated WUE)
Leaf N concentration
Leaf osmotic potential

Roots
Specific root length
Rooting depth

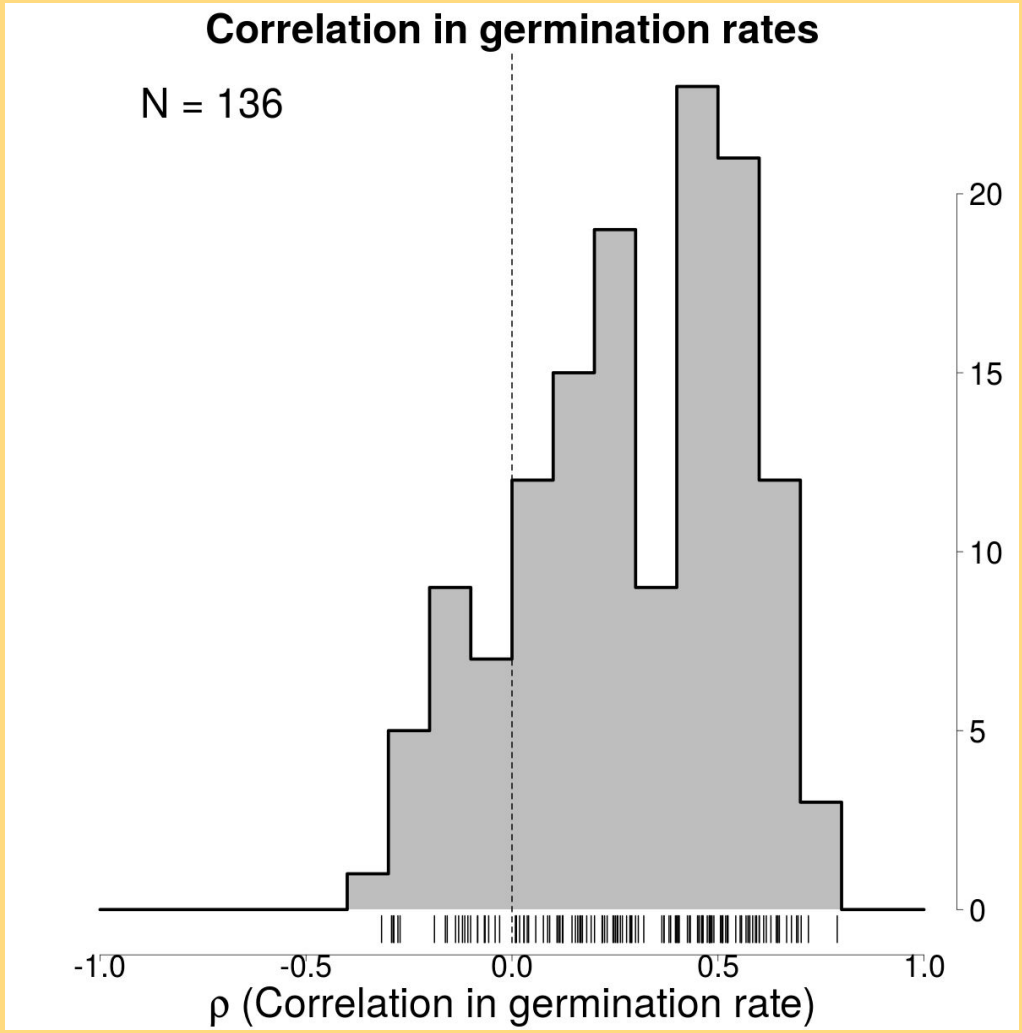


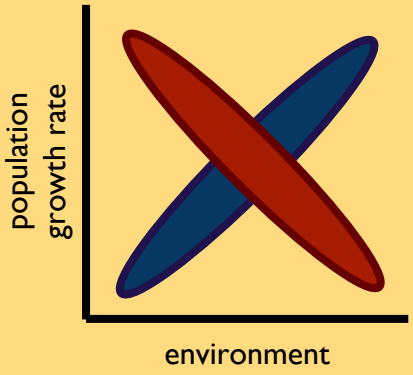
Reproduction
Seed mass
Fruiting phenology

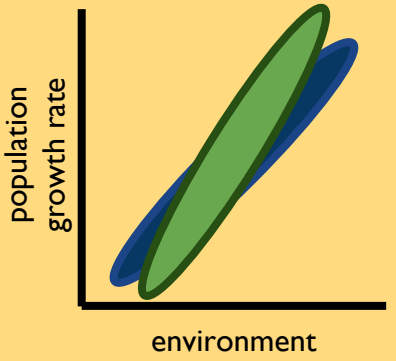
Whole-plant
Maximum height
Canopy shape index

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?

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Jamil et al. 2012 J. Veg. Sci

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

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Jamil et al. 2012 J. Veg. Sci

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.

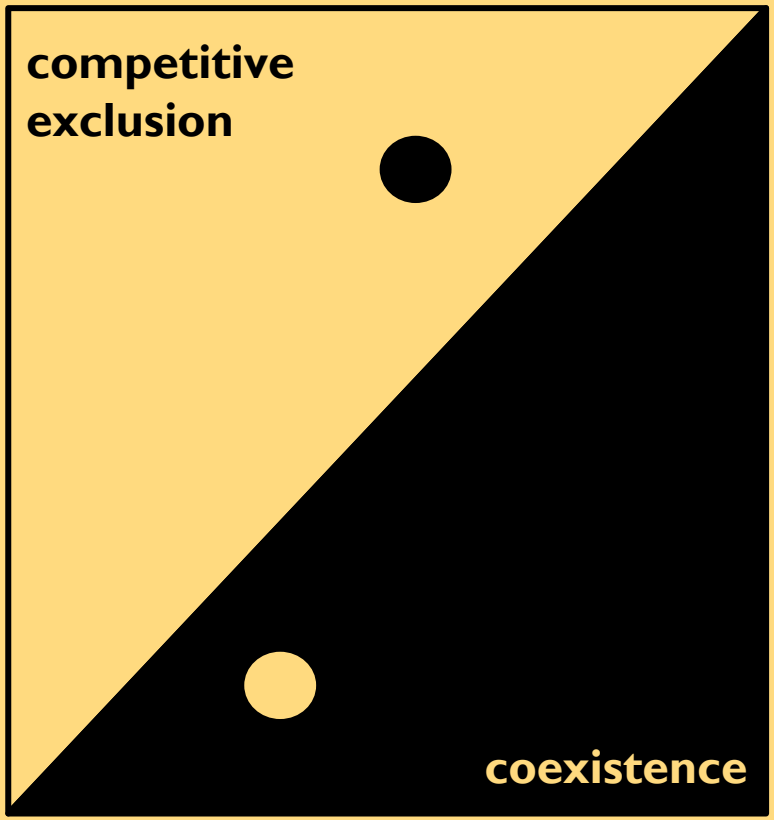
Siefert et al. 2015 Ecol. Letters

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

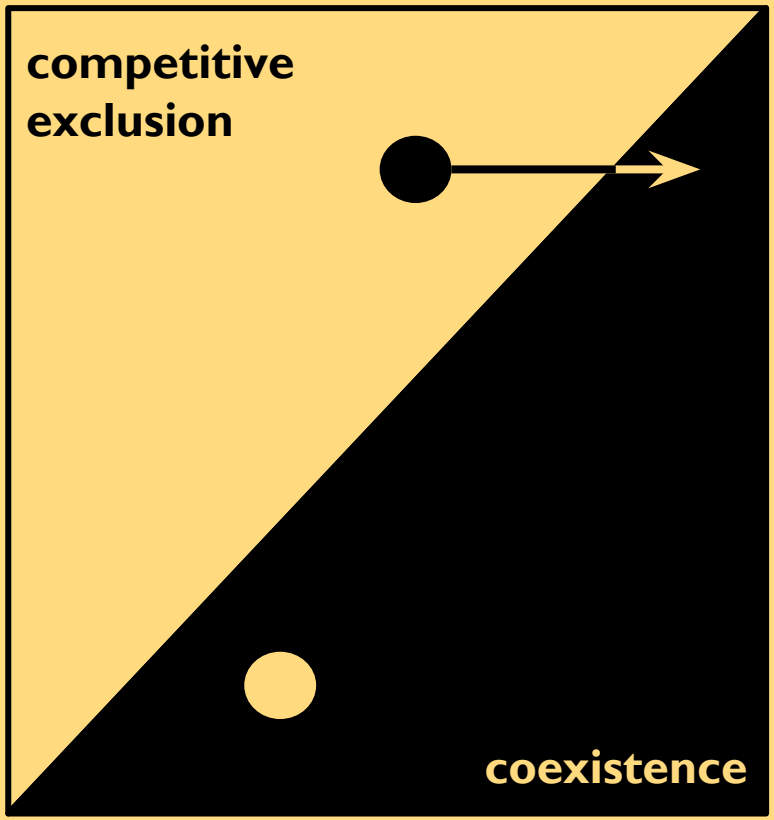
ITV may promote or destabilize coexistence



