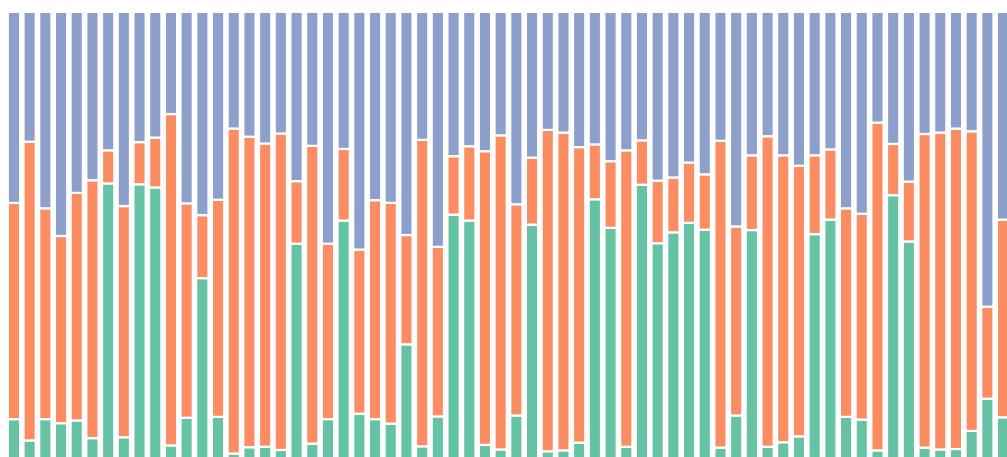


# Identifying Models of Trait-Mediated Community Assembly

using random forests and  
approximate Bayesian computation

Megan Ruffley, Katie Peterson,

Bob Week, David C. Tank,  
Luke J. Harmon



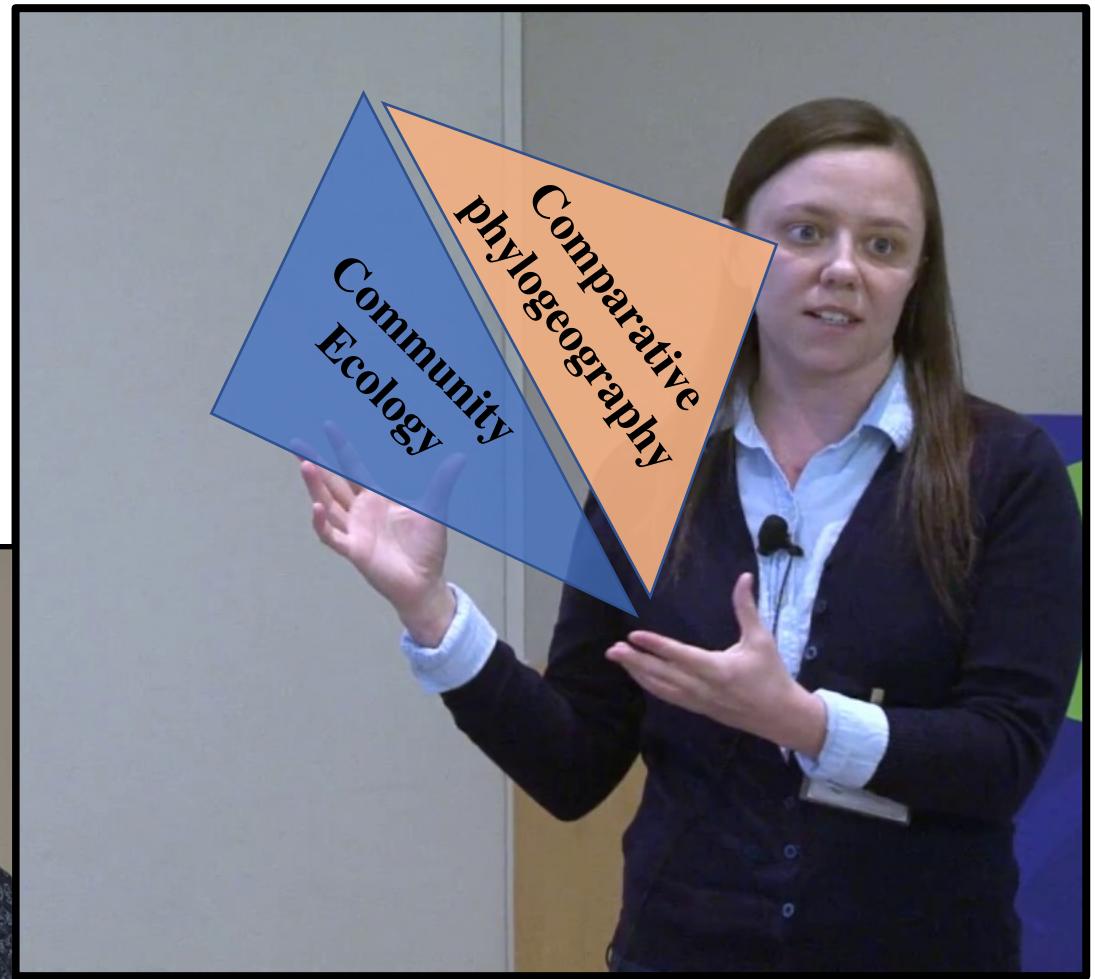
- Megan Ruffley (she/her)
- University of Idaho
- Institute for Bioinformatics and Evolutionary Studies (**Ibest**)
- Bioinformatics and Computation Biology
- Plants
- Roller Derby



David C. Tank

Jack Sullivan

Luke J. Harmon



# Interested in identifying neutral and non-neutral processes of assembly

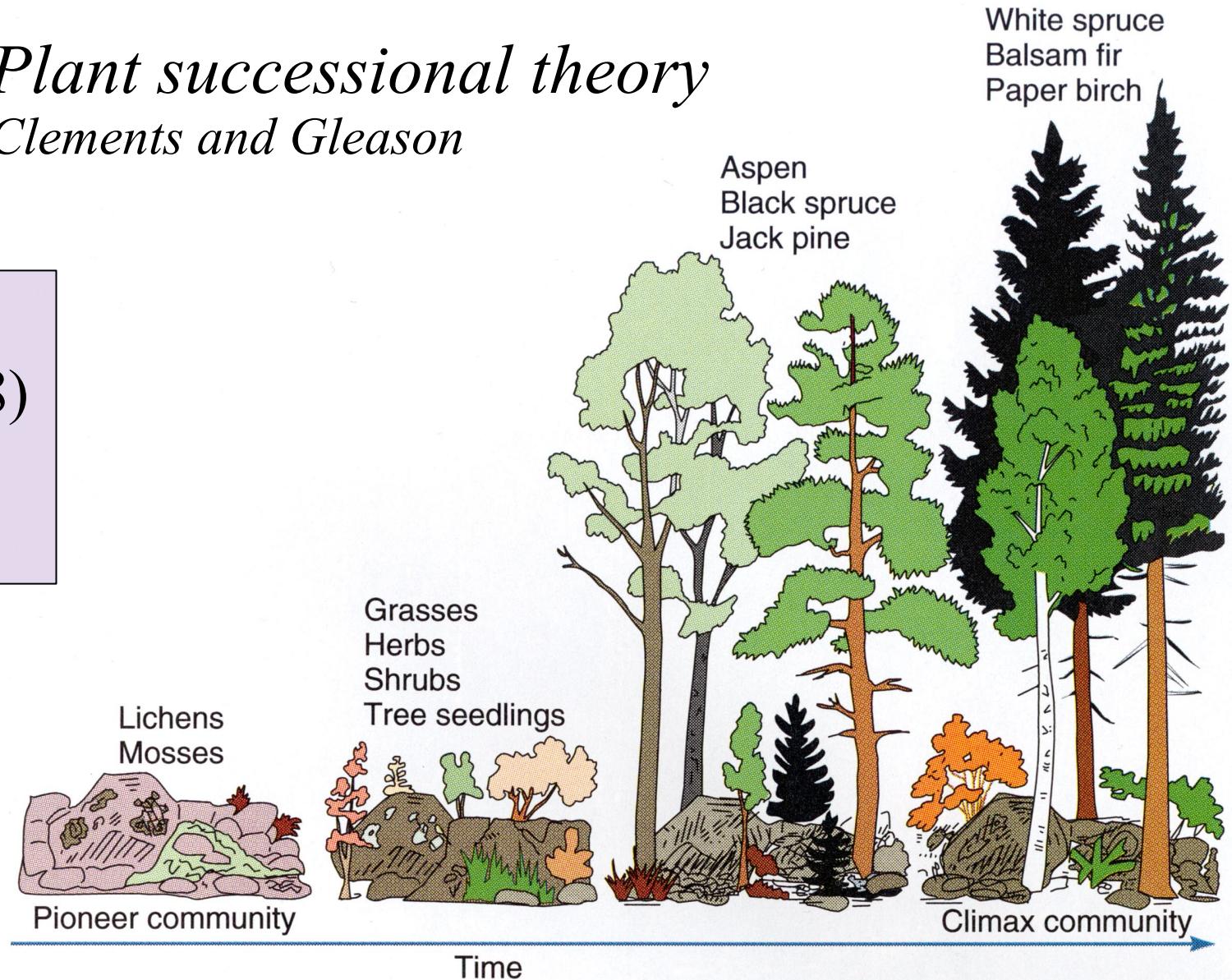


*“The processes that determine the patterns of the number and composition of co-occurring species have been central to community ecology for decades...” Chase 2003.*

## *Plant successional theory*

Clements and Gleason

Are communities a result of  
*deterministic* (Clements 1938)  
or *stochastic* (Gleason 1927)  
processes?



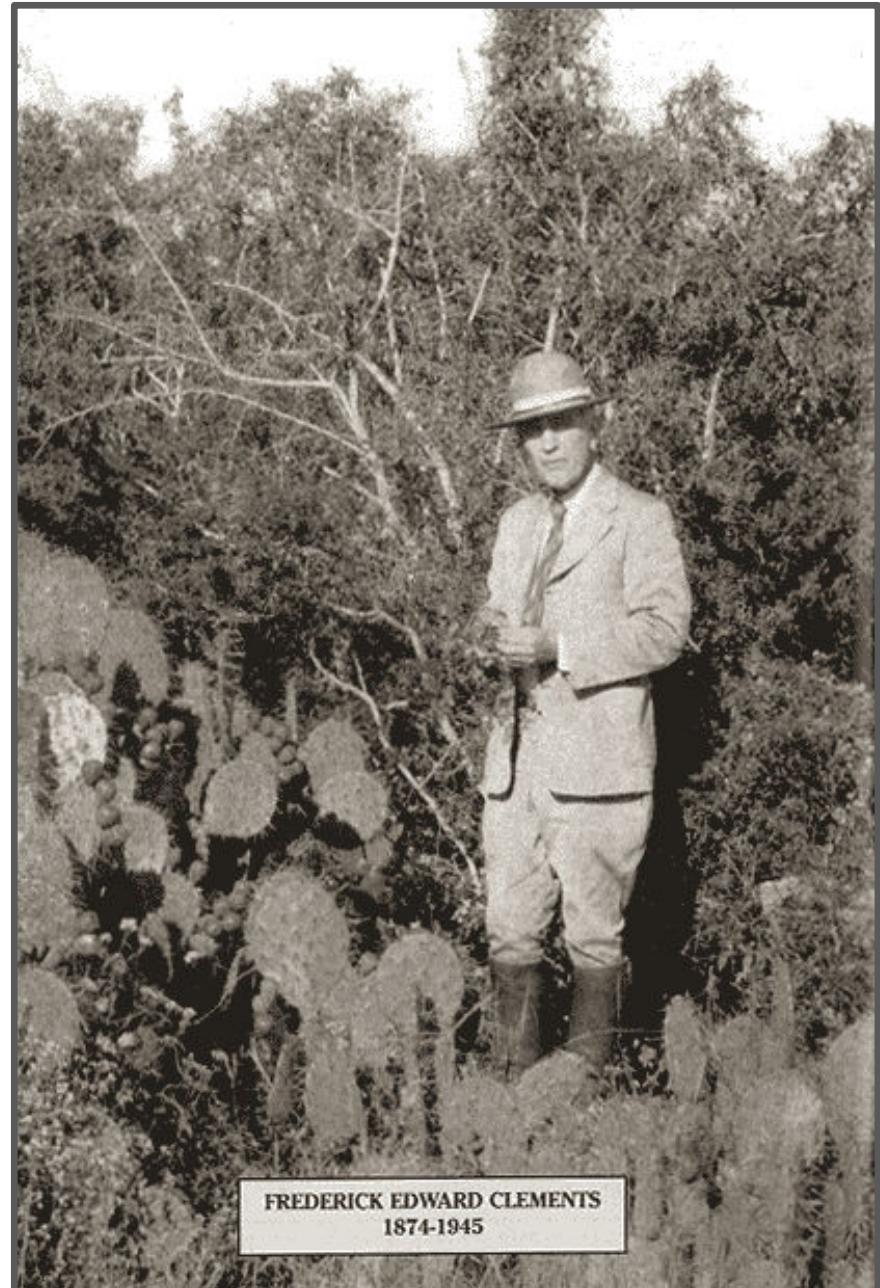
## Frederic Clements (1916)

“Succession is deterministic”

-stable ‘climax’ community that is in perfect balance with the climate

“Communities are super-organisms”

