Estimating species-specific competition coefficients with a Bayesian hierarchical model of the neighborhood effect of competition on tree growth

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Introduction

- Competition is an important interaction which structures many communities
- We want to understand how well competitive interactions are explained by different theories: neutral, limiting similarity, competitive hierarchy, intransitive loops, cause versus effect,…
- One way to tease apart these theories is by estimating the pair-wise competitive interactions between species at a single trophic level within a community.

Introduction

$$\begin{bmatrix} \lambda_{11} & \lambda_{12} & \cdots \\ \lambda_{21} & \lambda_{22} & \cdots \\ \vdots & \vdots & \ddots \end{bmatrix}$$

Matrix of competitive interactions, λ_{ij} is the effect of species *j* on species *i*.

Introduction

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Matrix of competitive interactions, λ_{ij} is the effect of species *j* on species *i*. Here we are going to measure the neighborhood effect of tree species *j* on the diameter growth of tree species *i*.

Introduction

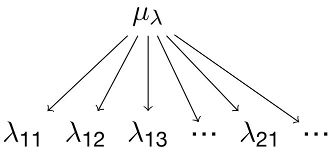
Estimating the full matrix of λ values is difficult. How have others dealt with this?

- Canham et al. (2006) neighborhood competition index. Frequentist likelihood to estimate λs for common species-pairs and ignored rare ones.
- Uriarte et al. (2010) don't estimate each λ, but tested models with λ as a function of phylogenetic or trait-based similarity between species.
- Tatsumi et al (2016) use a Bayesian hierarchal approach. Tested different theories of competition which imposed different structure on the λ matrix.

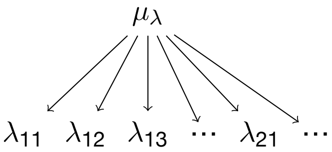
Hierarchal models

$$\lambda_{11} \quad \lambda_{12} \quad \lambda_{13} \quad \cdots \quad \lambda_{21} \quad \cdots$$

Hierarchal models



Hierarchal models



μ_λ is a hyperparameter. If the sample size for λ_{ij} is small, it “borrows” information from other pairs via the hyperparameter. If the sample size is large, there is less “borrowing.”

Model formulation

$$\text{Growth} \sim \text{Norm}(\beta_{0i} + \beta_{1i}\text{DBH} + \sum_j \lambda_{ij}\text{BA}_j, \sigma_y)$$

Where i is the species of the focal individual, j is species of the neighbor, and BA_j is the sum of the basal area of individuals of that species within 7.5 m of the focal individual.

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Where i is the species of the focal individual, j is species of the neighbor, and BA_j is the sum of the basal area of individuals of that species within 7.5 m of the focal individual. Also have the hyperparameters,

$$\beta_{0i} \sim \text{Norm}(\mu_{0\beta}, \sigma_{0\beta})$$
$$\beta_{1i} \sim \text{Norm}(\mu_{1\beta}, \sigma_{1\beta})$$
$$\lambda_{ij} \sim \text{Norm}(\mu_{\lambda}, \sigma_{\lambda})$$

Different groupings

- To test different theories of competition we let the notion of 'species' vary:
  - Species
  - Family
  - A group based of species with similar functional traits
- We form our trait-based groups from height, specific leaf area, and wood density. Kunstler et al. (2016) found these were important to competition.
- Trait values taken from the TRY plant trait database (Kattge et al. 2011).

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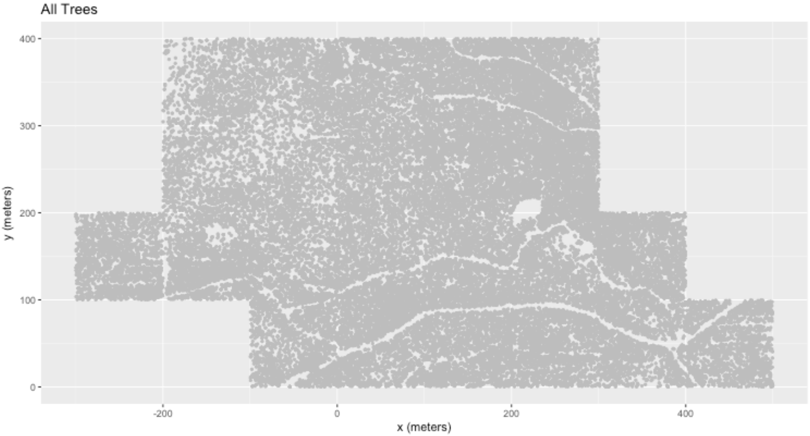
Models to be compared