fitness difference

stabilizing niche difference

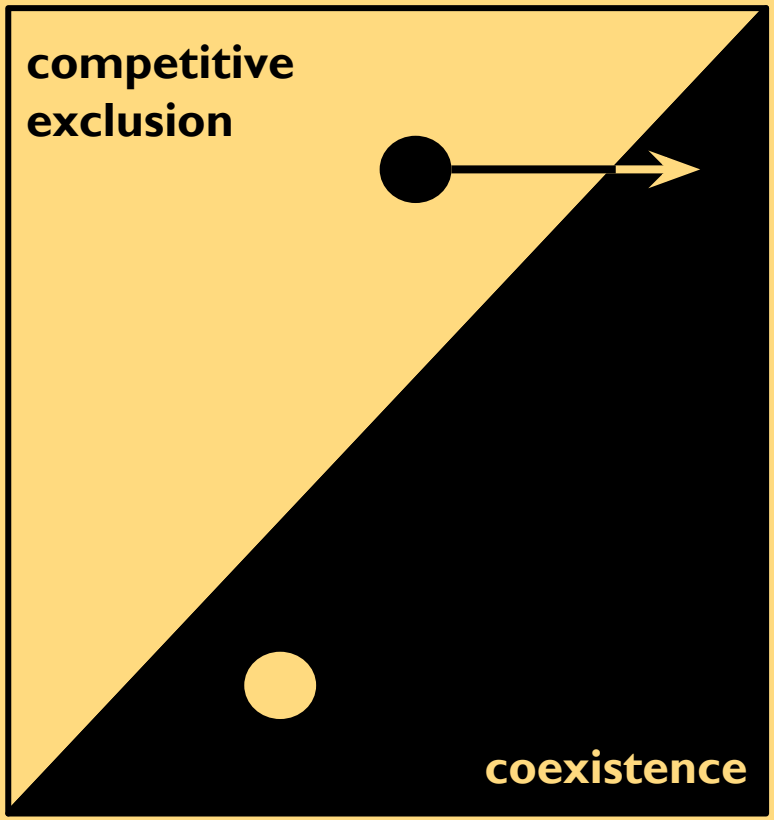
ITV may promote or destabilize coexistence