-Communities are dependent on the species interactions among members

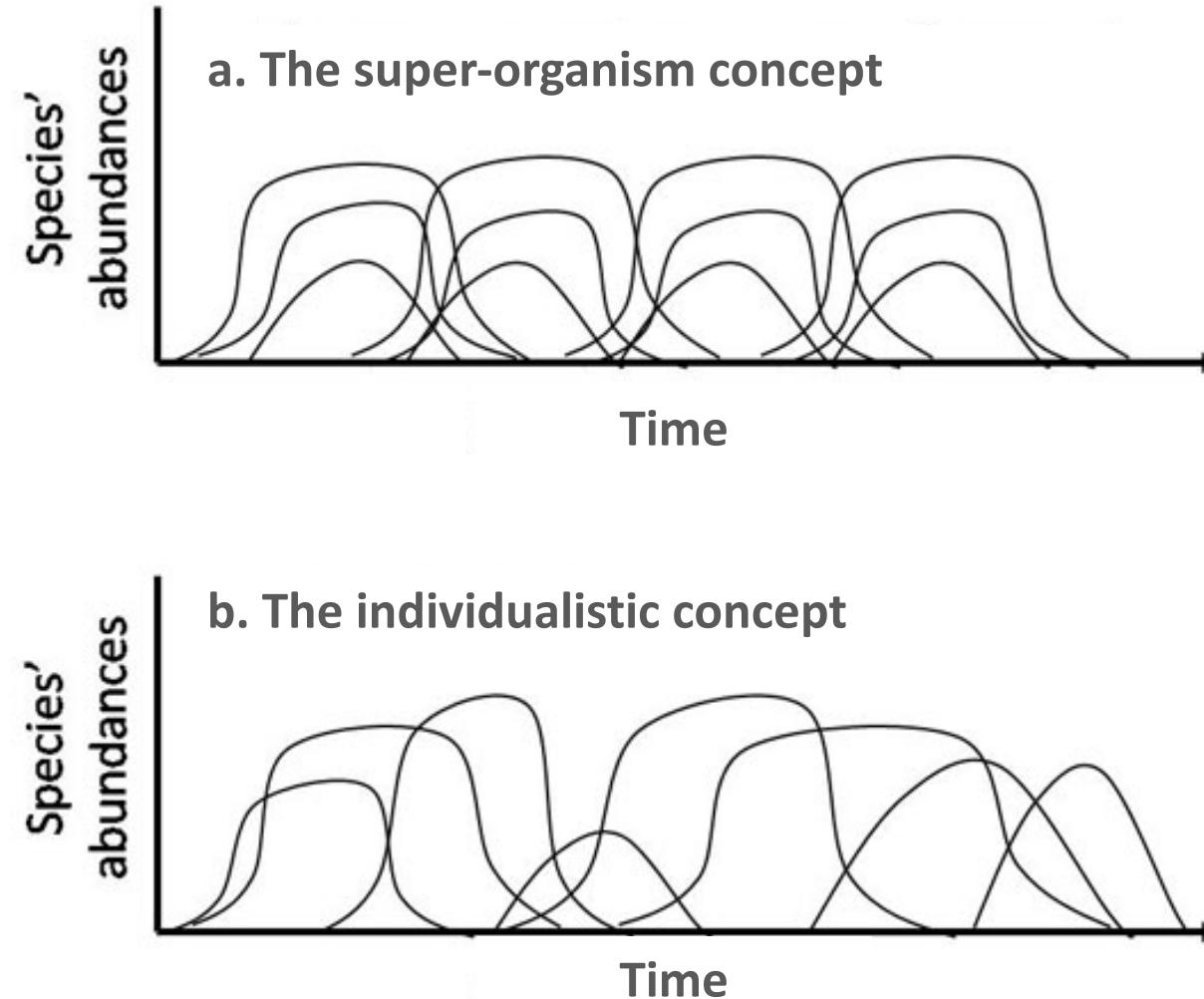


FREDERICK EDWARD CLEMENTS  
1874-1945

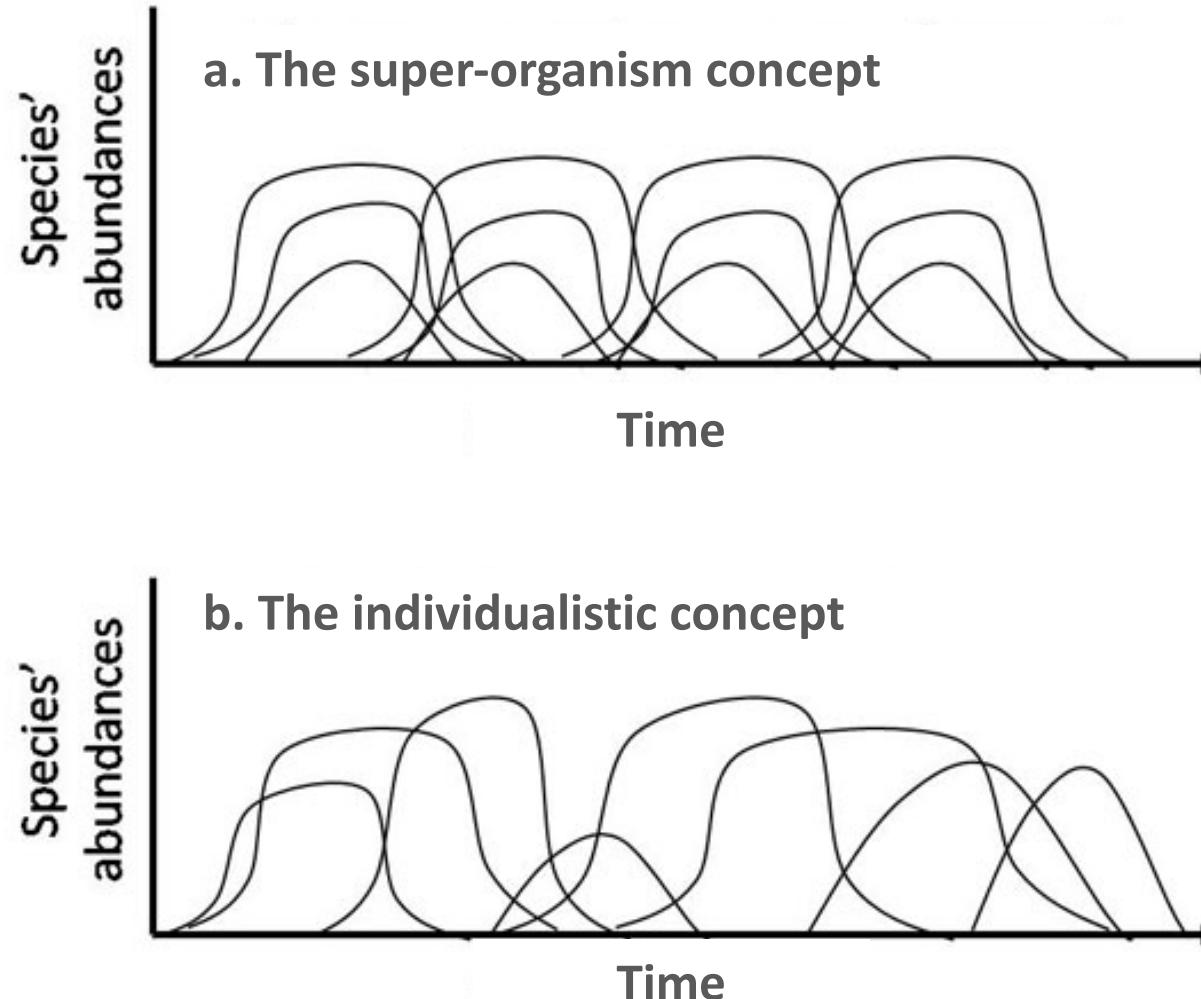


## Henry Gleason (1917)

- “Each species is an independent entity”
  - distribution of each species is due to genetics, physiology, life history, and relations to abiotic and biotic factors
  - communities are just a consequence of independent interactions among species and their environment



(A) Groups of species are tightly associated, and are supplanted by other groups of tightly associated species. (B) Individual species independently respond to environmental conditions. Each curve on the graphs represents the abundance of a single species.



\*\*note on  
phylogeographic  
concordance

(A) Groups of species are tightly associated, and are supplanted by other groups of tightly associated species. (B) Individual species independently respond to environmental conditions. Each curve on the graphs represents the abundance of a single species.

# Assembly “rules”

- Jared Diamond 1975 – the community is a product of the species pool, the environment, and the interactions amongst species.
- Problem was, if all of these things seems similar, why were communities behaving differently? \*\*cough\*\* (gleason)

# Assembly “rules”

- The whole debate begins again in a slightly different context.
- 1.) 1:1 match between species and environment, even if the timing of species entering a community is different
  - (Neill 1975, Tilman et al. 1986, Sommer 1991, Law & Morton 1996)
- 2.) depends on what species get there first (multiple state equilibria)
  - (Luh and Pimm 1993, Law 1999, Robinson and Dickerson 1988, Drake 1991, Samuels & Drake 1997)

# Assembly “rules”

- The whole debate begins again in a slightly different context.
  - 1.) 1:1 match between species and environment  
species entering a community.
    - (Neill 1975, Tilman 1982, Law 1999, Morton 1996)
  - 2.) different species get there first (multiple state equilibria)
    - (Law 1999, Tilman 1993, Law 1999, Robinson and Dickerson 1988, Drake 1991, Samuels & Drake 1997)
- \*\*Evidence has been found for both arguments\*\*

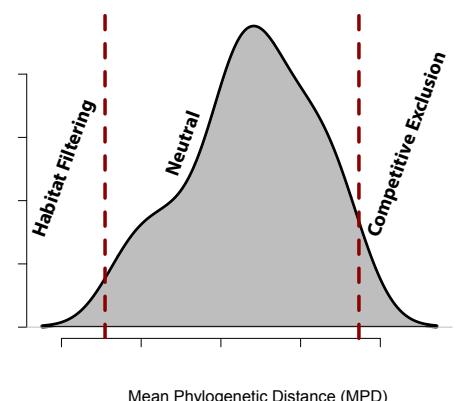
# Measure Community Structure

- Species/genus ratios
  - Moreau 1948, Simberloff 1970
- Abundance distributions
  - Simpson 1949, Magurran 1988
- Higher Taxonomic diversity metrics
  - Faith 1992, Gotelli & Colwell 2001
- Functional traits information
  - MacArthur & Levins 1967; Weiher *et al.* 1999; McGill *et al.* 2006

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Null Models in Community Ecology (Gotelli & Graves 1996)

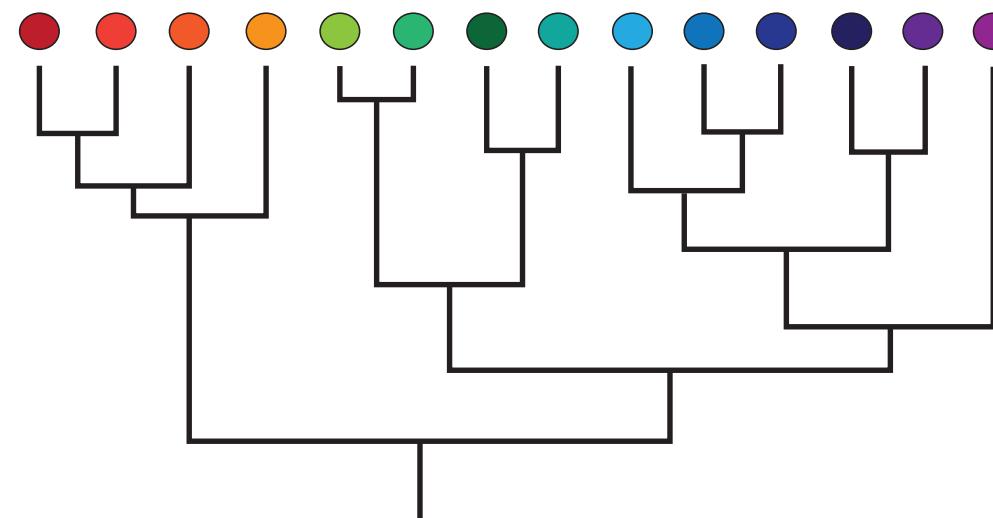


# Phylogenetic Community Ecology

- We should use phylogenies in community ecology!
  - Brooks & McLennan 1991, Losos 1996, Thompson et al. 2001
- The phylogeny encapsulates information about the functional traits important for assembly, as they are “phylogenetic conserved”
  - \*\*assumption

# Phylogenetic Community Ecology

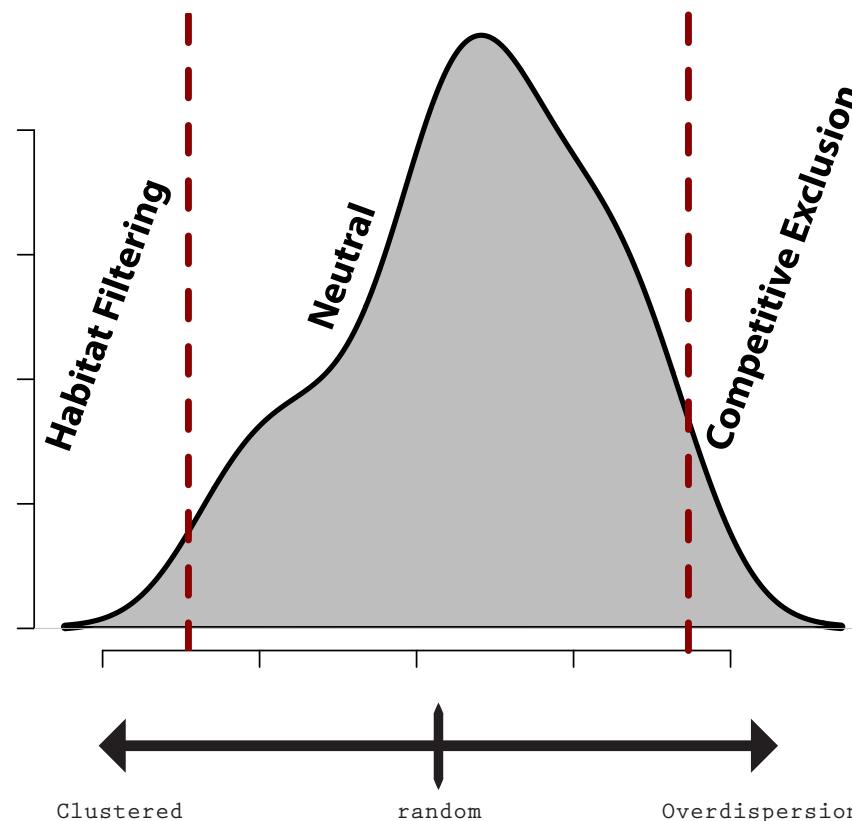
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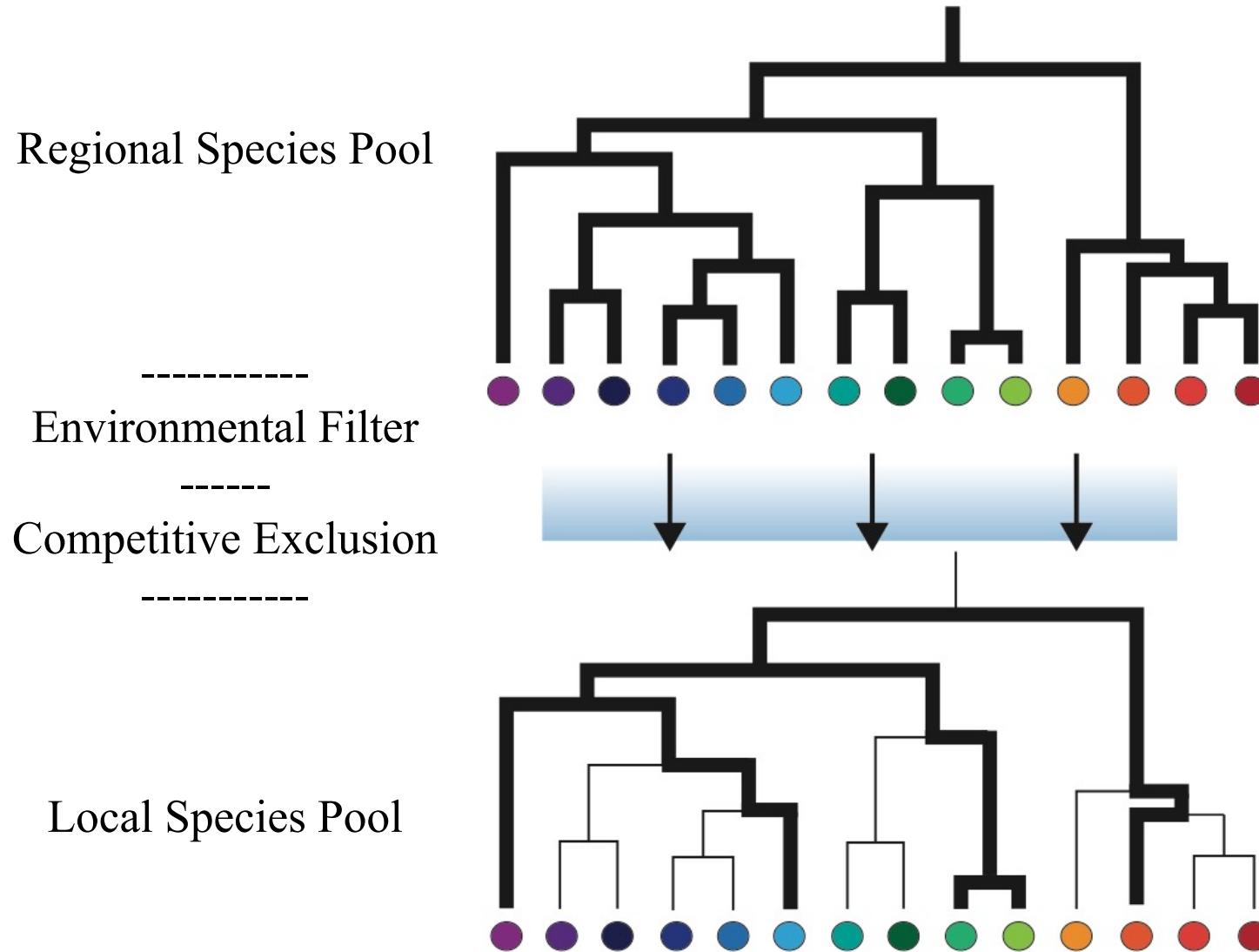


Webb et al. 2002

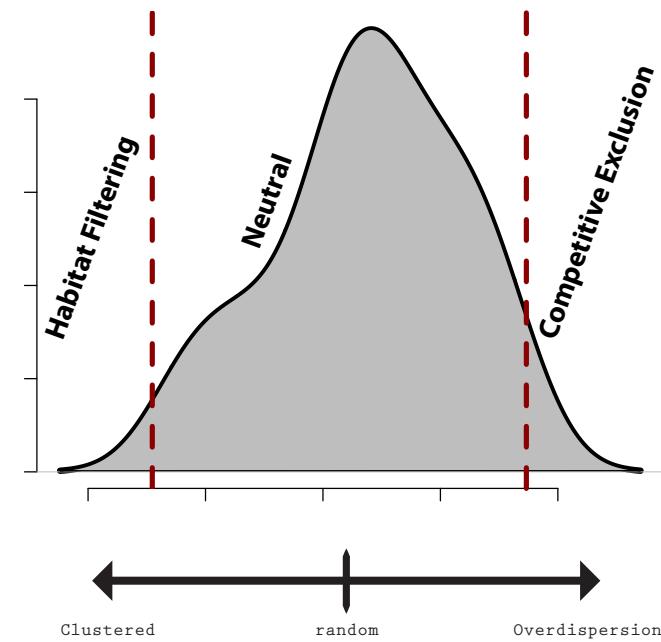
# Phylogenetic Community Ecology

- Is the distribution of species in a community nonrandom with respect to phylogeny?





