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

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Ecological Society of America
Portland, OR
August 10, 2017
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.
Matrix of competitive interactions, $\lambda_{ij}$ is the effect of species $j$ on species $i$. 

$$
\begin{bmatrix}
\lambda_{11} & \lambda_{12} & \ldots \\
\lambda_{21} & \lambda_{22} & \ldots \\
\vdots & \vdots & \ddots 
\end{bmatrix}
$$
Matrix of competitive interactions, $\lambda_{ij}$ 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 $i$. 

$$
\begin{bmatrix}
\lambda_{11} & \lambda_{12} & \ldots \\
\lambda_{21} & \lambda_{22} & \ldots \\
\vdots & \vdots & \ddots
\end{bmatrix}
$$
Estimating the full matrix of $\lambda$ values is difficult. How have others dealt with this?

- Canham et al. (2006) neighborhood competition index. Frequentist likelihood to estimate $\lambda$s for common species-pairs and ignored rare ones.

- Uriarte et al. (2010) don’t estimate each $\lambda$, but tested models with $\lambda$ as a function of phylogenetic or trait-based similarity between species.

- Tatsumi et al (2016) use a Bayesian hierarchical approach. Tested different theories of competition which imposed different structure on the $\lambda$ matrix.
Hierarchical models

\[ \lambda_{11} \quad \lambda_{12} \quad \lambda_{13} \quad \ldots \quad \lambda_{21} \quad \ldots \]
Hierarchal models

\[
\begin{align*}
\mu &
\end{align*}
\]

\[
\lambda_{11} \quad \lambda_{12} \quad \lambda_{13} \quad \cdots \quad \lambda_{21} \quad \cdots
\]

is a hyperparameter. If the sample size for \( ij \) is small, it "borrows" information from other pairs via the hyperparameter. If the sample size is large, there is less "borrowing."
Hierarchical models

\[ \mu, \lambda \]

\[ \lambda_{11}, \lambda_{12}, \lambda_{13}, \ldots, \lambda_{21}, \ldots \]

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Model formulation

\[
\text{Growth} \sim \text{Norm}(\beta_0i + \beta_1iDBH + \sum_{j} \lambda_{ij}BA_j, \sigma_y)
\]

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.
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 \( \text{BA}_j \) is the sum of the basal area of individuals of that species within 7.5 m of the focal individual. Also have the hyperparameters,

\[
\begin{align*}
\beta_{0i} & \sim \text{Norm}(\mu_0, \sigma_0) \\
\beta_{1i} & \sim \text{Norm}(\mu_1, \sigma_1) \\
\lambda_{ij} & \sim \text{Norm}(\mu, \sigma) 
\end{align*}
\]
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).
Models to be compared

- Null: Each species gets its own response to competition. $\lambda$ is $33 \times 1$
- Trait grouped: Clustered species based on values for those three traits and form six clusters. $\lambda$ is $6 \times 6$
- Family: $\lambda$ is $19 \times 19$
- Species: $\lambda$ is $33 \times 33$
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
Cross validation scheme
Cross validation scheme
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.
- 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

- Black cherry
- Red maple
- Oak
- Hickory

DBH (cm)
Number in 1cm bin
0 20 40 60 80
0 200 400 600 800

Number in 1cm bin vs. DBH (cm)
Stem size distribution

![Graph showing stem size distribution for different tree species]

- Black cherry
- Red maple
- Oak
- Hickory

Number in 1cm bin vs DBH (cm)
Oak decline in the plot

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

<table>
<thead>
<tr>
<th>Taxon</th>
<th>2003</th>
<th>2008</th>
<th>2014</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black/red oak</td>
<td>0.40</td>
<td>0.36</td>
<td>0.33</td>
</tr>
<tr>
<td>White oak</td>
<td>0.21</td>
<td>0.20</td>
<td>0.19</td>
</tr>
<tr>
<td>Black cherry</td>
<td>0.14</td>
<td>0.16</td>
<td>0.17</td>
</tr>
<tr>
<td>Red maple</td>
<td>0.11</td>
<td>0.12</td>
<td>0.15</td>
</tr>
<tr>
<td>Hickories</td>
<td>0.09</td>
<td>0.09</td>
<td>0.09</td>
</tr>
</tbody>
</table>
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.
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)
We use wide, uninformative priors for the hyperparameters.