fitness difference

stabilizing niche difference

ITV may promote or destabilize coexistence



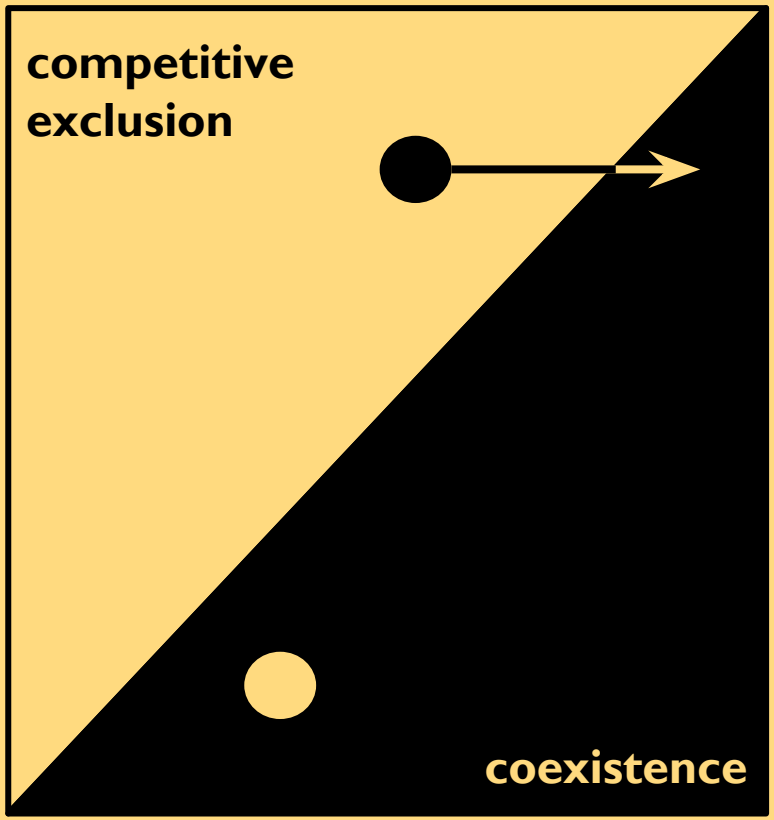
fitness difference

stabilizing niche difference

Growing without competitors

low stabilizing niche differences

ITV may promote or destabilize coexistence



fitness difference

stabilizing niche difference

Growing without competitors

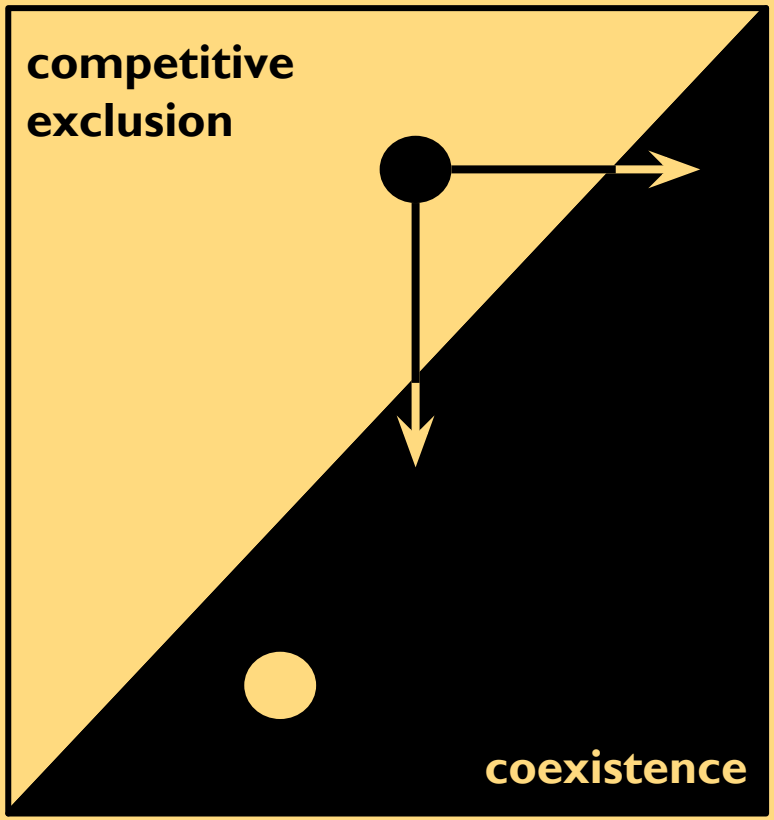
low stabilizing niche differences

Growing in competition

high stabilizing niche differences

Clark 2010 Science

ITV may promote or destabilize coexistence

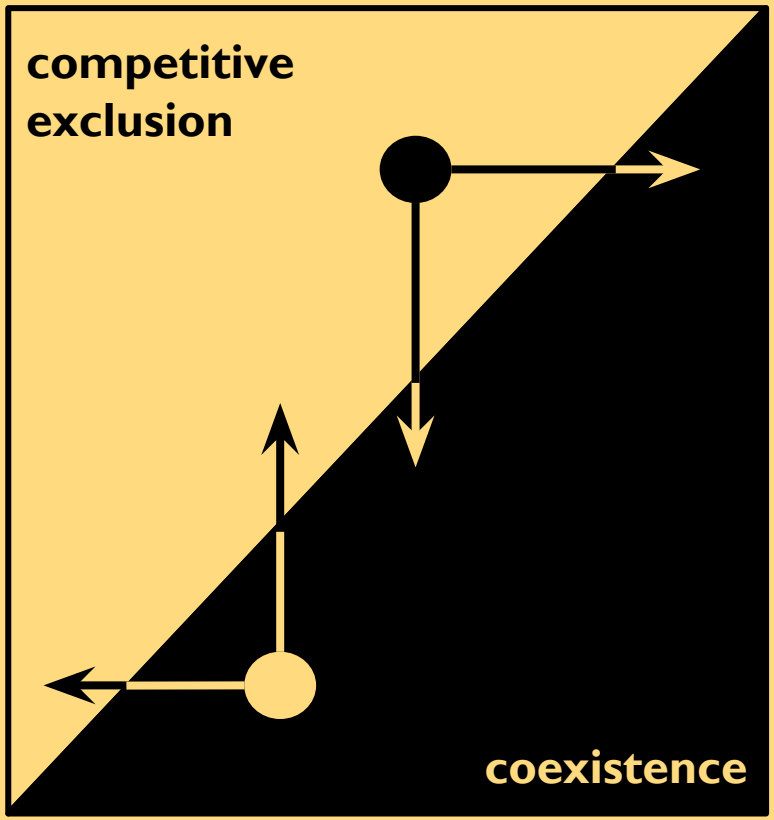


fitness difference

stabilizing niche difference

Fridley et al. 2007 J. Ecology

ITV may promote or destabilize coexistence

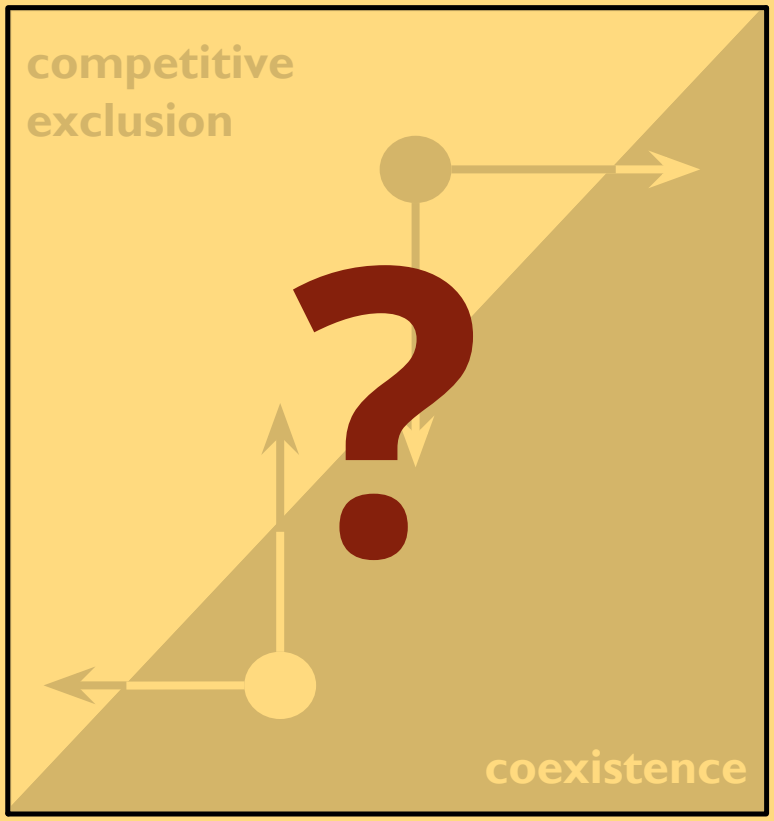


fitness difference

stabilizing niche difference

Hart et al. 2016 Ecology Letters

ITV may promote or destabilize coexistence



Outstanding questions

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

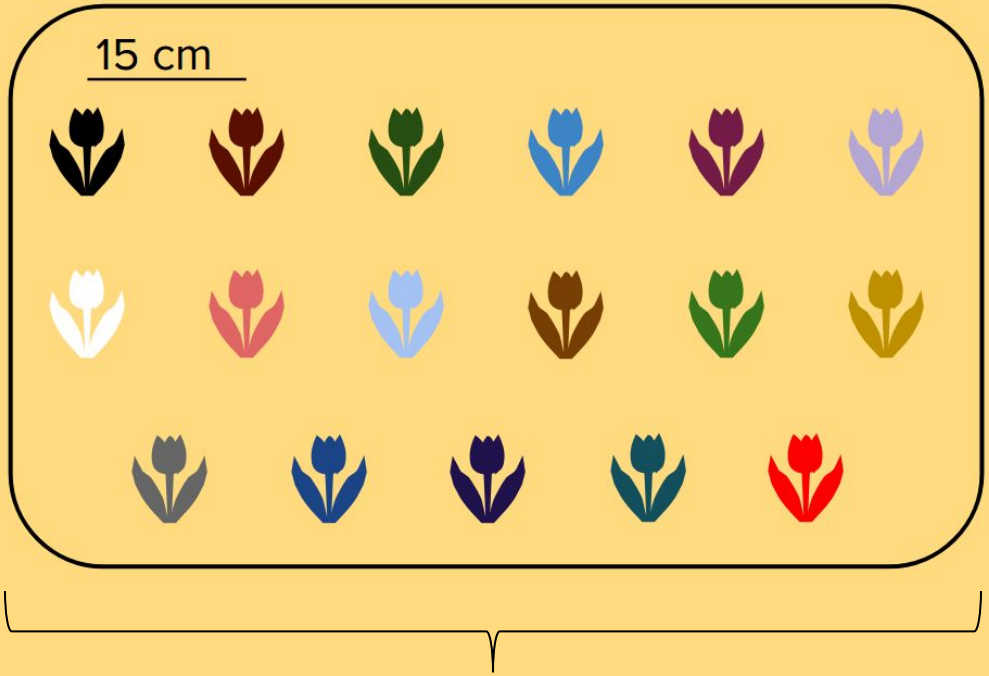
Can observed ITV change the outcome of competition?

Chapter questions

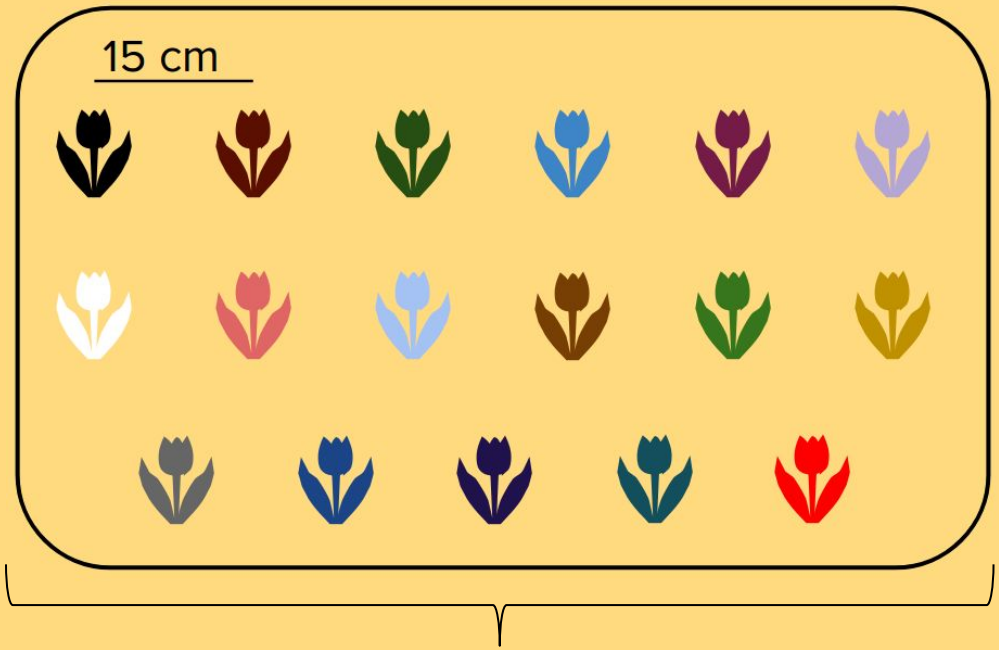
1. What is the structure of trait variation across an environmental gradient?