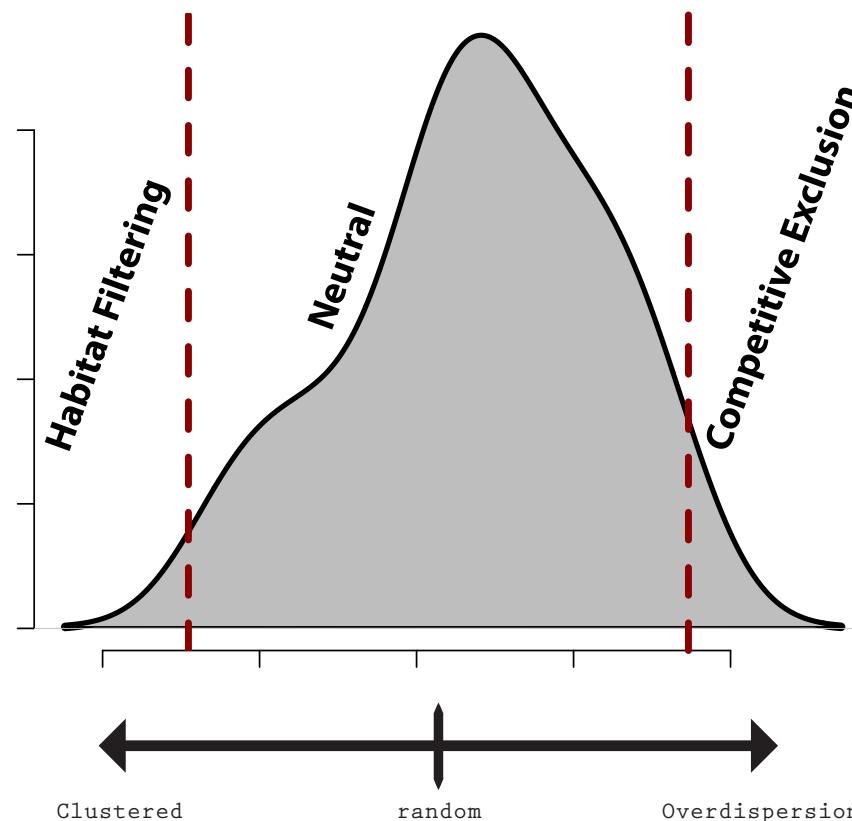
## Phylogenetic dispersion metrics: Mean Phylogenetic Distance (MPD)



# Non-neutral Assembly Models

- Is the distribution of species in a community nonrandom with respect to phylogeny?

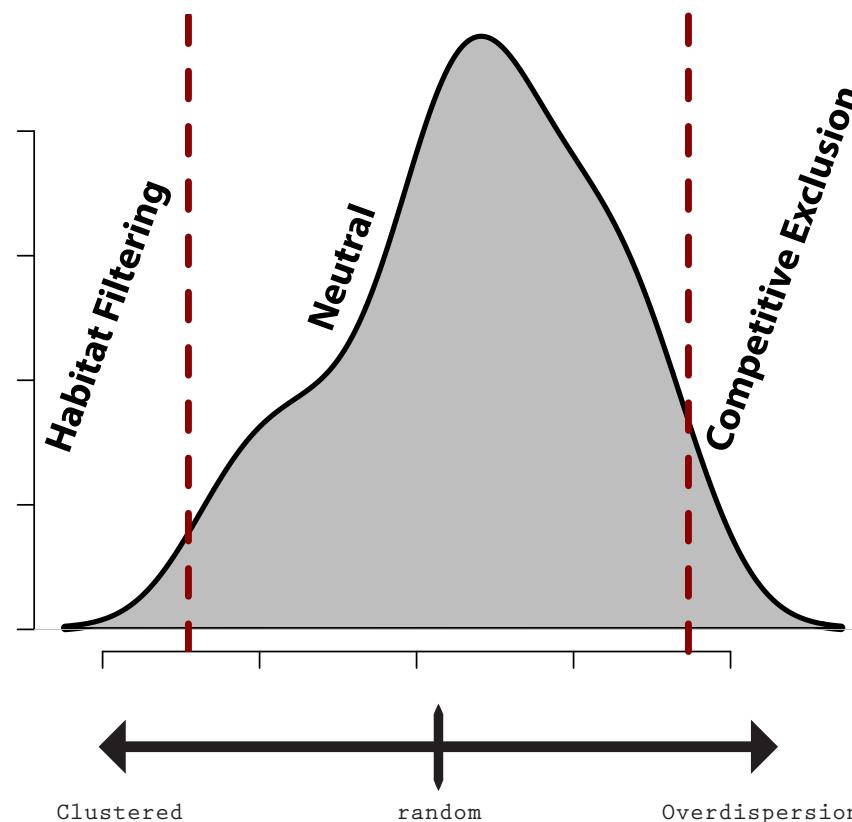
**Habitat Filtering** – species fail to establish in community due to incompatibility with relevant environmental factors (Bazzaz 1991)



# Non-neutral Assembly Models

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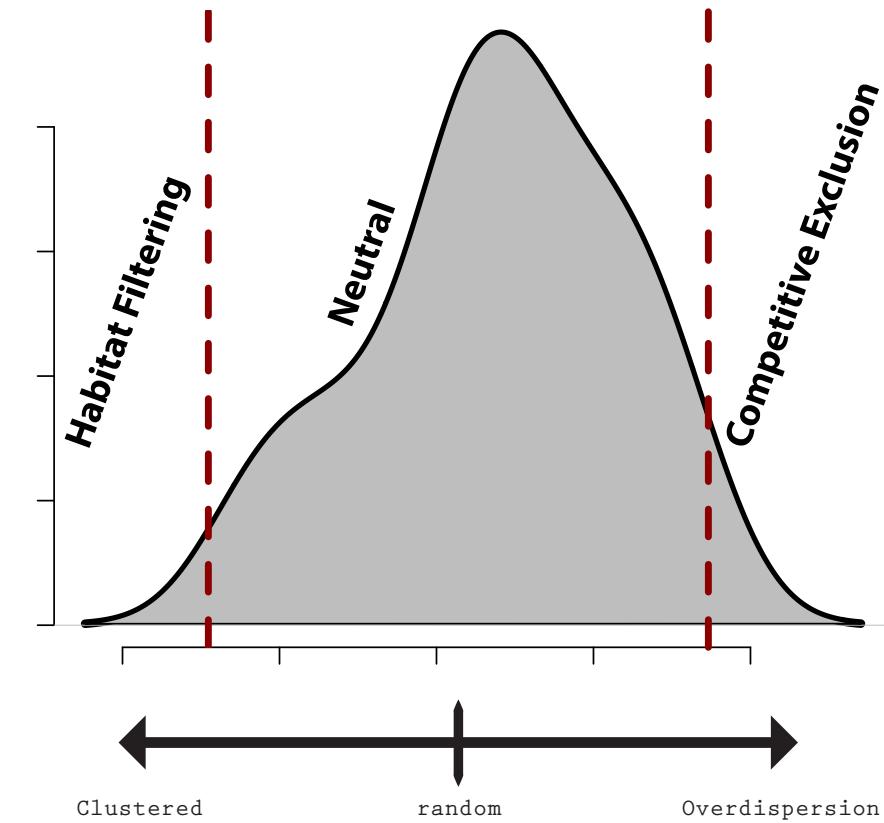
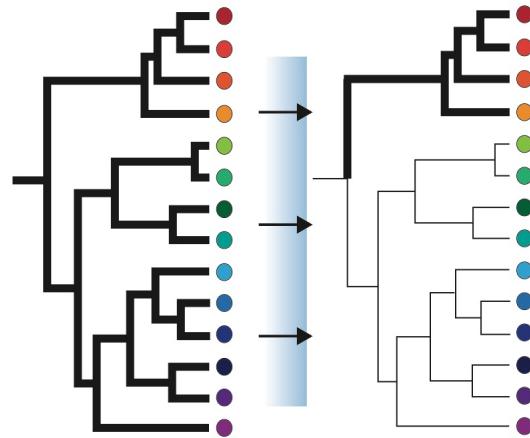
**Habitat Filtering** – species fail to establish in community due to incompatibility with relevant environmental factors (Bazzaz 1991)



**Competitive Exclusion** – species fail to establish in a community when they cannot out-compete another species for their desired niche (MacArthur & Levins 1967)

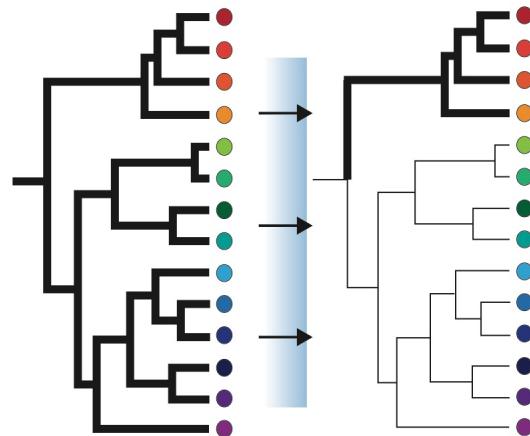
*Traits are phylogenetically conserved*

Habitat Filtering =  
phylogenetic underdispersion

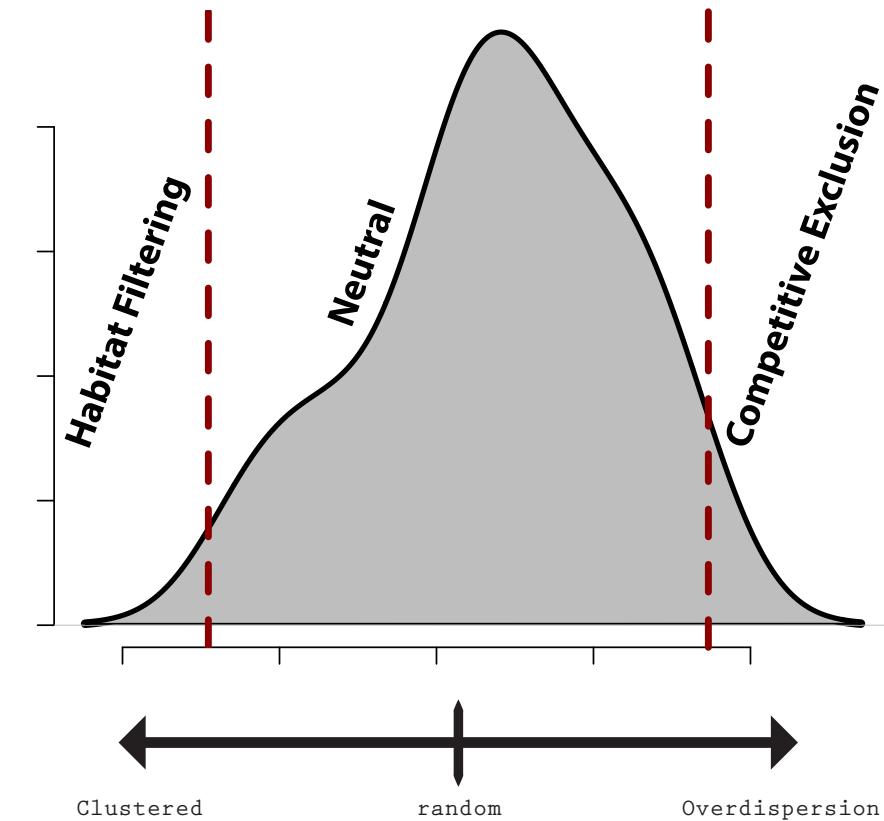
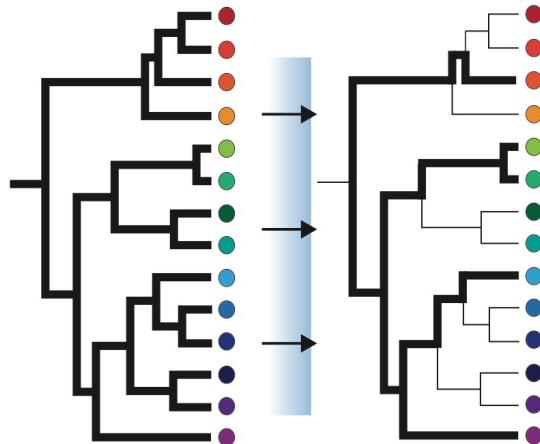


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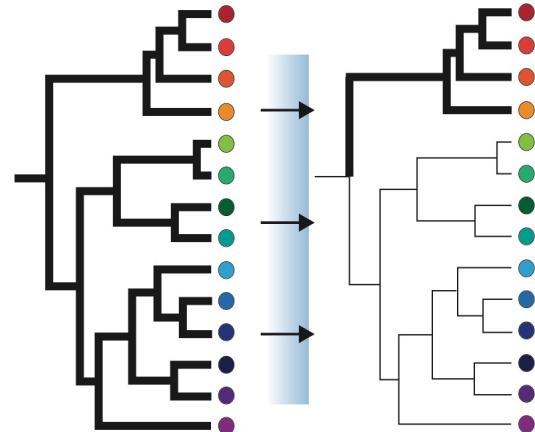