- Null: Each species gets its own *response* to competition. λ is 33×1
- Trait grouped: Clustered species based on values for those three traits and form six clusters. λ is 6×6
- Family: λ is 19×19
- Species: λ is 33×33

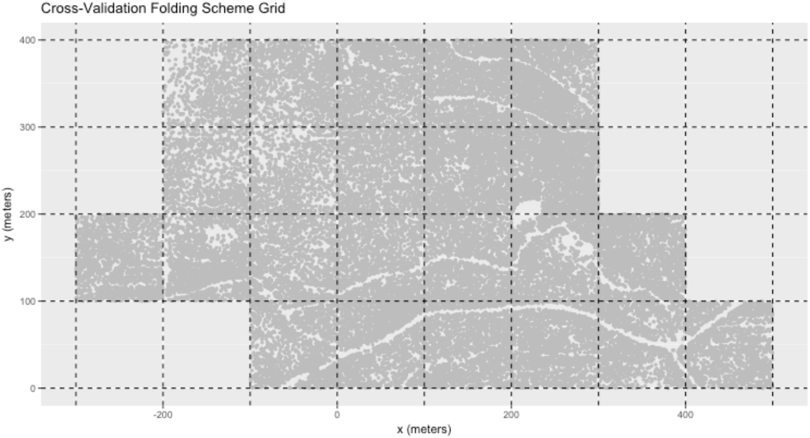
Model comparison

- Previous studies have used information theoretic criteria to compare models (e.g., AIC or DIC). These compare the likelihood of each model with a penalty for the number of parameters.
- Here we will compare with out-of-sample prediction.
- Options for this are cross validation with folds of the data or leave one out.
- We take a spatial fold approach because LOO would be too computationally intensive.

Cross validation scheme



Cross validation scheme



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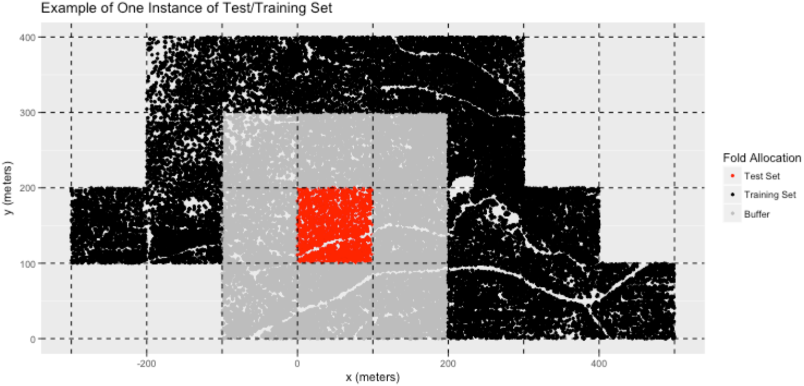