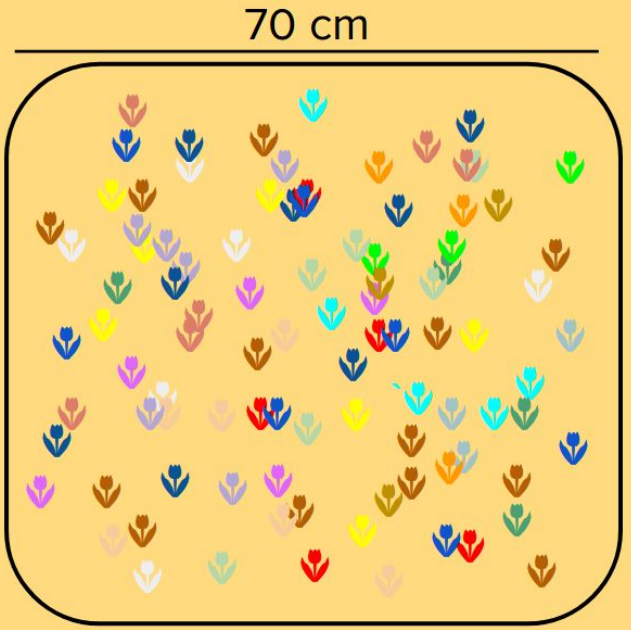
2. Do species shift their ecological strategies in competition, and how might this influence the outcome of competition?

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

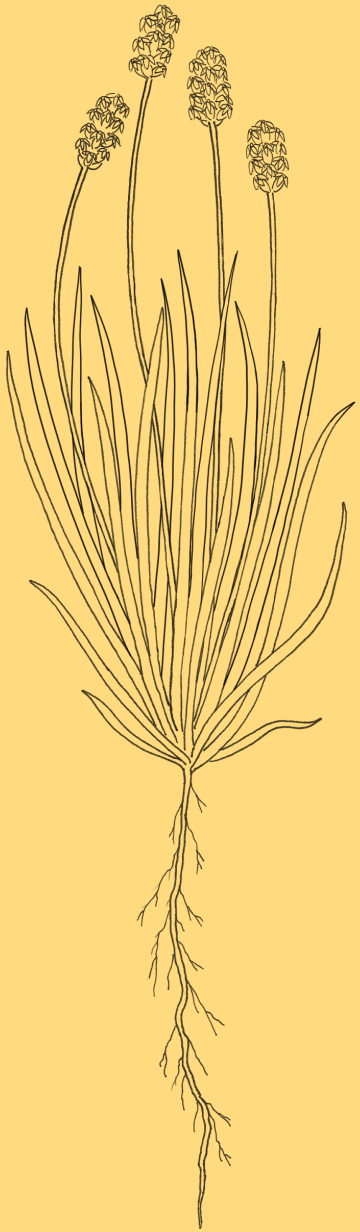


At one site, plants were grown with and without competitors





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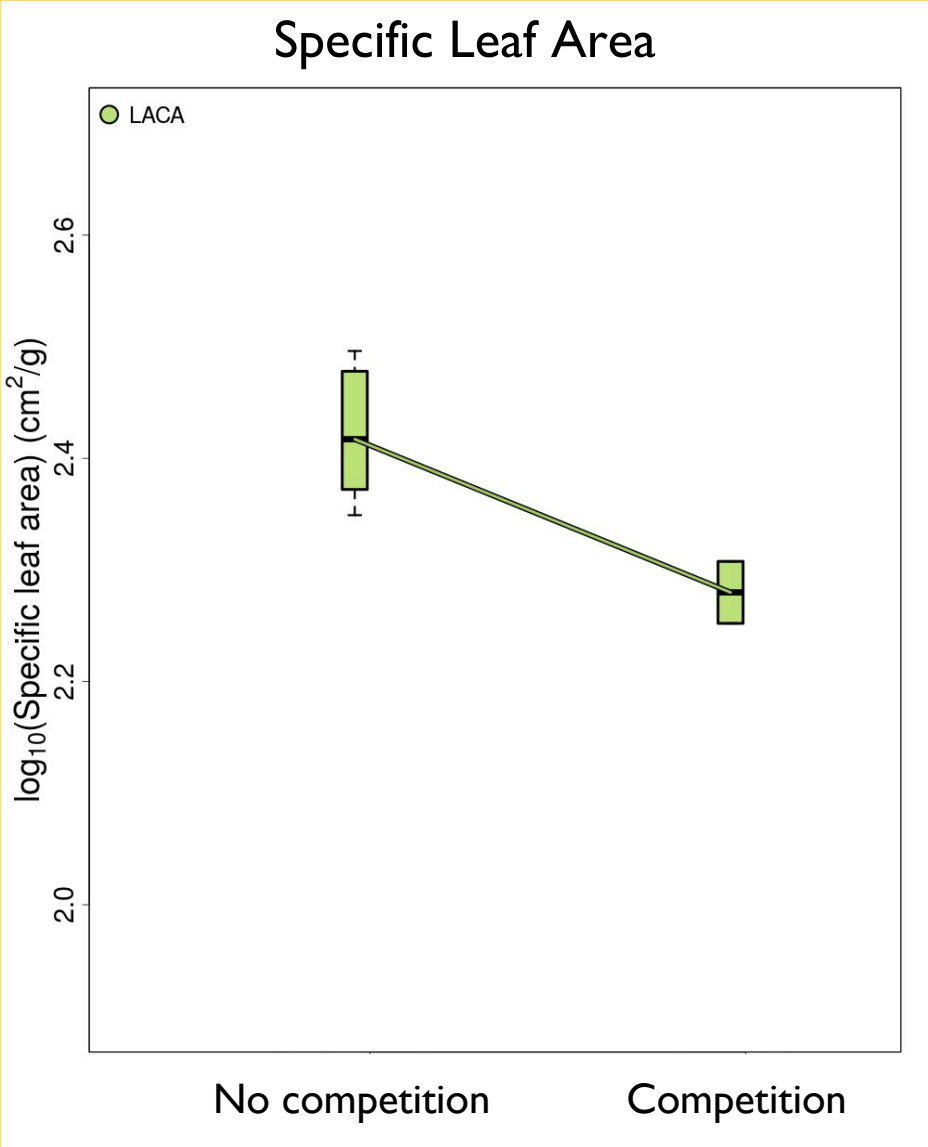
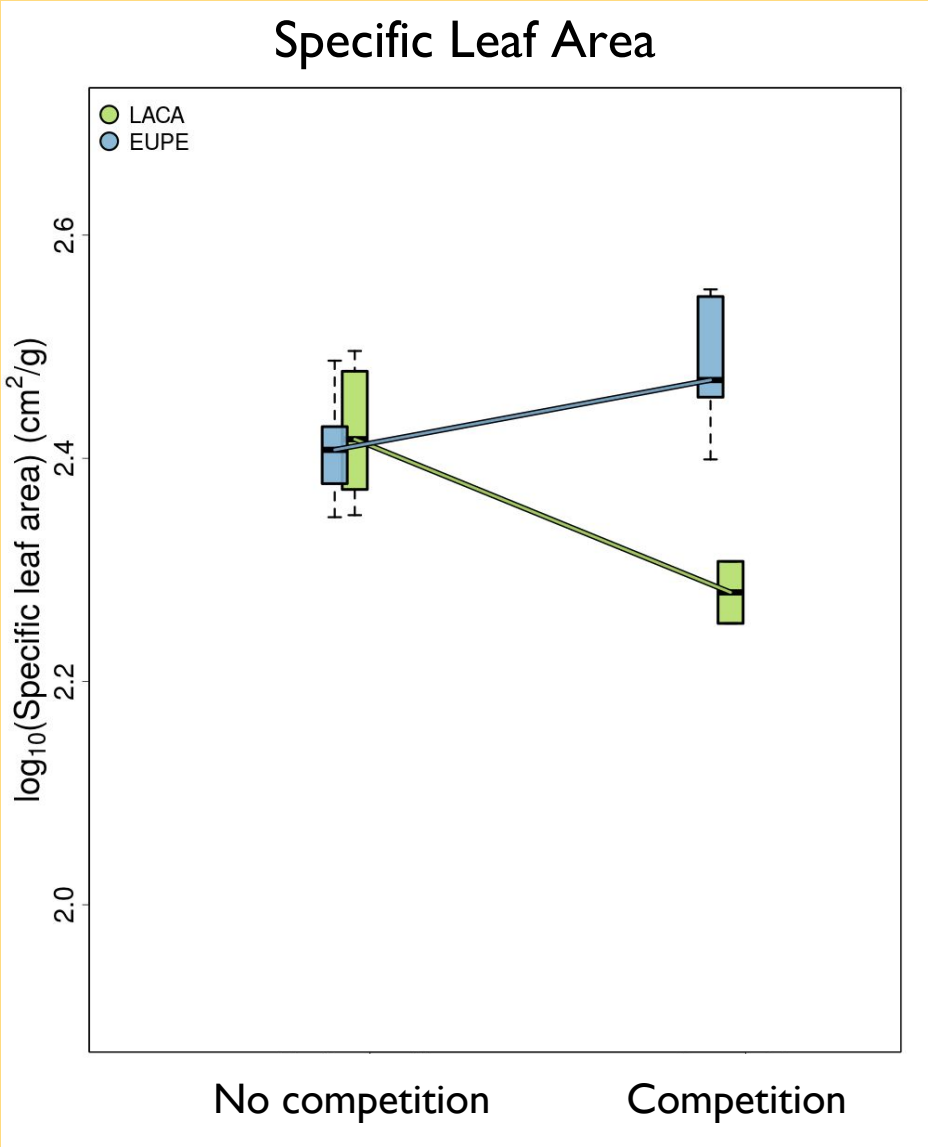
$$trait_{i,j} \sim \overbrace{a}^{\text{trait mean}} + \underbrace{b_0 x_i}_{\text{species effect}} + \overbrace{c_0 z_j}^{\text{environment effect}} + \underbrace{c_1 x_i z_j}_{\text{interaction}} + \overbrace{\epsilon_{\alpha j} + \epsilon_{\beta i} + \gamma_i}^{\text{error terms}}$$