\[
\begin{align*}
\mu_{0\beta} &\sim \text{Norm}(0, 100) \\
\mu_{1\beta} &\sim \text{Norm}(0, 100) \\
\mu_{\lambda} &\sim \text{Norm}(0, 100) \\
\sigma_y &\sim \text{Uniform}(0, 10000) \\
\sigma_{0\beta} &\sim \text{Uniform}(0, 10000) \\
\sigma_{1\beta} &\sim \text{Uniform}(0, 10000) \\
\sigma_{\lambda} &\sim \text{Uniform}(0, 10000) 
\end{align*}
\]
Convergence
Convergence

\[ \lambda_{\text{sapindaceae}} \]

-0.5
-1.0
-1.5

\[ \text{chain} \]
1
2
3
4

\[ 0 \quad 250 \quad 500 \quad 750 \quad 1000 \]
Actual versus out-of-sample predicted growth

![Diagram showing the comparison between actual growth and predicted growth.](image-url)
Model results comparison

<table>
<thead>
<tr>
<th></th>
<th>Null</th>
<th>Trait groups</th>
<th>Family</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAE</td>
<td>0.130</td>
<td>0.128</td>
<td>0.126</td>
<td>0.127</td>
</tr>
<tr>
<td>MSE</td>
<td>0.069</td>
<td>0.068</td>
<td>0.067</td>
<td>0.067</td>
</tr>
<tr>
<td>Slope</td>
<td>0.126</td>
<td>0.156</td>
<td>0.156</td>
<td>0.161</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.095</td>
<td>0.108</td>
<td>0.105</td>
<td>0.109</td>
</tr>
</tbody>
</table>
Example posterior estimate of $\lambda$

For the null model with a $33 \times 1 \lambda$-matrix.

![Graph showing density of $\lambda_{i1}$ with peak at $n = 6894$.]
Example posterior estimate of $\lambda$

For the null model with a $33 \times 1$ $\lambda$-matrix.

![Density plot showing two distributions for Black cherry and Red maple with sample sizes $n = 6894$ and $n = 4945$ respectively.](image)
Example posterior estimate of $\lambda$
For the null model with a $33 \times 1$ $\lambda$-matrix.
Example posterior estimate of $\lambda$

For the null model with a $33 \times 1$ $\lambda$-matrix.
Estimates of $\lambda$s from the family model

<table>
<thead>
<tr>
<th>Family</th>
<th>Density</th>
<th>N = 2000</th>
<th>Bandwidth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fagaceae</td>
<td></td>
<td>0.004639</td>
<td></td>
</tr>
<tr>
<td>Juglandaceae</td>
<td></td>
<td>0.01054</td>
<td></td>
</tr>
<tr>
<td>Rosaceae</td>
<td></td>
<td>0.01488</td>
<td></td>
</tr>
<tr>
<td>Sapindaceae</td>
<td></td>
<td>0.02086</td>
<td></td>
</tr>
</tbody>
</table>

Effect of ... On ...

- Fagaceae
- Juglandaceae
- Rosaceae
- Sapindaceae
Conclusions, limitations, possible extensions

- **Conclusions**
  - Powerful approach to estimate competition coefficients.
  - Interesting that we did not see the importance of traits that others did (Uriarte et al. 2010, Kunstler et al. 2016)

- **Limitations**
  - This approach does not directly measure competition.
  - 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.
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Acknowledgments

- Work supported by the Edwin S. George Reserve Fund, USDA McIntyre–Stennis Grant, and the Middlebury College Faculty Professional Development Fund.

- John Vandermeer, Chris Dick, and Ivette Perfecto are collaborators on the Big Woods plot

- Many students who helped census the plot: Omodele Ajagbe, Bob Barretto, Hillary Butterworth, Richard Byler, Vera Chan, Ben Crotte, David Hudson, Lindsay Ford, Katie Gallagher, Jasmine Gramling, Kate Heflick, Rodica Kocur, Carley Kratz, Rachael Lacey, Isaac Levine, Kathleen Parks, Andrew Phillips, Jayna Sames, Margot Sands, John Schroeder, Leah Spaulding, Ethan Strayer, Jordan Trejo, Justin Waraniak, Padhma Venkitapathy, Connor Velzy, and Ash Zemenick.