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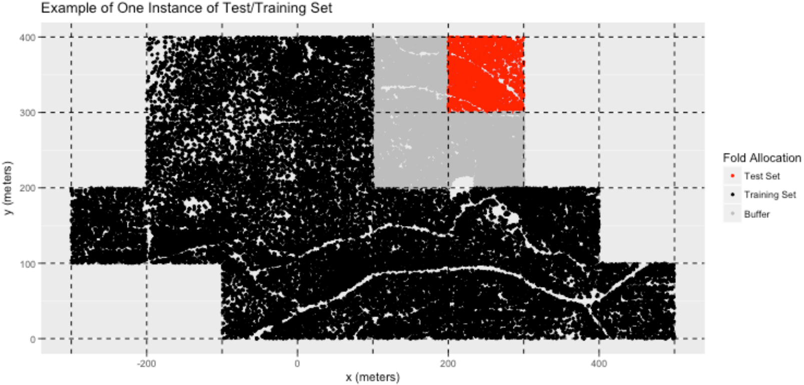
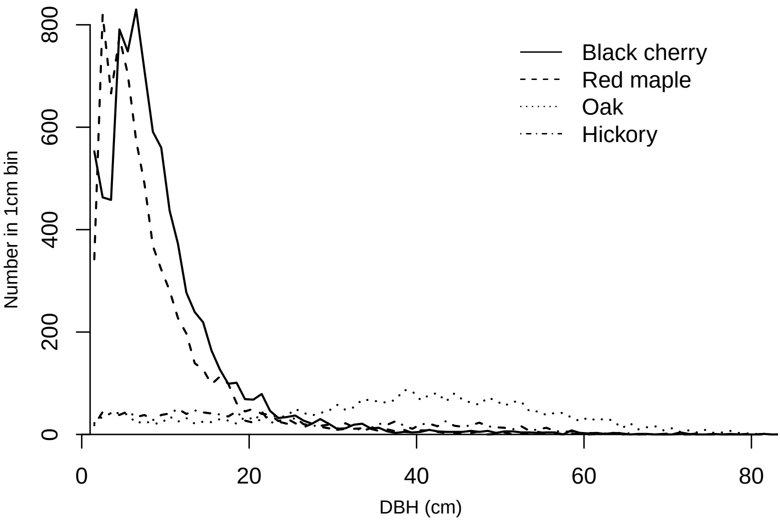


Big Woods plot at the Edwin S. George Reserve

- Edwin S George Reserve, 500 ha, in southeast Michigan. Administered by the University of Michigan.
- Big Woods plot is 23 ha, all stems greater than 1 cm DBH tagged, identified and mapped. >40,000 stems.
- Censuses in 2003 (only 12 ha), 2008, and 2014.
- Part of the Smithsonian Institute's ForestGEO network of plots.
- Oak-hickory dominated canopy: *Quercus rubra*, *Q. velutina*, *Q. rubra x velutina*, *Q. alba*, *Carya ovata*, *C. cordiformis*, and *C. glabra*.
- Subcanopy dominated by *Acer rubrum* and *Prunus serotina*.

Stem size distribution



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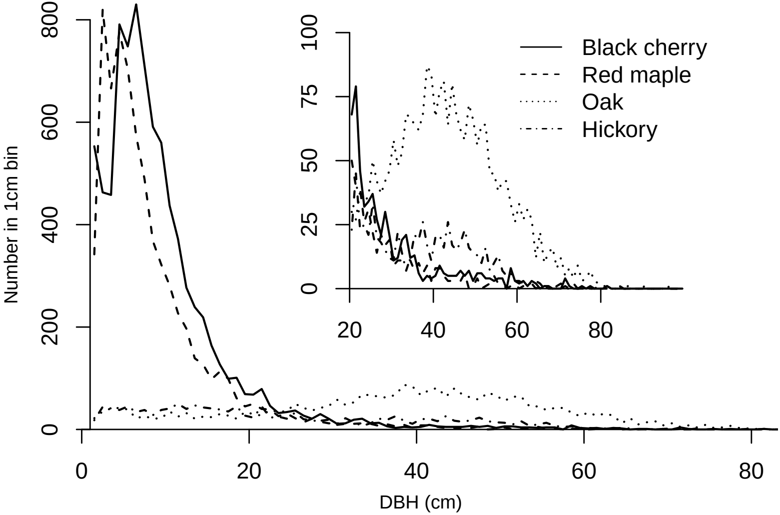


Oak decline in the plot

Proportion of stems >20 cm DBH belonging to each taxon over the three censuses:

	2003	2008	2014
Black/red oak	0.40	0.36	0.33
White oak	0.21	0.20	0.19
Black cherry	0.14	0.16	0.17
Red maple	0.11	0.12	0.15
Hickories	0.09	0.09	0.09

Big Woods plot at the Edwin S. George Reserve

Here we will model the diameter growth between 2008 and 2014 based on a focal tree's neighbors in 2008. There are 21,065 stems of 33 species.