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

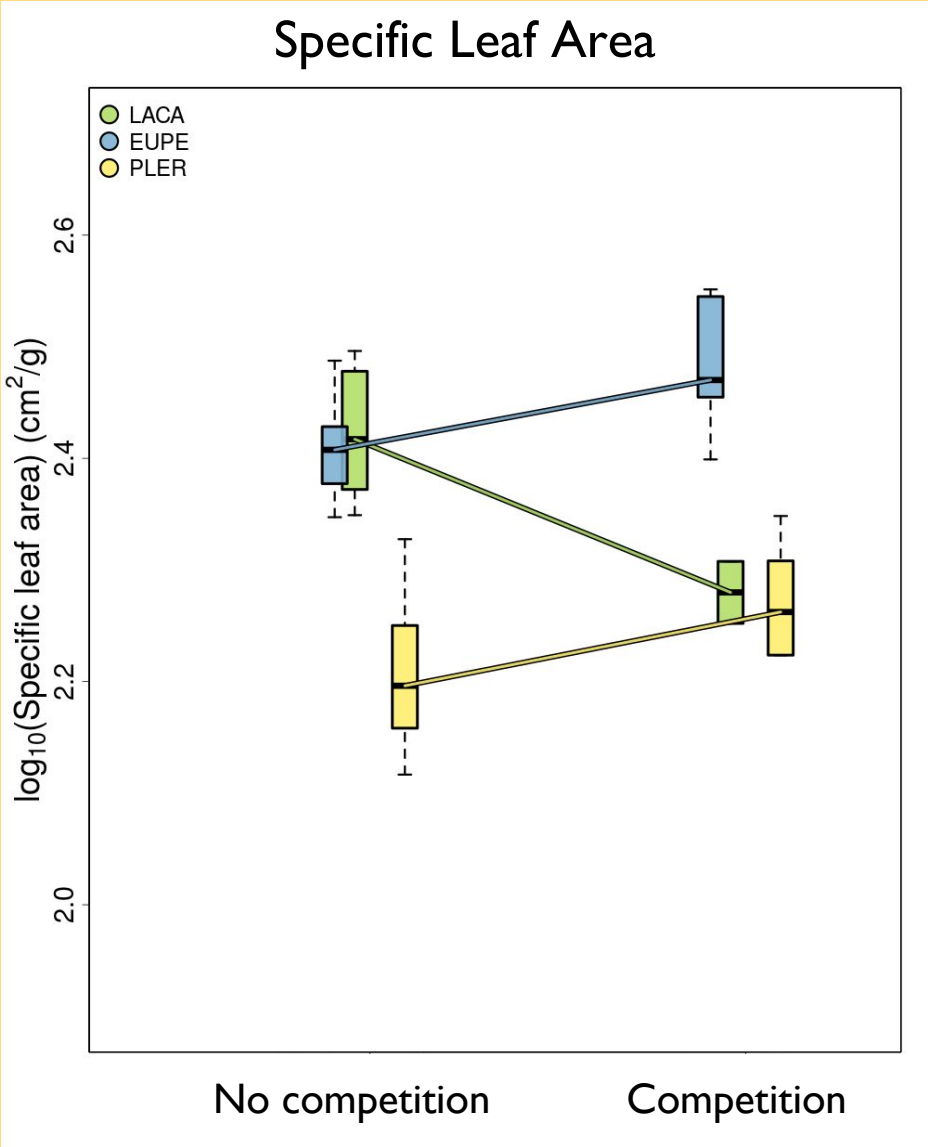
Trait changes in response to competition are species-specific



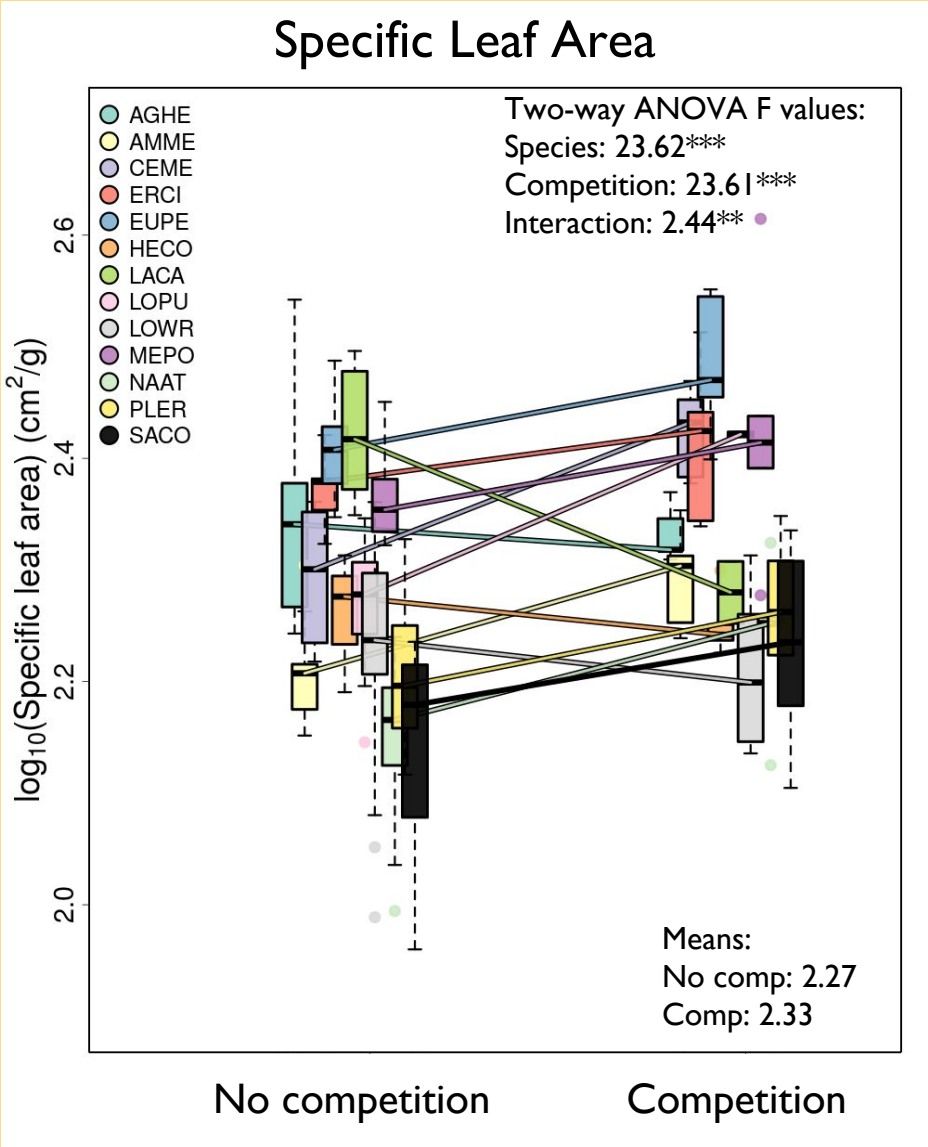
Trait changes in response to competition are species-specific