Competitive Exclusion =  
phylogenetic overdispersion

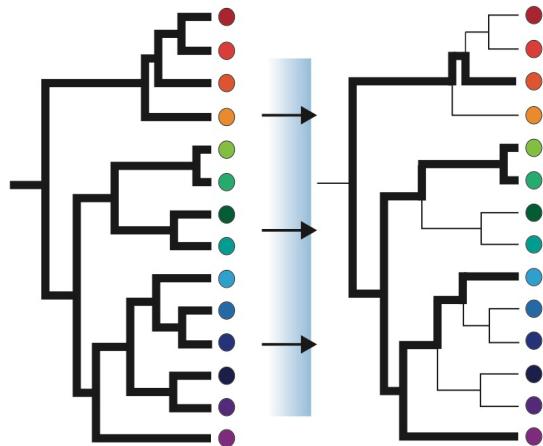


*Traits are phylogenetically conserved*

**Habitat Filtering =  
phylogenetic underdispersion**



**Competitive Exclusion =  
phylogenetic overdispersion**



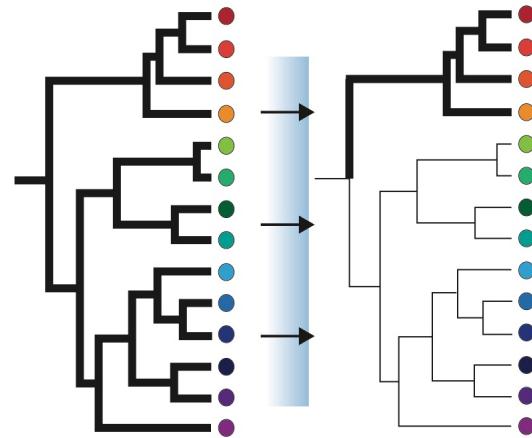
*Traits are phylogenetically convergent*

**Habitat Filtering =  
phylogenetic overdispersion**

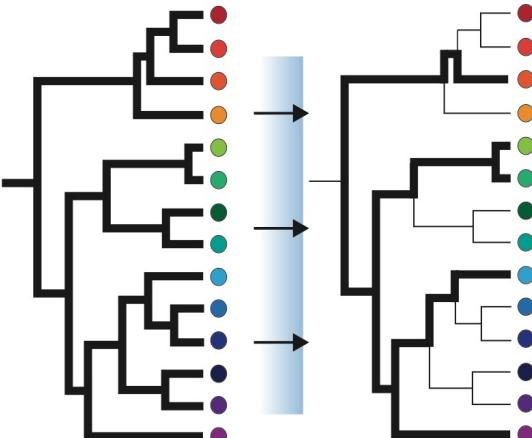
**Competitive Exclusion =  
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**Habitat Filtering =  
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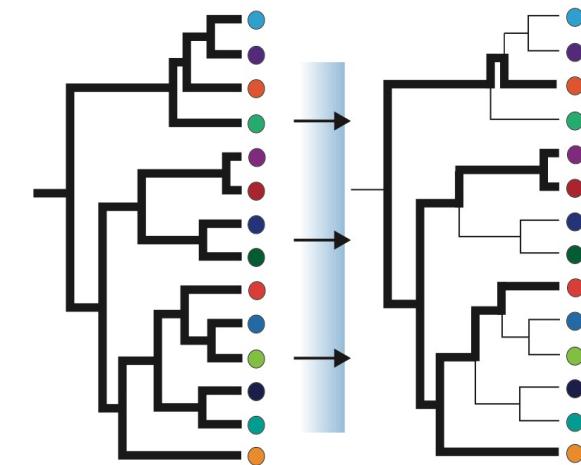


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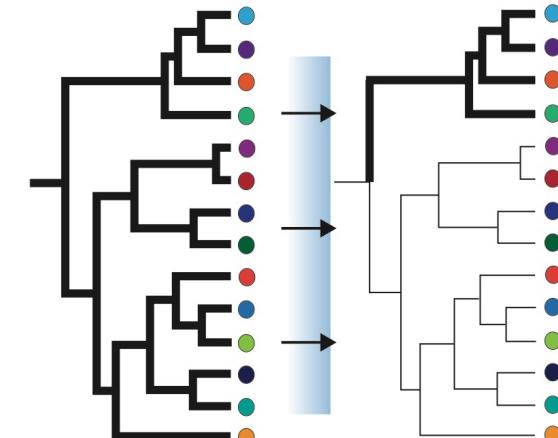


*Traits are phylogenetically convergent*

**Habitat Filtering =  
phylogenetic overdispersion**



**Competitive Exclusion =  
phylogenetic underdispersion**



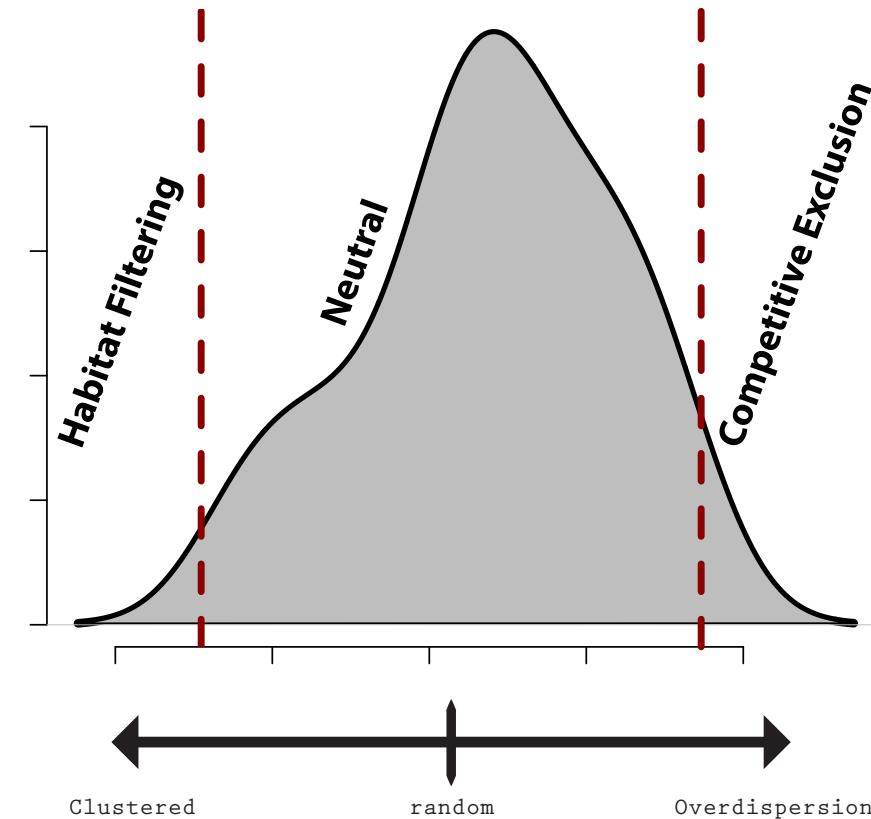
# Community Assembly Inference; dispersion metrics

- Phylogenetic Community Structure

Grandcolas 1998, Webb et al. 2000, 2002,  
Kraft et al. 2007

- Trait Community Structure

Weiher et al. 1999, McGill et al. 2006,  
Cornwell et al. 2006, Kraft et al. 2007



# Community Assembly Inference; dispersion metrics

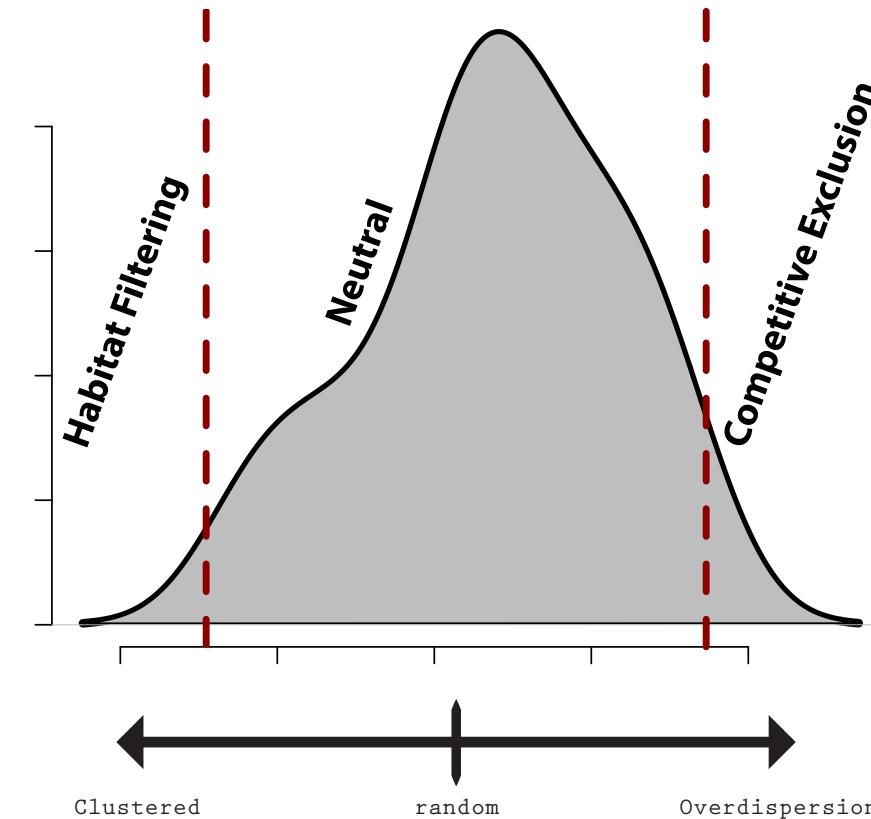
- Phylogenetic Community Structure

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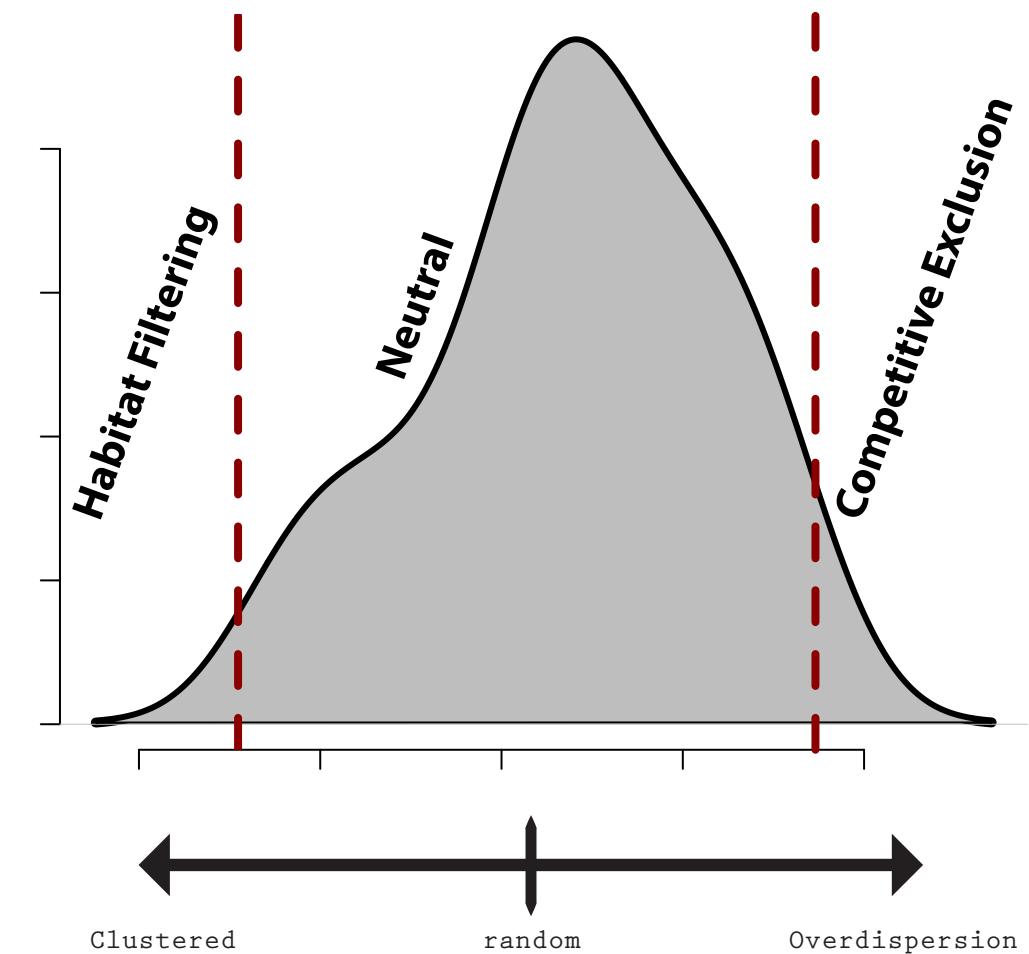
Weiher et al. 1999, McGill et al. 2006,  
Cornwell et al. 2006, Kraft et al. 2007

Weiher and Keddy 1995, Kraft et al.  
2007, 2010, Cavender-Bares et al.  
2009; Kemble 2009; Mayfield and  
Levine 2010; Gerhold et al. 2015



# Current Community Assembly Inference Methods

- Relying on often-violated assumptions
- Statistical significance != Biological significance
- Cannot simultaneously compare model support
- Not widely comparable across communities



# *CAMI development objectives*

- 1. Implement a model-based inference procedure*

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1. *Implement a model-based inference procedure*
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# *CAMI development objectives*

## *1. Implement a model-based inference procedure*

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- \*\*Cannot write down a likelihood, so we will need to use an approximate approach based on simulations*

# *CAMI development objectives*

1. *Implement a model-based inference procedure*
  - *Compare support for neutral and non-neutral models simultaneously*  
\*\**Cannot write down a likelihood, so we will need to use an approximate approach based on simulations*
2. *Parameterize the strength of the non-neutral assembly processes*

# *CAMI development objectives*

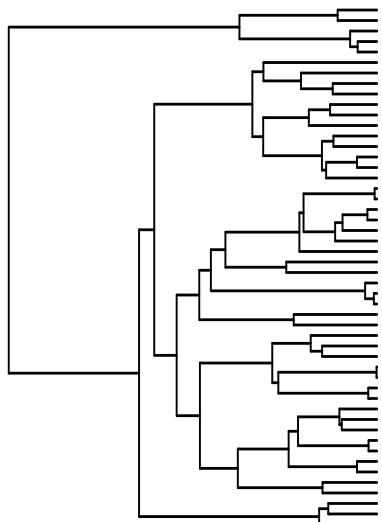
## **1. Implement a model-based inference procedure**

- *Compare support for neutral and non-neutral models simultaneously*
- *\*\*Cannot write down a likelihood, so we will need to use an approximate approach based on simulations*

## *2. Parameterize the strength of the non-neutral assembly processes*

# Objective 1: Implement a model-based inference procedure

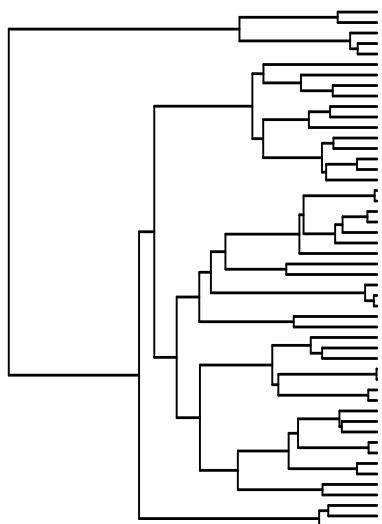
## 1.1 Regional community phylogeny: $N, \lambda, \mu$