RStan

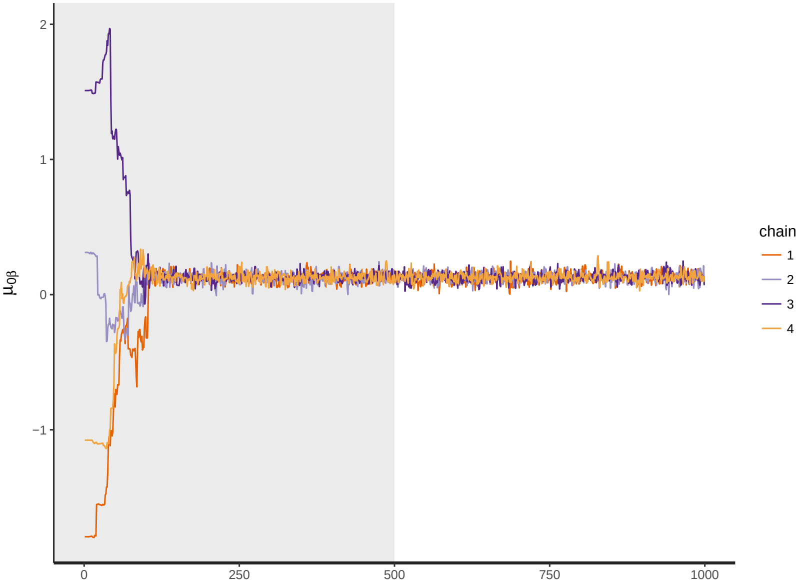
- Bayesian methods lend themselves well to hierarchical models.
- With Bayesian models, it's often difficult to compute analytic estimates of all parameters
- Instead, Markov Chain Monte Carlo (MCMC) methods draw a random sample from the posterior distributions of parameters. For example: the empirical mean of such a sample approximates the true posterior mean.
- "Bayesian inference Using Gibbs Sampling" (BUGS) was long the de facto tool for MCMC.
- Stan is a new alternative
  - Uses Hamiltonian MCMC instead
  - Is supported across many platforms: R, Python, MATLAB, Julia, Stata
  - Rstan (Stan Development Team 2016)

Priors

We use wide, uninformative priors for the hyperparameters.

$$\begin{aligned}
\mu_{0\beta} &\sim \text{Norm}(0, 100) \\
\mu_{1\beta} &\sim \text{Norm}(0, 100) \\
\mu_{\lambda} &\sim \text{Norm}(0, 100) \\
\sigma_{y} &\sim \text{Uniform}(0, 10000) \\
\sigma_{0\beta} &\sim \text{Uniform}(0, 10000) \\
\sigma_{1\beta} &\sim \text{Uniform}(0, 10000) \\
\sigma_{\lambda} &\sim \text{Uniform}(0, 10000)
\end{aligned}$$