Trait changes in response to competition are species-specific

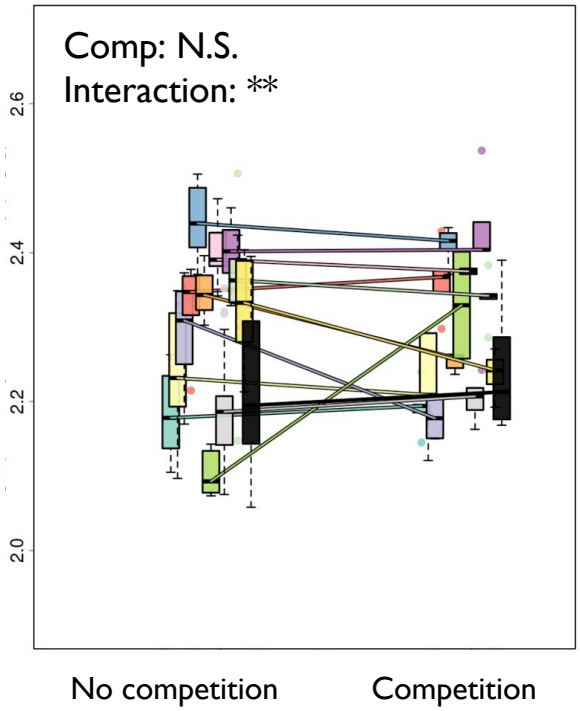


Trait changes in response to competition are species-specific

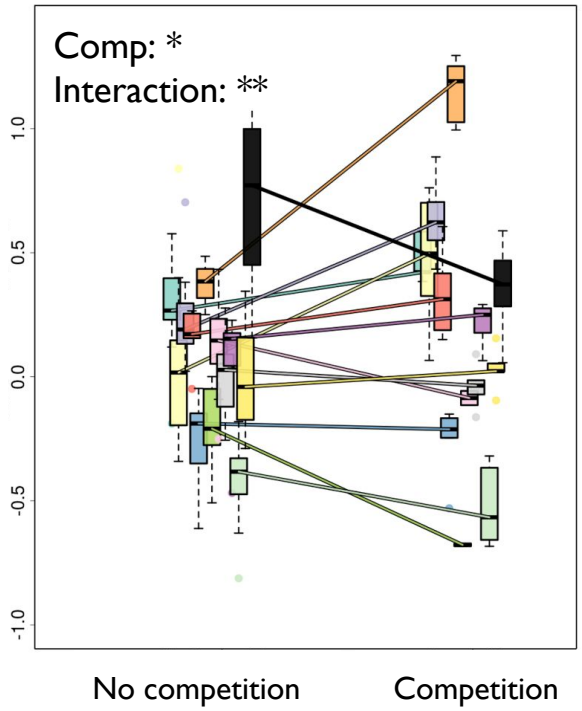


Trait changes in response to competition are species-specific

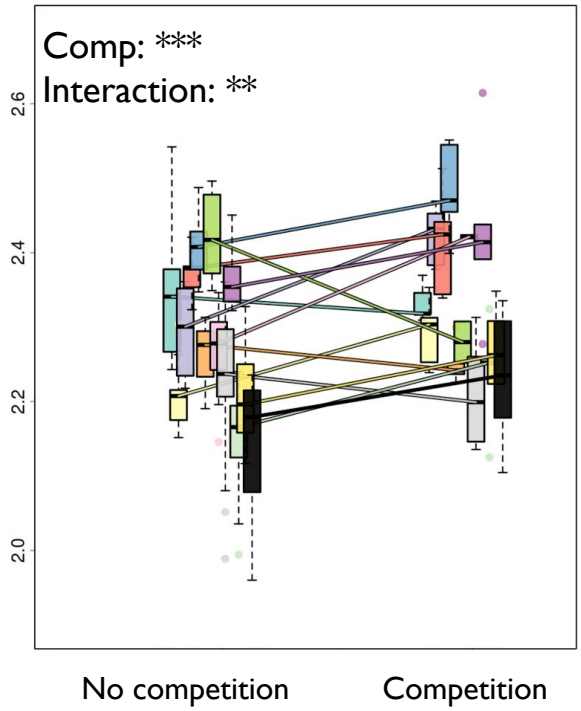
Leaf Dry Matter Content



Leaf Size



Specific Leaf Area



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

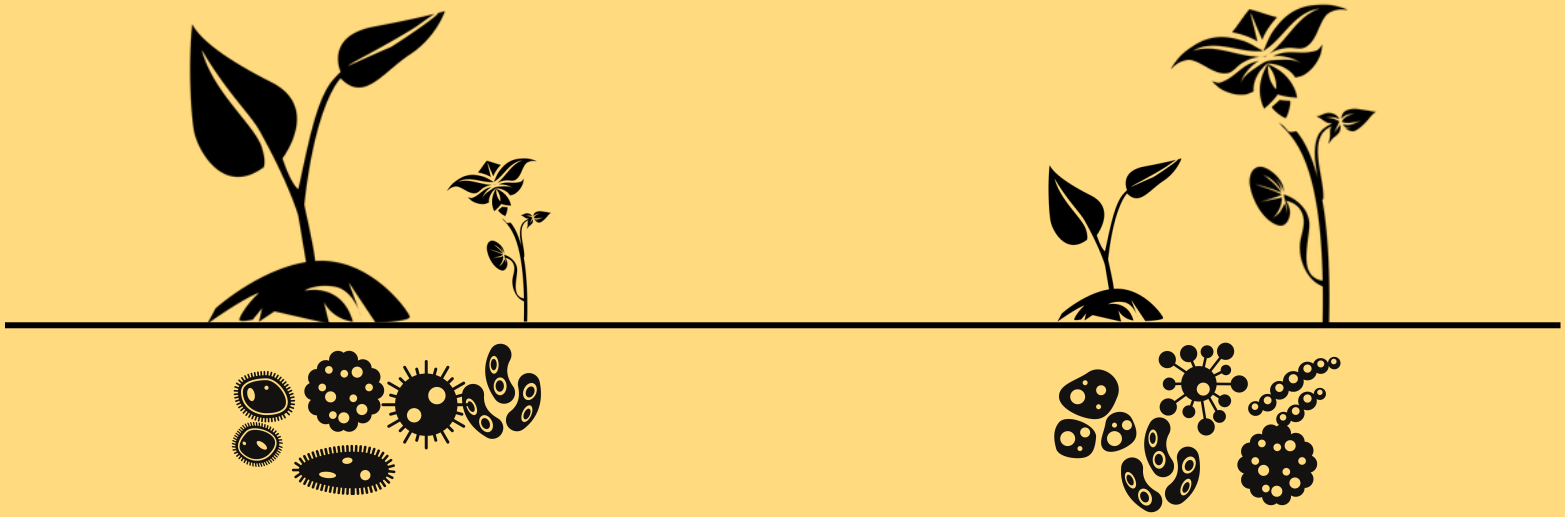
Plant ecologists lack a clear understanding of how some fundamental ecological processes structure communities

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.