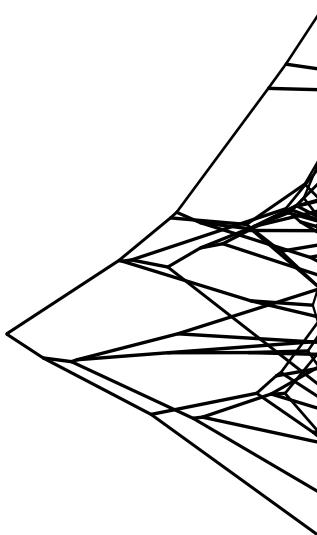
$N$	regional species pool
$\lambda$	speciation rate
$\mu$	extinction rate
$\sigma^2$	rate of character change
$\alpha$	strength of constraints (OU only)
$n$	local species pool
$t_E$	effect of environmental filtering
$t_C$	effect of competitive exclusions

# Objective 1: Implement a model-based inference procedure

1.1 Regional community phylogeny:  $N, \lambda, \mu$



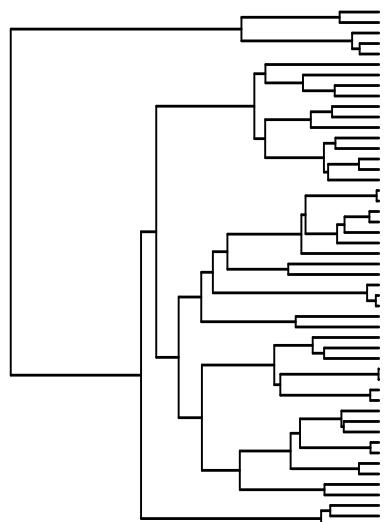
1.2 Trait evolution:  
 $\sigma^2, \alpha$



$N$	regional species pool
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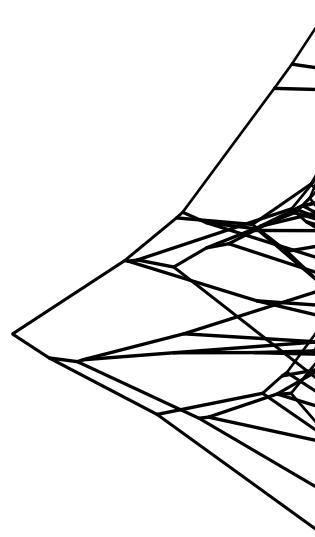
# *Objective 1: Implement a model-based inference procedure*

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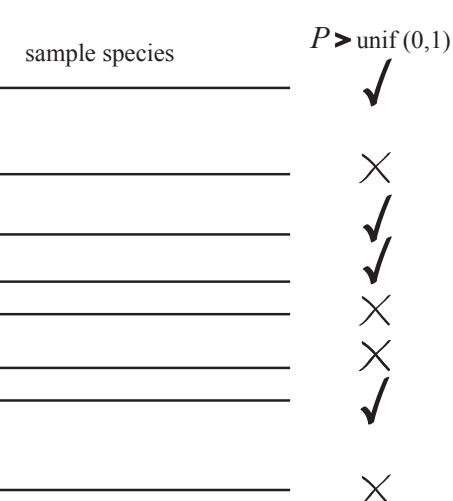


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1.2 Trait evolution:  $\sigma^2, \alpha$



1.3 Local community assembly:  $n, t_E, t_C$



$$P > \text{unif}(0,1)$$

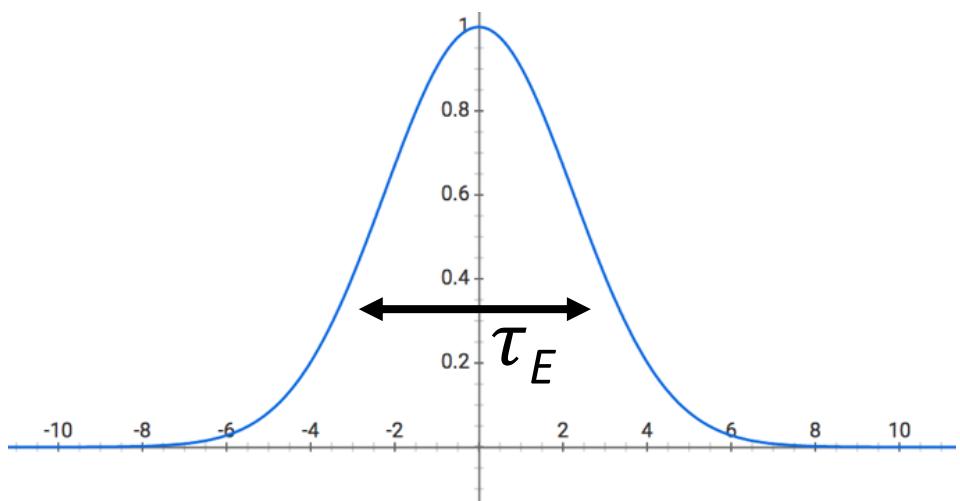
- Neutral
- Environmental Filtering
- Competitive Exclusion

*Objective 2: Parameterize the strength of the non-neutral assembly processes*

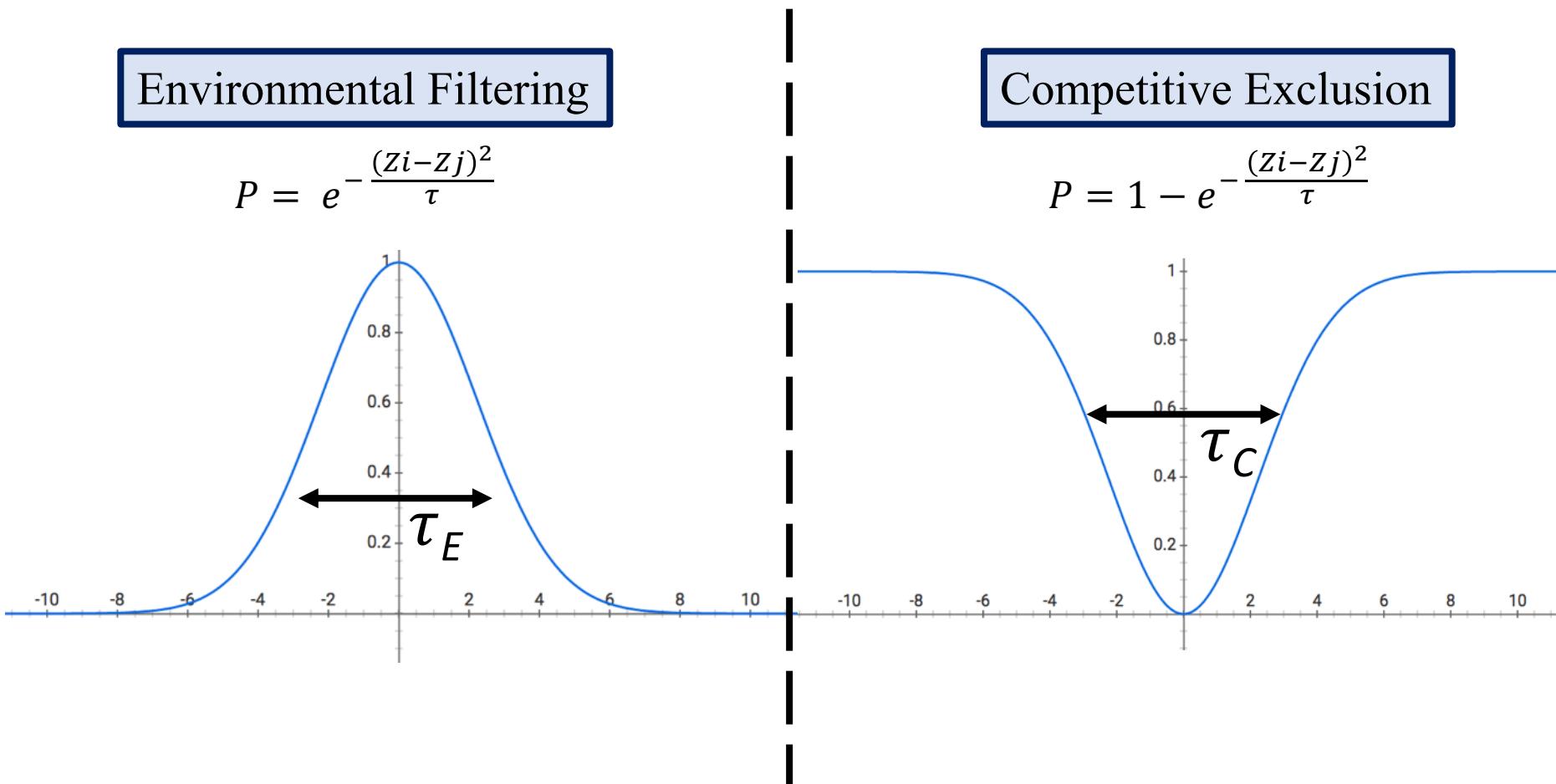
*Objective 2: Parameterize the strength of the non-neutral assembly processes*

Environmental Filtering

$$P = e^{-\frac{(Z_i - Z_j)^2}{\tau}}$$

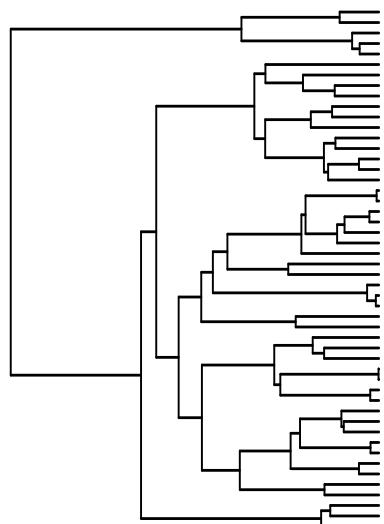


*Objective 2: Parameterize the strength of the non-neutral assembly processes*



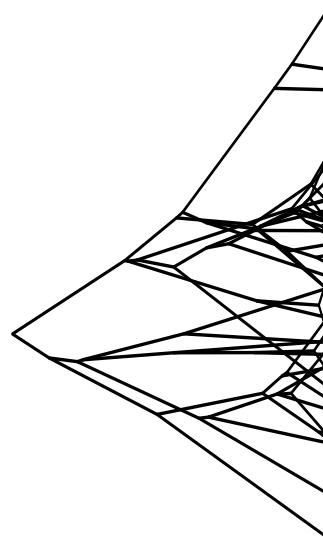
# *Objective 1: Implement a model-based inference procedure*

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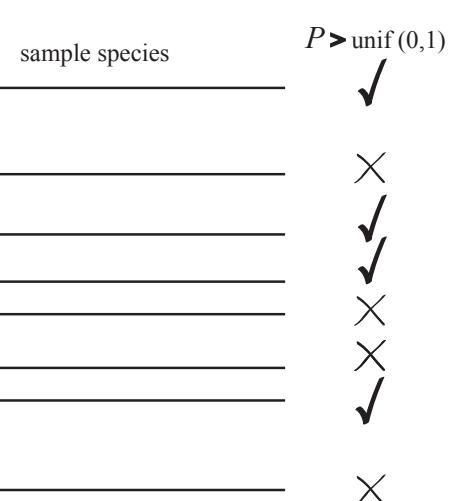


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1.2 Trait evolution:  $\sigma^2, \alpha$

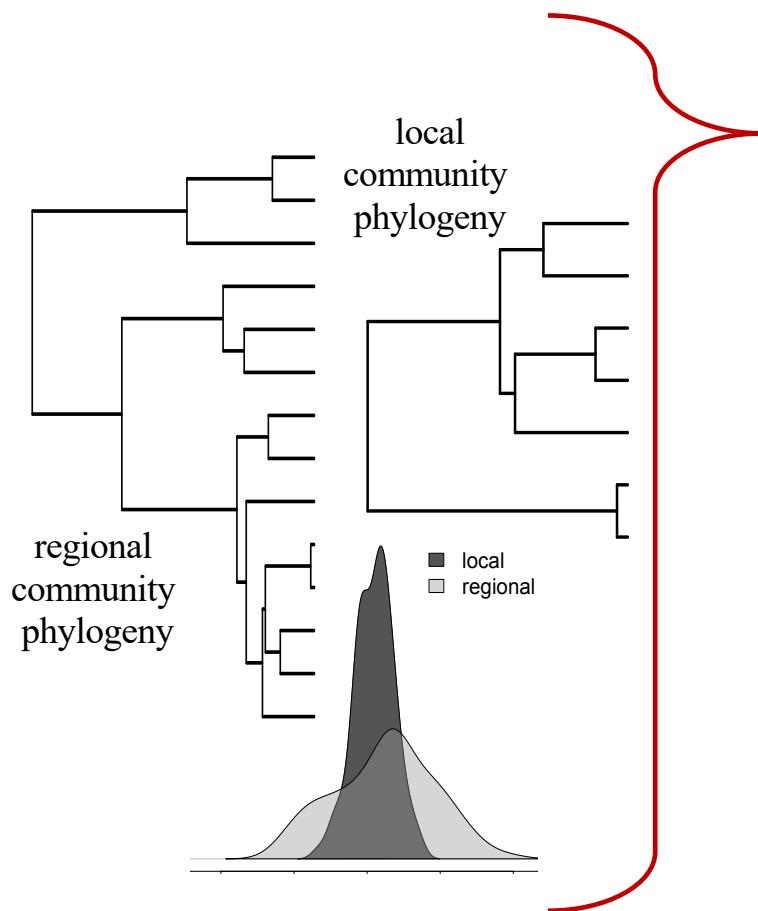


1.3 Local community assembly:  $n, t_E, t_C$



- Neutral
- Environmental Filtering
- Competitive Exclusion

# *Objective 1: Implement a model-based inference procedure*



Simulation #	SS.1	SS.2	SS.3	.....	SS.30	Model
1	29.3201204	0.047795881	2.202369339	0.024039567	-0.551807157	Neutral
2	58.01018705	0.05683677	4.296006276	0.014001377	-0.141285853	Neutral
3	28.35028897	0.057748823	2.565336481	0.02472052	0.543737366	Neutral
4	54.4519145	0.058161893	4.462506196	0.006577184	-0.297716652	Neutral
5	29.52415799	0.0449925	1.332280042	-0.027307941	-0.424597011	Neutral
6	13.8002455	0.043015337	3.827085961	0.052868925	0.00038215	Filtering
7	68.51513963	0.05221236	3.773466742	0.006122832	-0.373019012	Filtering
8	6.409247373	0.067539483	1.27370363	0.056550081	-0.419361409	Filtering
9	7.869379132	0.044893904	1.621625795	0.005944114	-0.225941885	Filtering
10	56.74215972	0.042376631	3.870139564	-0.010551762	1.612683176	Filtering
11	32.21489305	0.039088122	4.436192932	-0.005017495	-0.608370405	Competition
12	35.31406132	0.055897014	1.802319164	0.00665565	0.575928644	Competition
...	15.17747744	0.052302964	2.833102254	-0.007315425	-0.343133625	Competition
10,000	176.8646799	0.046759559	3.404803136	0.003965272	-0.492954288	Competition

# *Objective 1: Implement a model-based inference procedure*

## *Model-selection using approximate approaches*

- randomForests (*Breiman 2001, Breiman and Cutler 2007*)\*\*
- Approximate Bayesian Computation (ABC; *Beaumont, et al. 2002, Csilléry, et al. 2012*)