Convergence



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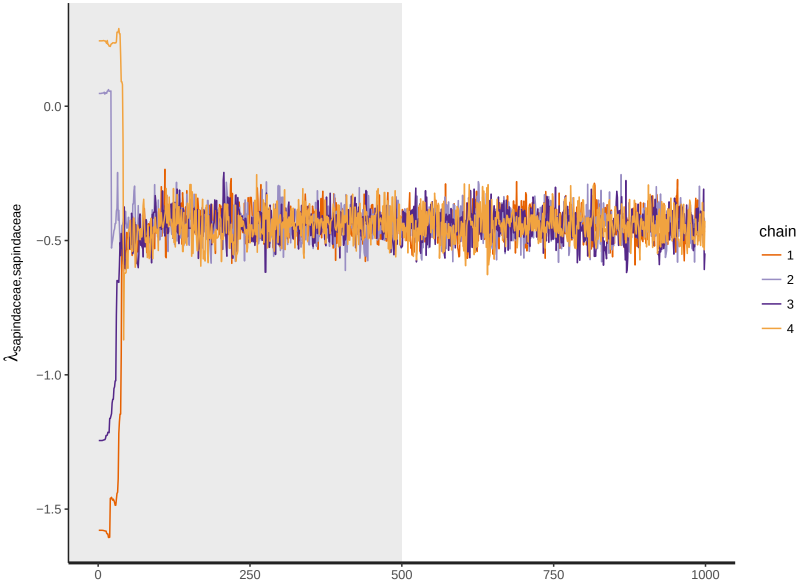
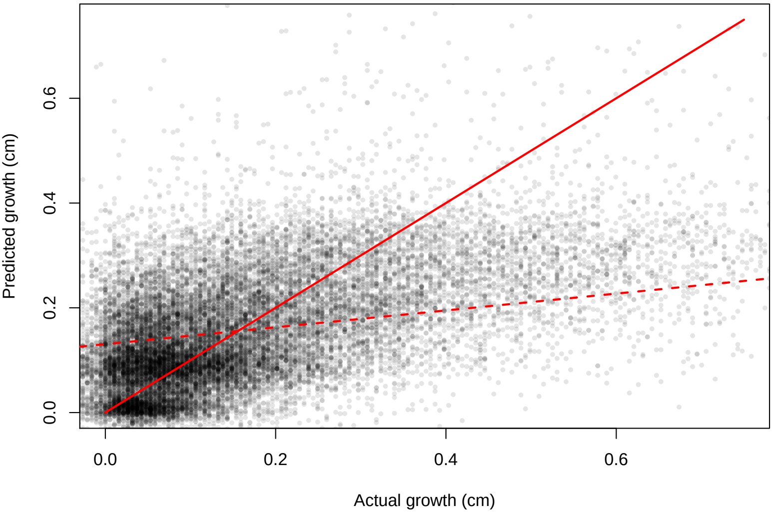


Actual versus out-of-sample predicted

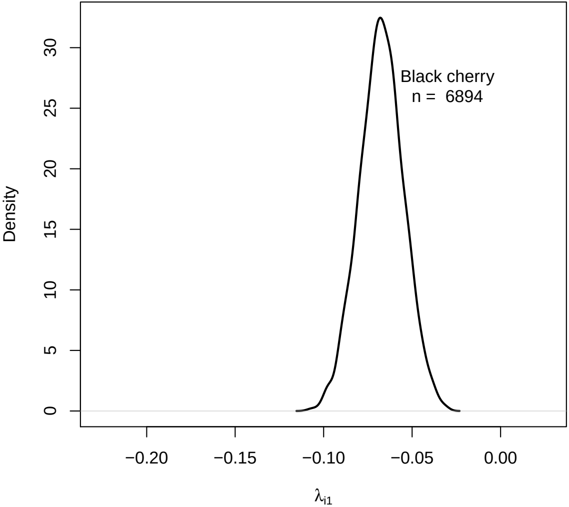


Model results comparison

	Null	Trait groups	Family	Species
MAE	0.130	0.128	**0.126**	0.127
MSE	0.069	0.068	**0.067**	**0.067**
Slope	0.126	0.156	0.156	**0.161**
R^2	0.095	0.108	0.105	**0.109**

Example posterior estimate of λ

For the null model with a 33×1 λ-matrix.



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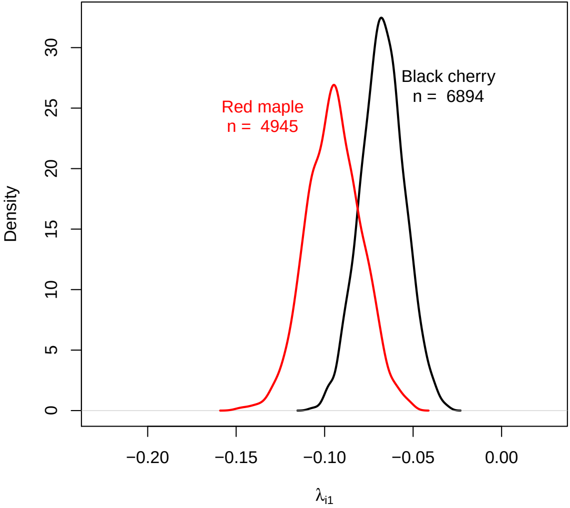