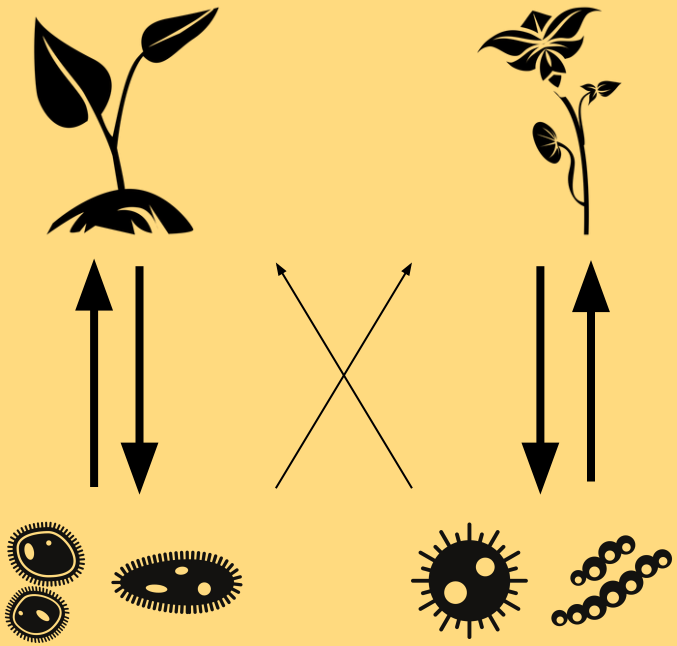
Van der Putten et al. 1993 Nature; Redman 2002 Science; Mangan et al. 2010 Nature

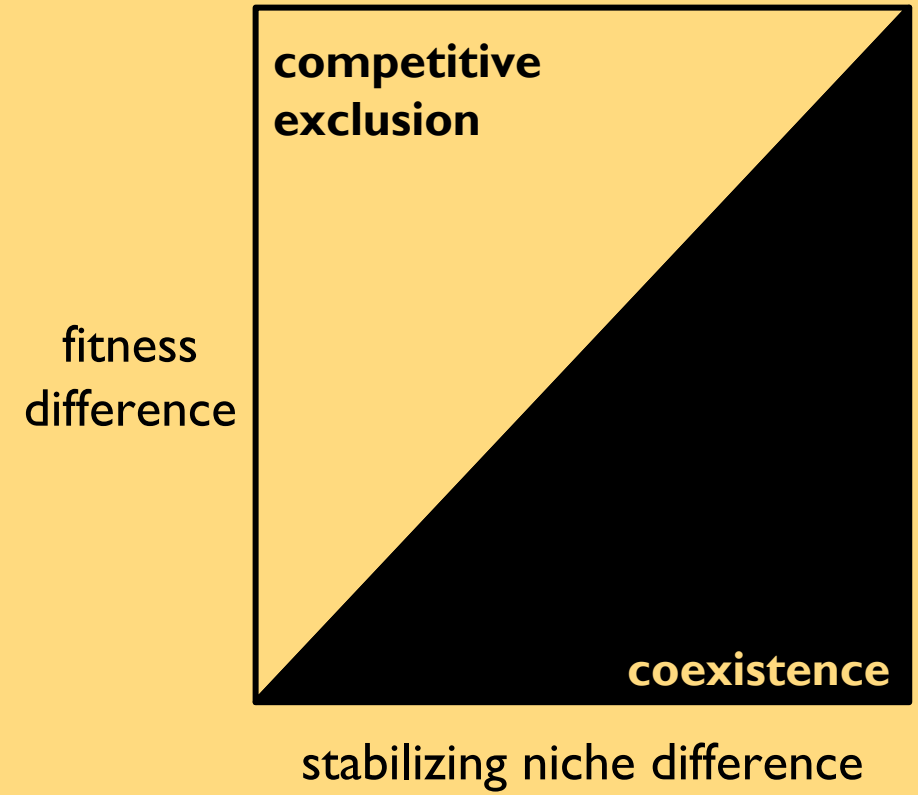
Plant-soil feedbacks can promote plant species coexistence

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

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

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

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

Chesson & Kuang (2008) Nature

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

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

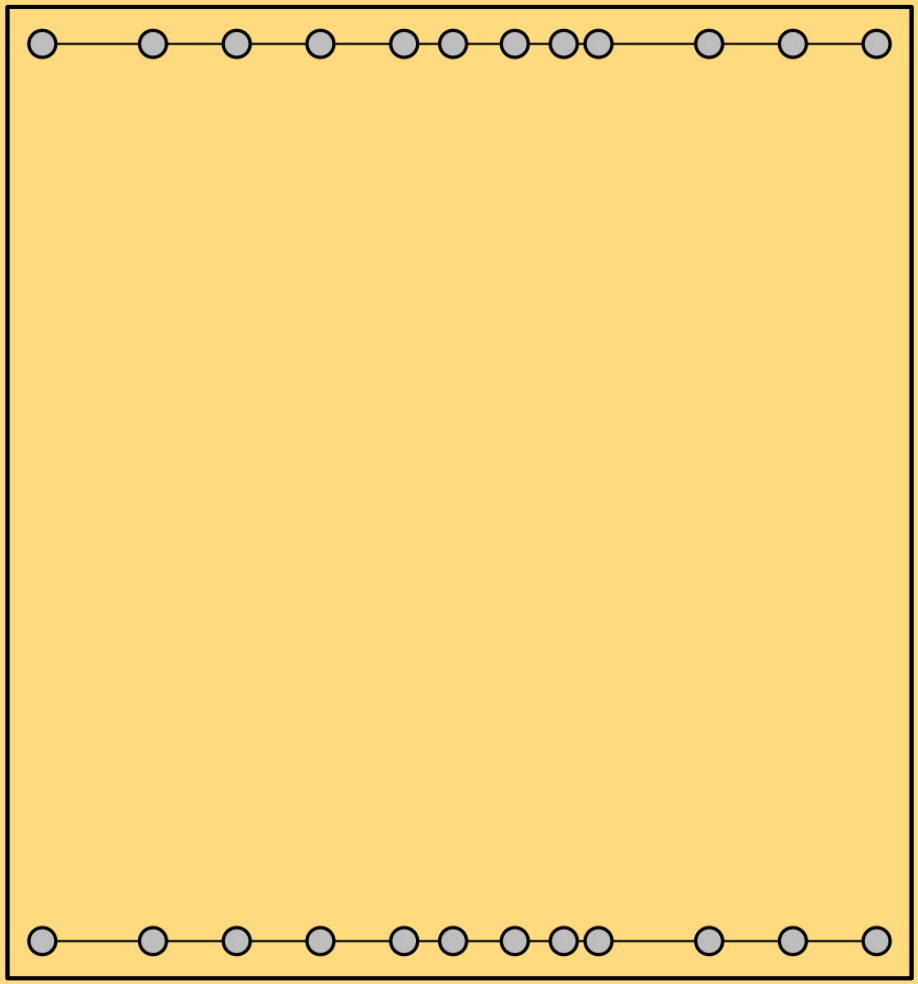
Species fitness = $\frac{\sum_l \frac{C_{jl} v_l}{\alpha_l^R} - \sum_m \frac{a_{jm}}{\alpha_m^P} - \mu_j}{\sqrt{\left(\sum_l \frac{c_{jl}^2 v_l}{r_l^R \alpha_l^R} + \sum_m \frac{a_{jm}^2 w}{r_m^P \alpha_m^P}\right)}}$