<i>Simulation #</i>	<i>SS.1</i>	<i>SS.2</i>	<i>SS.3</i>	.....	<i>SS.30</i>	<i>Model</i>
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6	13.8002455	0.043015337	3.827085961	0.052868925	0.00038215	Filtering
7	68.51513963	0.05221236	3.773466742	0.006122832	-0.373019012	Filtering
8	6.409247373	0.067539483	1.27370363	0.056550081	-0.419361409	Filtering
9	7.869379132	0.044893904	1.621625795	0.005944114	-0.225941885	Filtering
10	56.74215972	0.042376631	3.870139564	-0.010551762	1.612683176	Filtering
11	32.21489305	0.039088122	4.436192932	-0.005017495	-0.608370405	Competition
12	35.31406132	0.055897014	1.802319164	0.00665565	0.575928644	Competition
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10,000	176.8646799	0.046759559	3.404803136	0.003965272	-0.492954288	Competition

# *Results*

- 1. Power Analysis*
- 2. Parameter Estimation*

# Results

## 1. Power Analysis

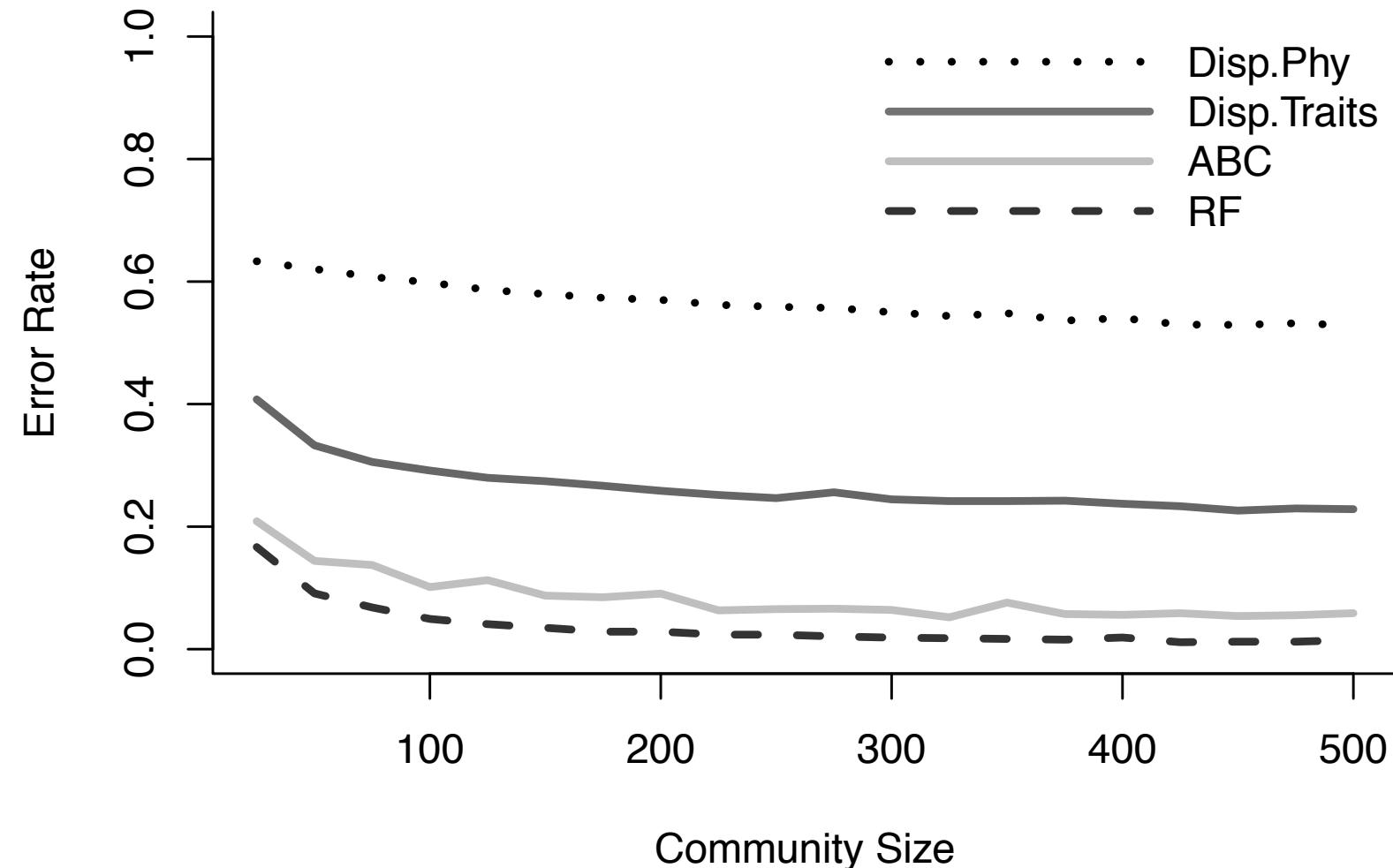
- **Dispersion Metrics**

*Phylogenetic data*

*Functional trait data*

- **randomForest (RF)**
- **ABC**

# Results: Power Analysis



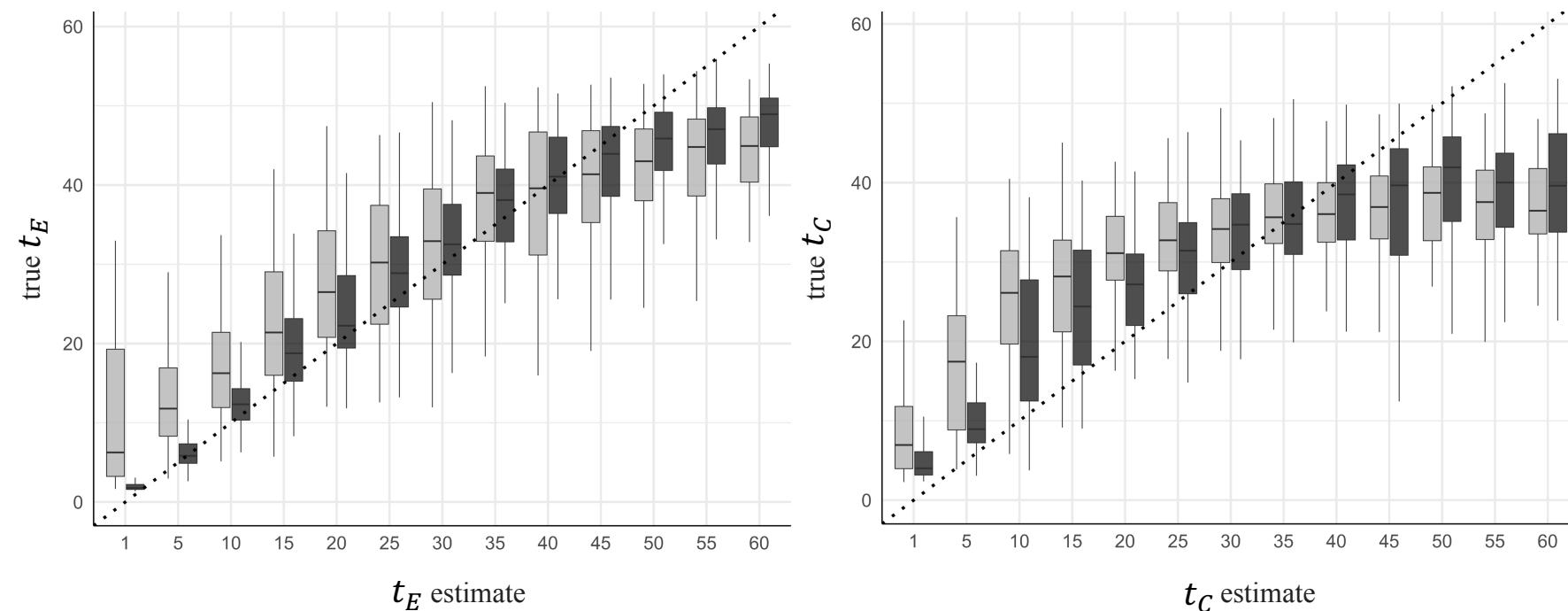
# Results

*1. Power Analysis*

**2. Parameter Estimation**

*-Estimate  $\tau_E$  and  $t_C$*

# Results: Parameter Estimation



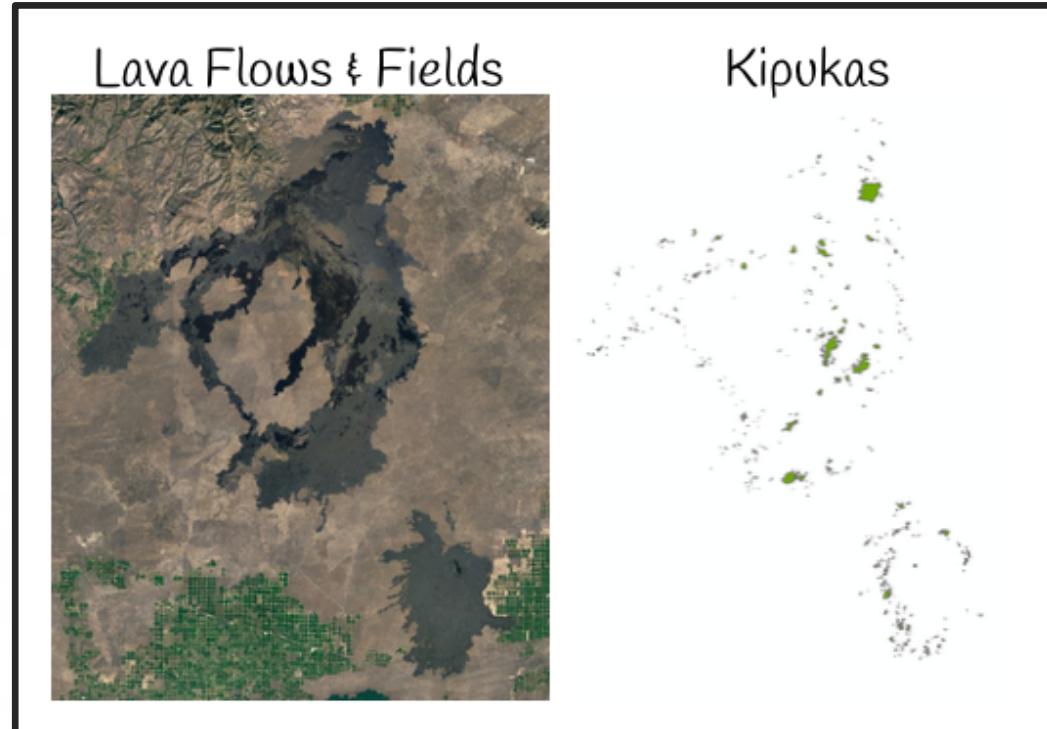
# CAMI introductory tutorial

- [compphylo.github.io/Oslo2019/CAMI\\_files/CAMI\\_1.html](https://compphylo.github.io/Oslo2019/CAMI_files/CAMI_1.html)

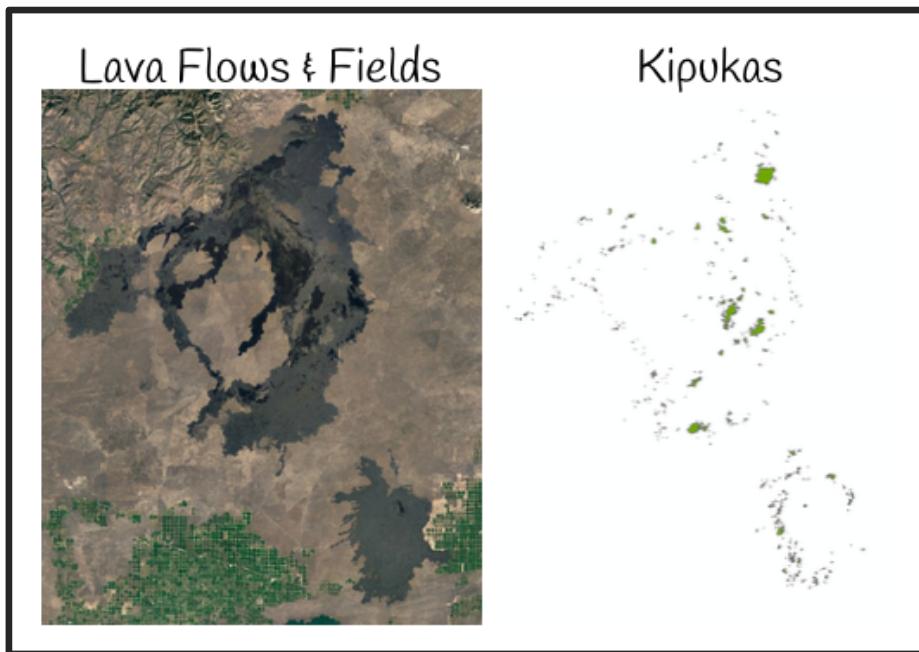
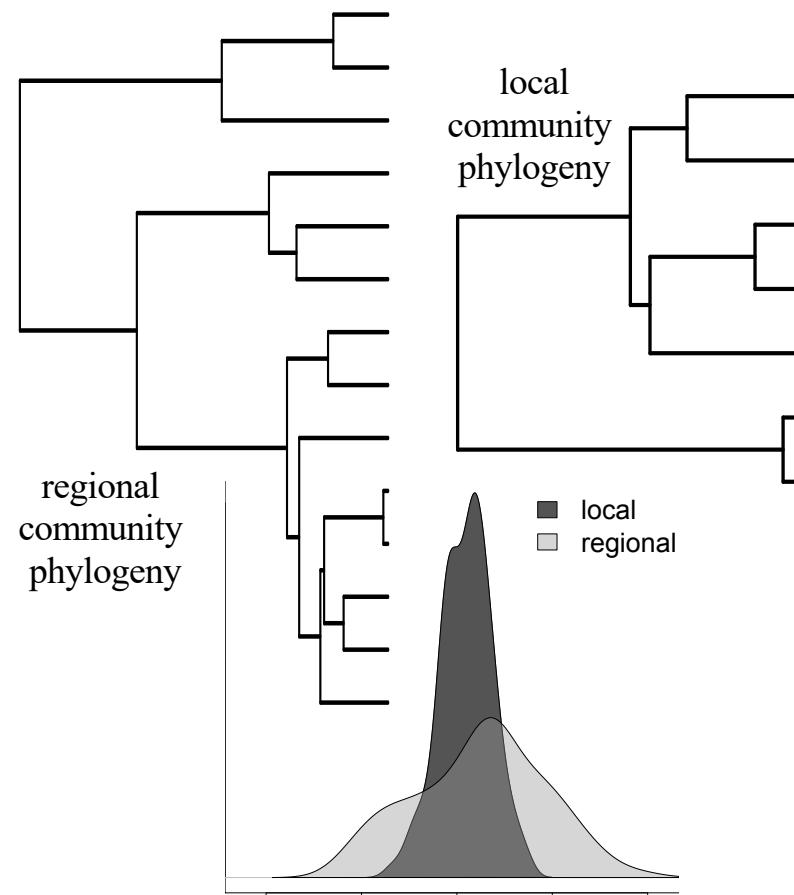
# Results: Lava-flow Islands in Craters of the Moon National Monument and Preserve



Katie Peterson  
Dr. Christine Parent lab  
University of Idaho



# Results: Lava-flow Islands in Craters of the Moon National Monument and Preserve



# *Results: Lava-flow Islands in Craters of the Moon National Monument and Preserve*



Smith, S. A., and J. W. Brown. 2018. Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany* 105(3): 302-314.