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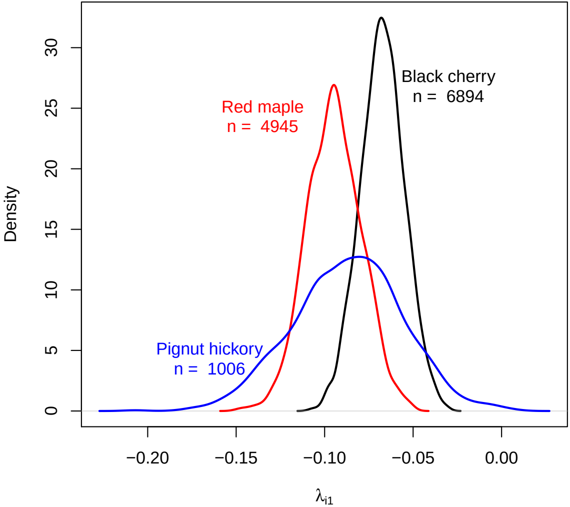

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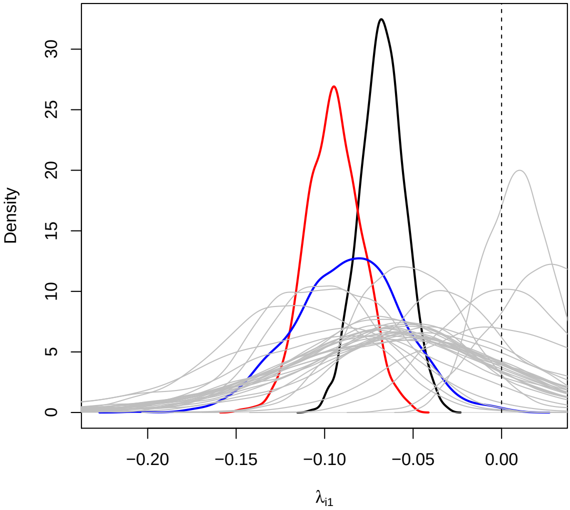
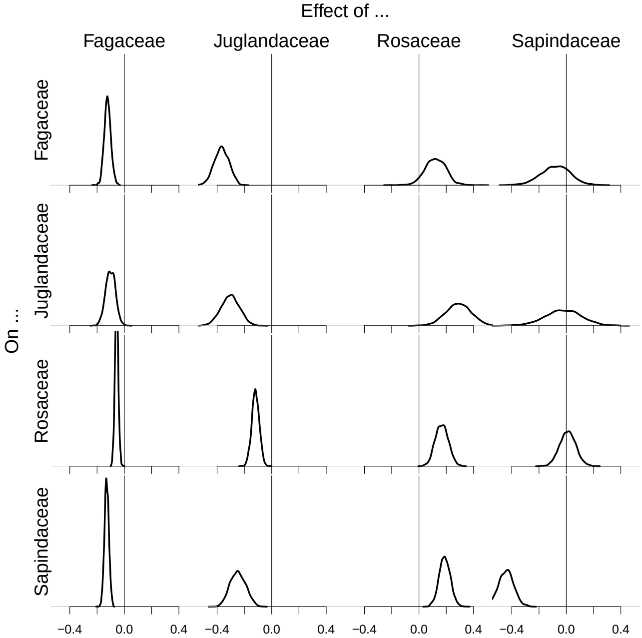


Estimates of λs from the family model



Conclusions, limitations, possible extensions

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  - Powerful approach to estimate competition coefficients.
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  - Could be seeing some other spatial signal going on. Maybe black cherry individuals grow in favorable locations.
- Possible extensions
  - Similar formulation for effect of neighbors on survival. (e.g., Lasky et al. 2014) or recruitment
  - Two-level hierarchal structure
  - Extend to other CTFS ForestGEO plots.

Acknowledgments

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