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



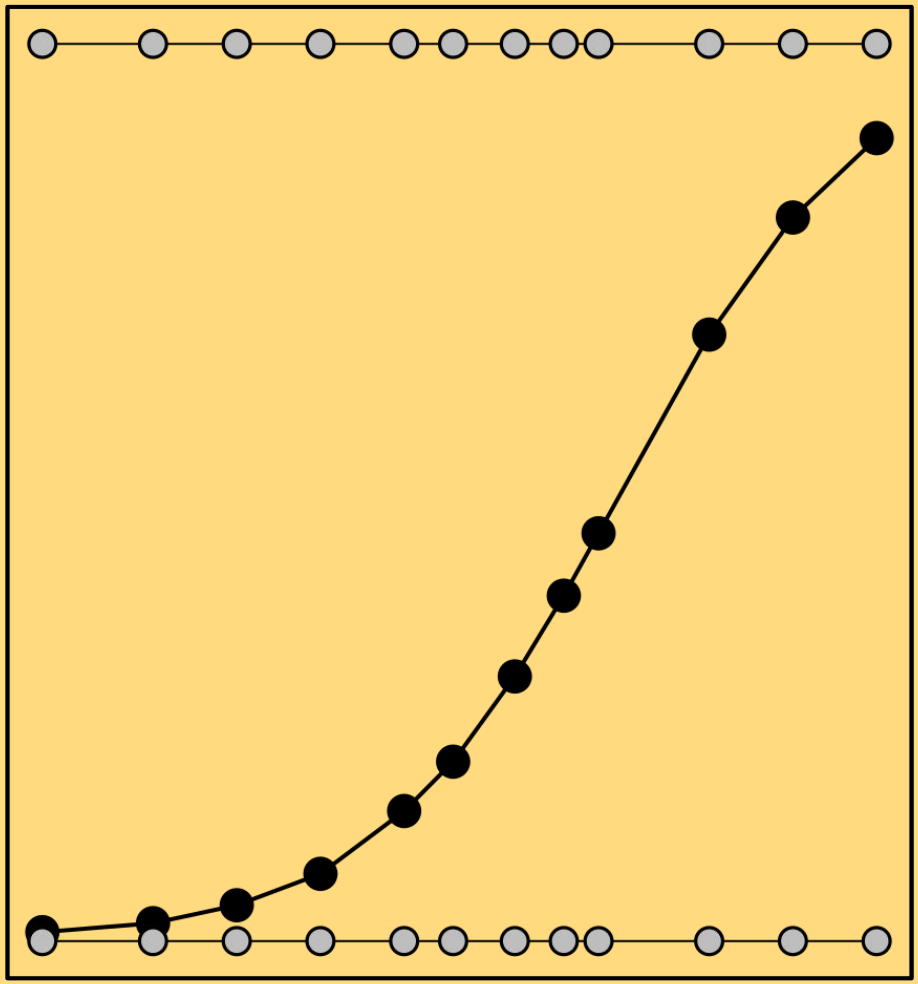
niche differences

Niche differences due to natural enemies

Niche differences due to resource use

resource replacement rate (r^R)

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



niche differences

resource replacement rate (r^R)

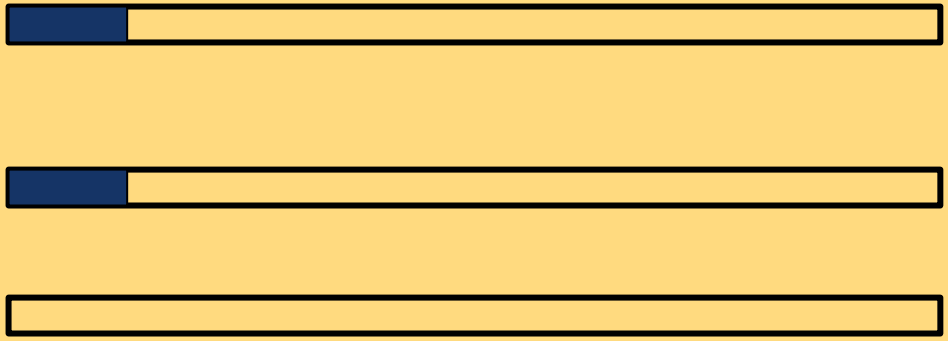
Niche differences due to natural enemies

Niche differences due to resource use

Modeling

Literature review

Writeup



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

Dissertation Questions

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

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

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

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

A better understanding of the impact of how these processes shape natural communities will help progress towards a **theoretically justified and predictive community ecology**

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

Acknowledgements

Kraft Lab
Nathan Kraft
Claire Fortunel
Andy Kleinhesselink
Ian McFadden
Suzanne Ou
Mary Van Dyke
Marcel Vaz

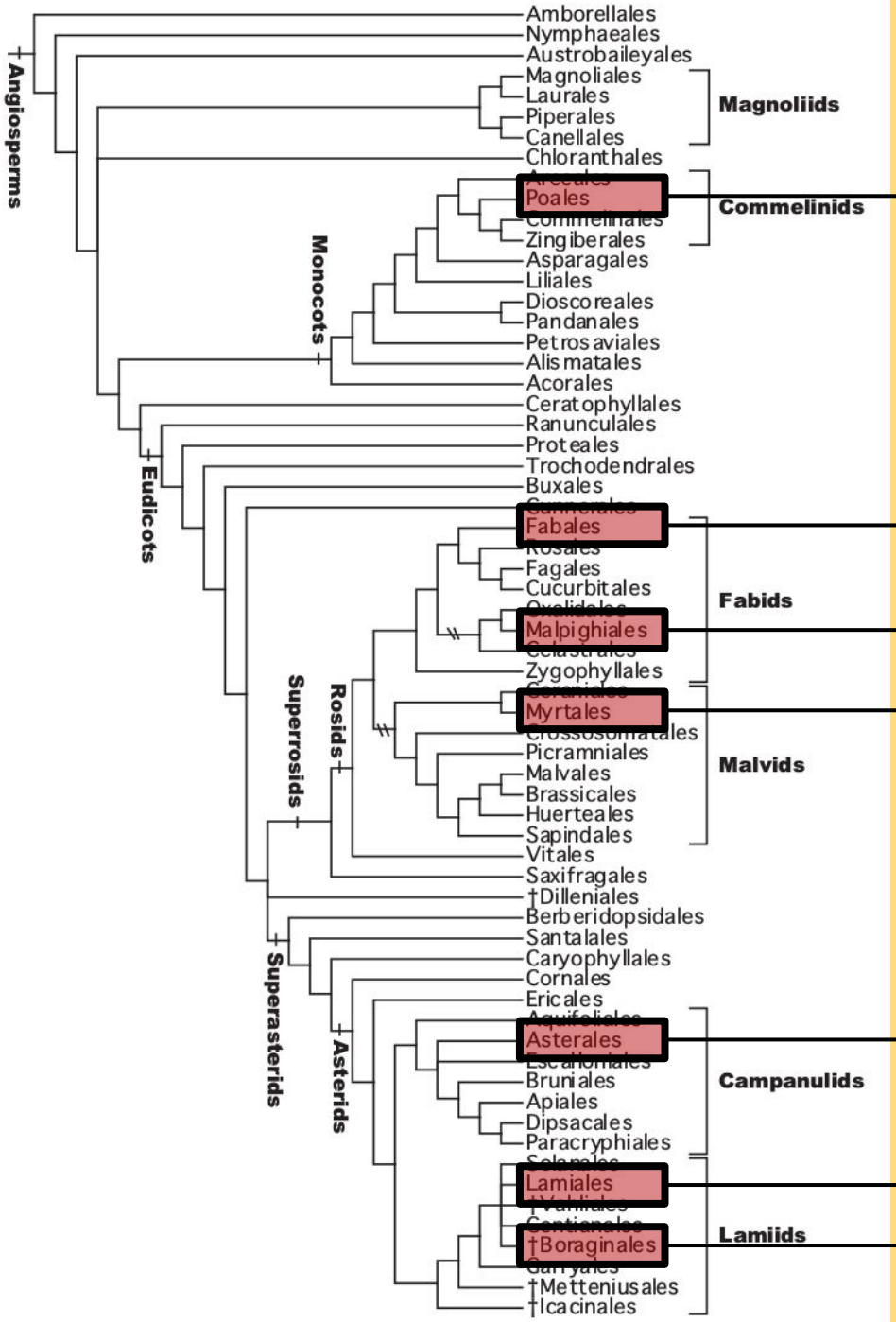
Collaborators
Jonathan Levine
Will Petry
Oscar Godoy
Renato Guidon
Amanda Friese
Jordan Moberg-Parker
Mirjam von Rütte

Committee
Jennifer Martiny
Lawren Sack
Felipe Zapata

UCLA
Emily Curd
Zack Gold
Sack Lab
Rachel Meyer

UCLA Undergrads
Clare Camilleri
Angela Chen
Bastien Dehaut
Aoife Galvin
Xin Yi Yan

Funding



Poaceae

Fabaceae

Euphorbiaceae

Onagraceae

Asteraceae

Lamiaceae; Plantaginaceae

Boraginaceae

Phylogeny: APG IV