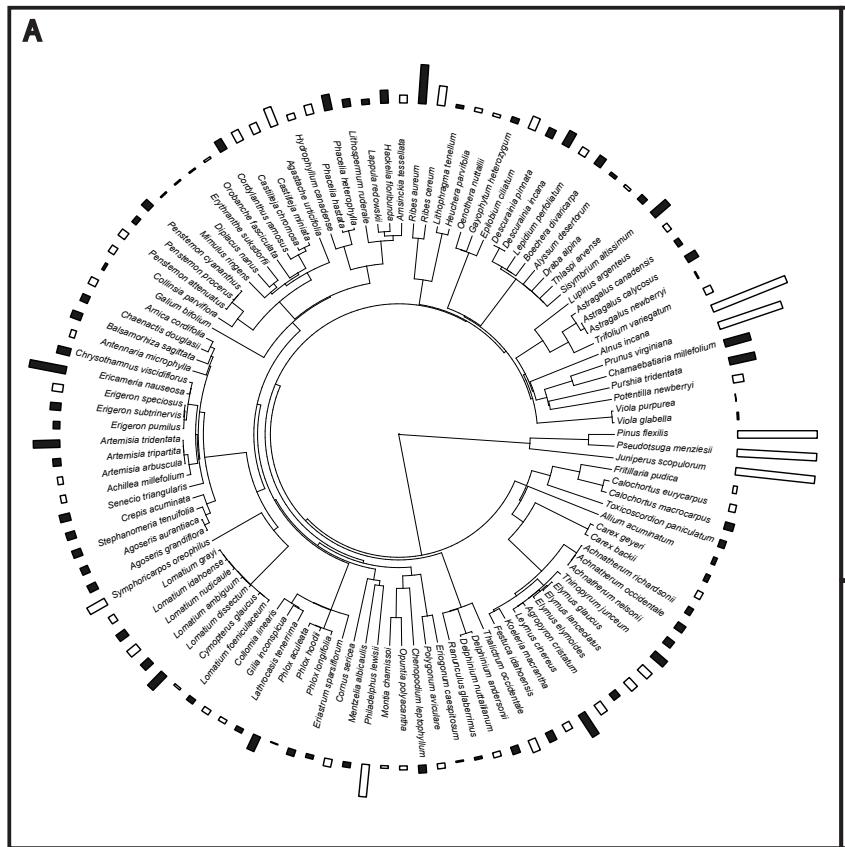
- Spermatophyta phylogeny  
79,881 tips
- Discarded 79,768 tips (99.9%)

- 8 kipuka communities
- 113 species in regional community
- 18-60 species in local community

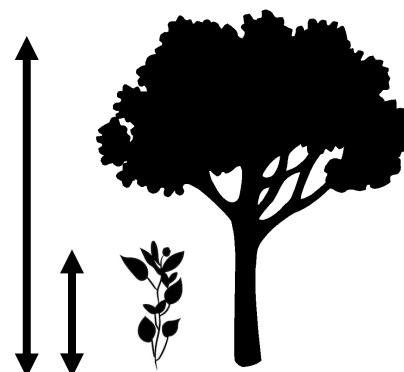
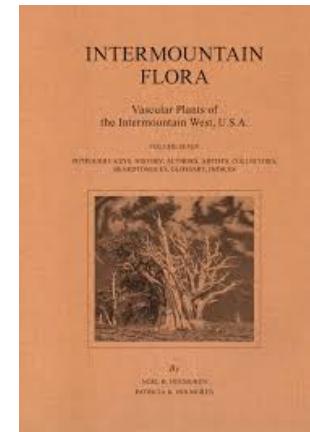
**Try it with your community!**

<https://github.com/ruffleymr/CommunityPhylogeneticExample>

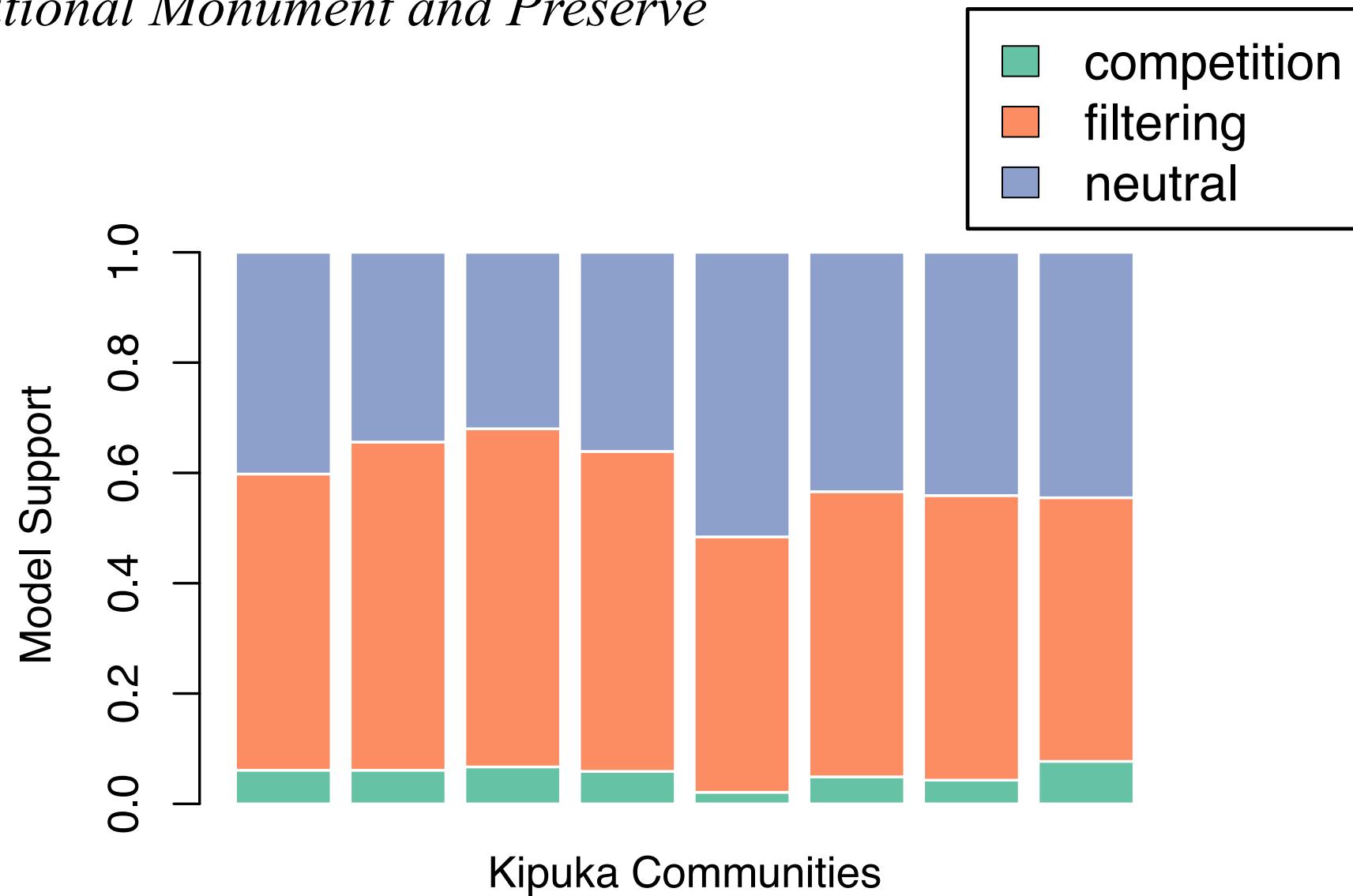
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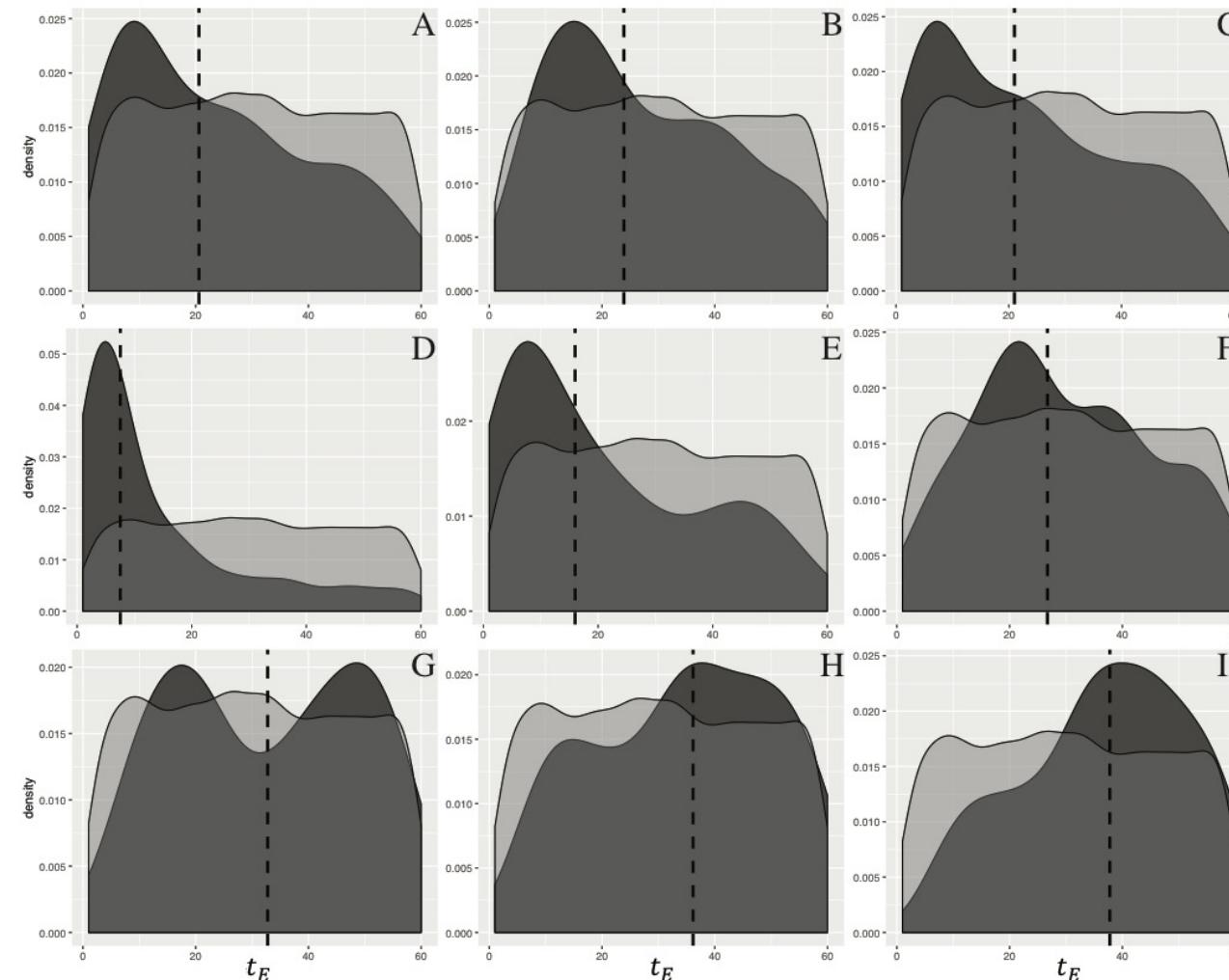
## Maximum vegetative height



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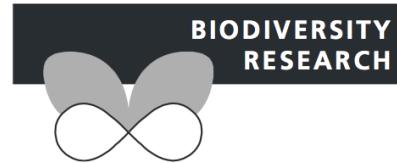


# CAMI tutorial 2: San Juan Islands

- [compphylo.github.io/Oslo2019/CAMI\\_files/CAMI\\_2.html](https://compphylo.github.io/Oslo2019/CAMI_files/CAMI_2.html)

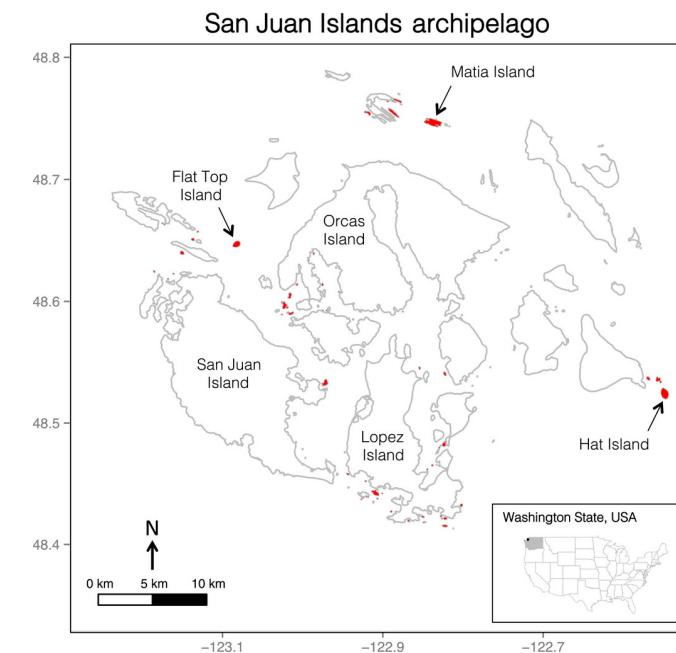
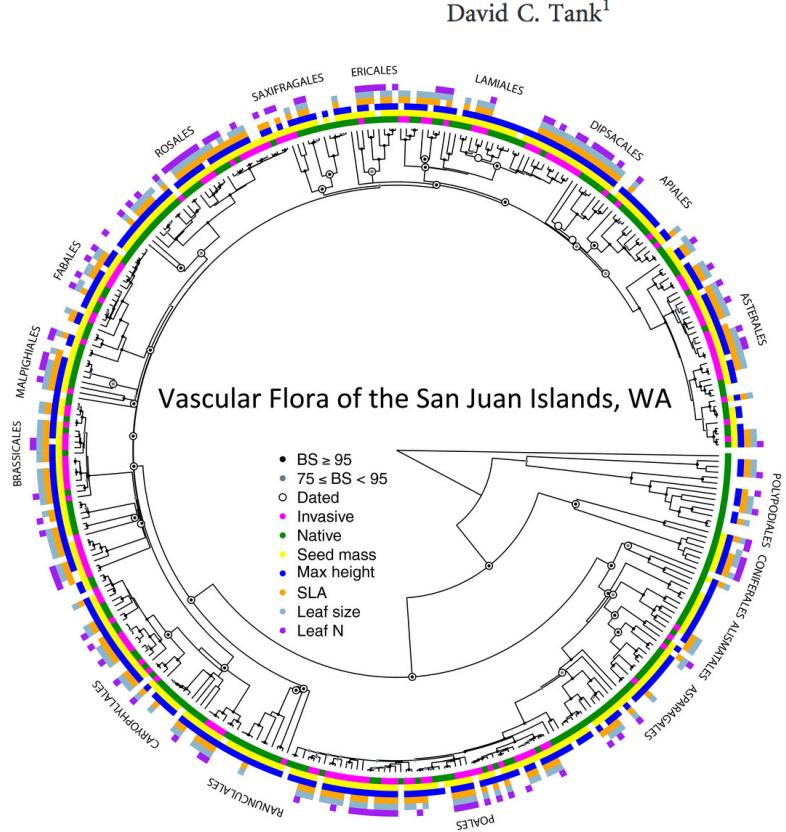
# Results: San Juan Islands in the Pacific Northwest

Diversity and Distributions, (*Diversity Distrib.*) (2016) **22**, 318–331



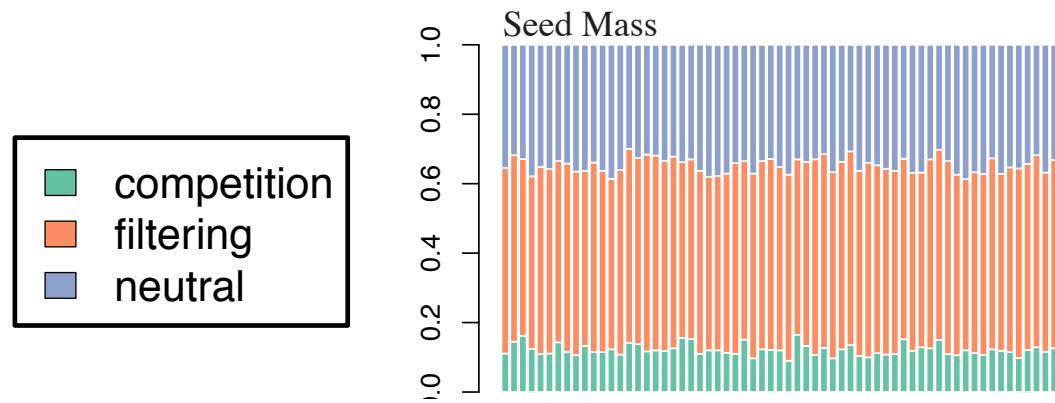
## Deconstructing Darwin's Naturalization Conundrum in the San Juan Islands using community phylogenetics and functional traits

Hannah E. Marx<sup>1\*</sup>, David E. Giblin<sup>2</sup>, Peter W. Dunwiddie<sup>2</sup> and David C. Tank<sup>1</sup>

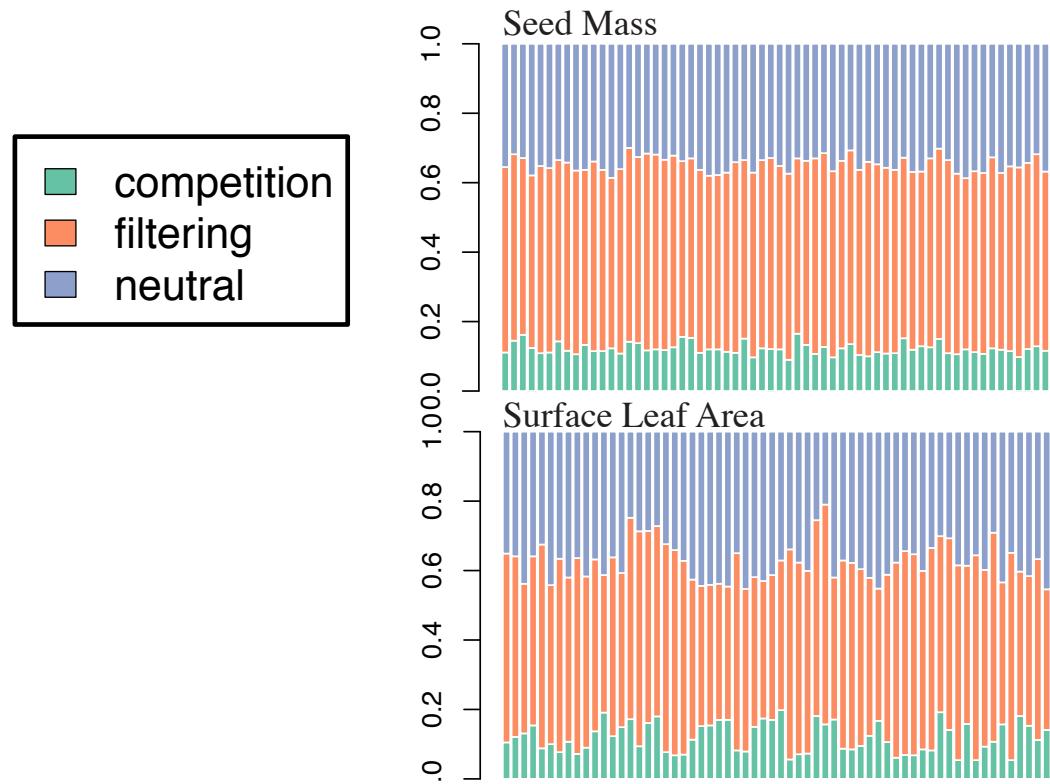


- 322 regional species
- 50 island communities
- 25-150 species in each
- 3 traits

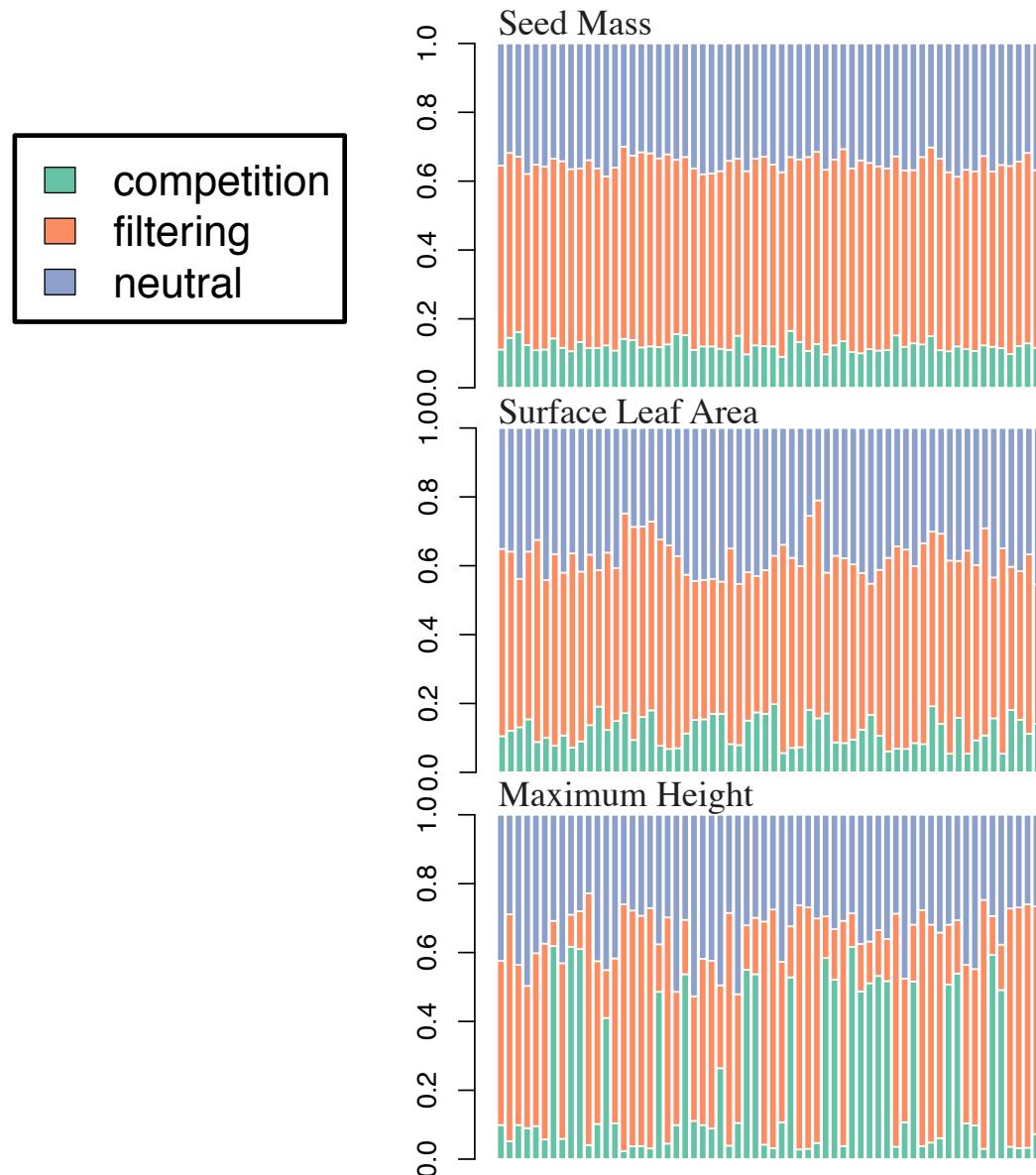
## Results: San Juan Islands in the Pacific Northwest



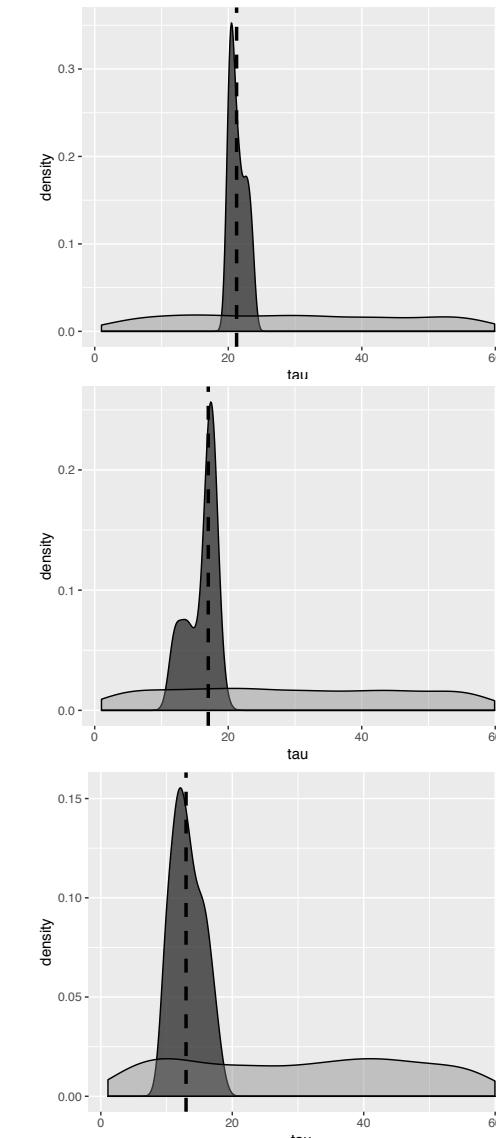
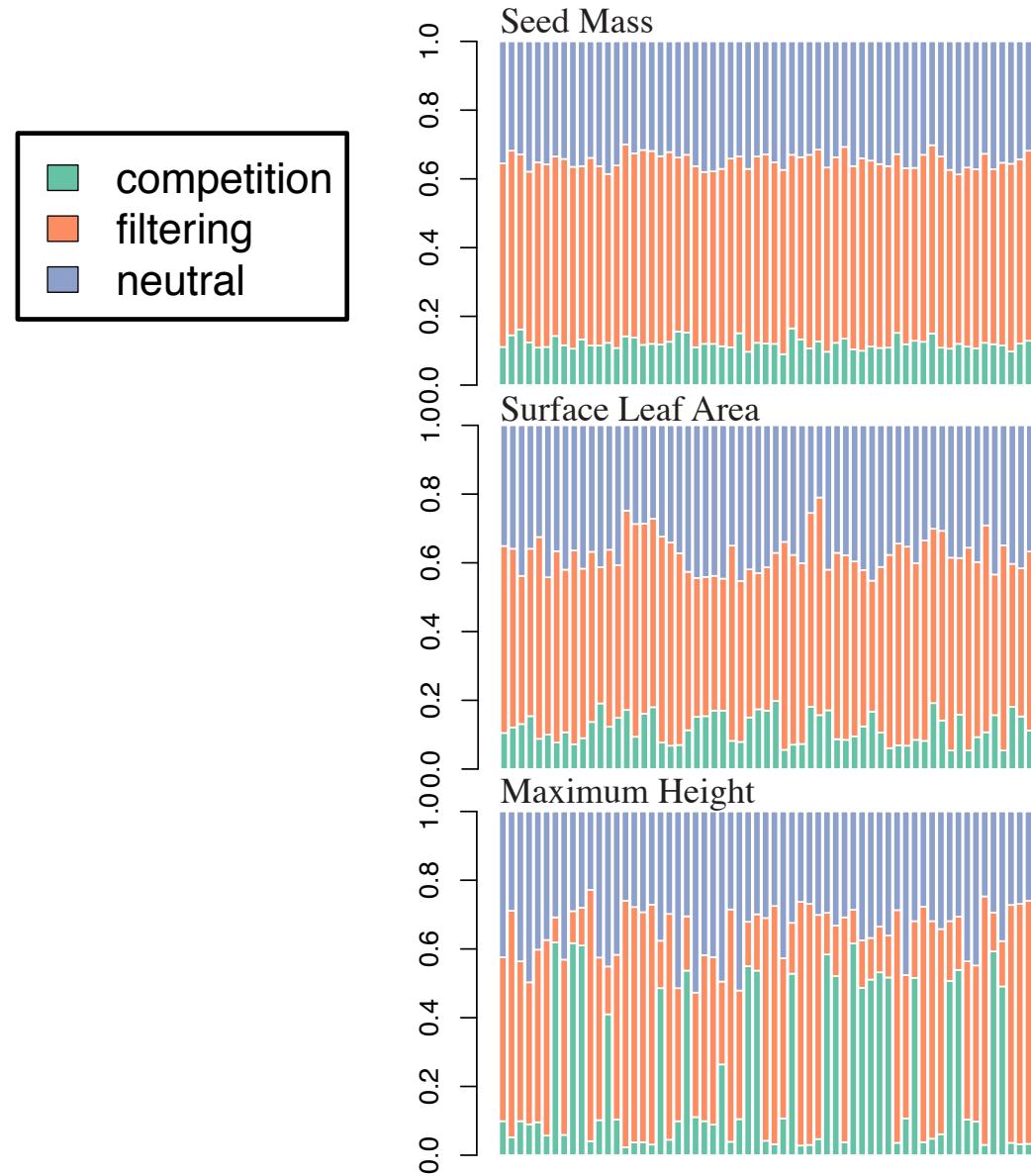
## Results: San Juan Islands in the Pacific Northwest



## Results: San Juan Islands in the Pacific Northwest



# Results: San Juan Islands in the Pacific Northwest



## *CAMI Conclusions*

- Simulate phylogenetic and phenotypic community assembly data under neutral and non-neutral models of assembly
- Implements a model-based inference procedure with parameter estimation

**CAMI: Community Assembly  
Model Inference**

R package and docs available now @  
<https://github.com/ruffleymr/CAMI>

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Received: 2 January 2017 | Accepted: 21 July 2017  
DOI: 10.1111/2041-210X.12918

### RESEARCH ARTICLE

Methods in Ecology and Evolution 

## **ecolottery: Simulating and assessing community assembly with environmental filtering and neutral dynamics in R**

François Munoz<sup>1</sup>  | Matthias Grenié<sup>2</sup> | Pierre Denelle<sup>2</sup> | Adrien Taudière<sup>2</sup> |  
Fabien Laroche<sup>2,3</sup> | Caroline Tucker<sup>2,4</sup> | Cyrille Violle<sup>2</sup> 

### APPLICATION

## **VirtualCom: a simulation model for eco-evolutionary community assembly and invasion**

Tamara Münkemüller<sup>1\*</sup> and Laure Gallien<sup>1,2,3</sup>



Article |  Full Access |

## A new modeling approach estimates the relative importance of different community assembly processes

Fons van der Plas , Thijs Janzen, Alejandro Ordóñez, Wimke Fokkema ... See all authors 

### REVIEW

Methods in Ec

## Inferring community assembly processes from macroscopic patterns using dynamic eco-evolutionary models and Approximate Bayesian Computation (ABC)

Mikael Pontarp<sup>1,2,3</sup>  | Åke Bränström<sup>4,5</sup> | Owen L. Petchey<sup>2</sup> 

# Identifying Models of Trait-Mediated Community Assembly

using random forests and  
approximate Bayesian computation

Megan Ruffley, Katie Peterson,

Bob Week, David C. Tank,  
Luke J. Harmon

