Data Description:

In the central Rocky Mountains of the western U.S., *Pinus ponderosa*, *Pinus contorta* and *Pseudotsuga menziesii* exhibit distinct ranges, yet show some overlap along montane ecotones (Rehfeldt et al. 2006). The overlapping ranges of these species suggest that, where they occur sympatrically, all species compete for similar resources. Estimating relative competitive dominance of each species along these ecotones is necessary for understanding interspecific competition in this system and for identifying environmental and physiological drivers of competitive advantages. Basal area is a strong indicator of competitive dominance, and the change in basal area across an ecotone may represent a species’ competitive ability across a gradient of environmental conditions (Stohlgren & Bachand 1997). Here, I use a hierarchical Bayesian regression approach to answer the two following questions:

1. **How does basal area of *P. ponderosa*, *P. contorta* and *P. menziesii* change across montane ecotones in the Beartooth Mountains, MT, and how does rate of change (turnover) vary among species?**
2. **What proportion of species turnover is explained by maximum annual temperature, minimum annual temperature and precipitation?**

To address these questions, basal area (BA) of each species was measured in five sampling plots spaced along each of six transect that spanned the width of montane ecotones. Climate data was extracted from the PRISM data set with an 800m resolution to characterize the climate associated with each transect. A hierarchical Bayesian regression approach was used to fit parameters to data using Gibb’s sampling and the effect of climate variables on species turnover was analyzed. The specific modeling approach is described below.

Model Description:

Basal area by species was calculated by plot from DBH field measurements. A nested linear model was constructed to characterize the change in species basal area across an ecotone. The model is distributed according to a multivariate Normal with three variables (individual species), each of which shows distinct and characteristic trends across transects. Because the model explains a global trend across all transects, a random effect term is incorporated to capture the differences in turnover between transects. Elevation by plot is believed to account for a range of environmental differences among plots and is thus used as the primary predictor. Climate is used to explain dominance trends among transects and is incorporated into the elevation effect. The simplified model is shown below:

\[ y_{ij} \sim N_3(\beta_0 + \alpha_j + \text{elev}_j(\beta_1 + A_1 \times \text{clim}_j), \text{prec}) \]
In this model, $i$ is equal to the transect number where $i=(1,\ldots,6)$ and $j$ is equal to the plot number where $j=(1,\ldots,5)$. The variable $y$ is equal to the basal area at plot $ij$ for species $n$ where $n=(1,\ldots,3)$ for *P. contorta*, *P. ponderosa*, and *P. menziesii*. The multivariate normal distribution is characterized by two parameters, the mean $\mu$ being equal to the linear function, and the variance $prec$ equal to the process error covariance, assuming that each species’ BA is not independent. $\beta_0$ and $\beta_1$ are intercepts and are ecologically irrelevant but computationally important. Elevation is explained by a nested linear model incorporating a climate effect ($A_1$) and the climate variable of interest (max temp., min temp., precipitation). The model incorporates a random effect parameter, $\alpha$, to account for variation in trends among transects.

Prior distributions are assigned to all parameters and are shown below:

- $\beta_0 \sim N_3(b_0, \nu b_0)$
- $\beta_1 \sim N_3(b_1, \nu b_1)$
- $A_1 \sim N_3(a_1, \nu a_1)$
- $prec \sim W(a_R, o_K)$
- $\alpha_{i,k} \sim N(0, \phi_K)$

Linear model parameters are distributed according to a multivariate Normal, while the process error covariance is distributed according to the Inverse Wishart, a distribution that is conjugate to the Normal and allows for calculation of a closed solution.

**Analysis:**

Parameters were fitted to data using standard Bayesian regression techniques. Weak priors were initially set to minimize their influence on parameter estimates. The model was coded in to Program R and a Gibb’s Sampler was used to estimate parameter distributions for each model using the R packages JAGS and CODA. Four independent Gibb’s chains were run for each parameter with 500,000 iterations and a burn in of 100,000 iterations. Convergence and autocorrelation were assessed visually, and parameter estimates were thinned to every 1000th value. Full Gibb’s chains were used to estimate mean parameter estimates and 95% credible intervals for each parameter. Predictions were made across each iteration of the sampler and averaged for a mean prediction of basal area for each species by plot.

A predictive loss method was used to estimate model fit for each of the three models. Predictive loss correctly accounts for models that include random effects by penalizing for model complexity rather than the number of parameters. Because all three models were equal in complexity, the second term of the equation acts as a constant and model comparison was completed based on only the first term of the predictive loss equation (residual term). The model that minimized residuals was thus deemed the strongest model.
**Results:**

Turnover rate predictions were comparable among all three models (fig. 1). Across all transects, *P. contorta* (Pico) and *P. menziesii* (Psme) showed a positive turnover rate, indicating an increase in basal area with increasing elevation. Mean turnover rate for *Pinus ponderosa* (Pipo) was slightly negative, indicating a decrease in basal area with increasing elevation. However, the credible interval for Pipo spanned both positive and negative values, and thus the dominance trend cannot be stated with confidence. The process error covariance (table 1) for each species shows generally negative relationships among species for all three models. This implies that turnover rates of different species are inversely related. However, the precipitation model gives a positive covariance for Psme and Pipo. Indeed, the Psme covariances were the weakest across all models suggesting that the relationship between *P. menziesii* basal area and that of *P. ponderosa* and *P. contorta* is variable and difficult to predict.

Climate effects were generally small for all three climate variables considered (fig. 2). Temperature showed a greater effect on turnover rate of all species in comparison to precipitation. However, temperature appeared to have a smaller effect on Pipo than on Pico and Psme, while precipitation had a much larger effect on Pipo than on Pico or Psme. This suggests that species show different sensitivities to individual climate variables.

The random effects term accounted for most of the variation in basal area across all three models. The random effects parameter accounts for variation among plots within a transect separately from the global trends across all transects. This suggests that finer-scale landscape variation is largely driving trends in species turnover rate.

Model fit was generally poor and did not differ significantly among models (fig. 3, table 2). The data are clearly zero inflated and thus require either transformation or an alternative model. Predictive loss analysis indicates a slightly better fit of temperature models over precipitation, though this is likely due to the greater effect of temperature on two species versus precipitation on only one.

In general, these results indicate that further model development is required to more accurately predict species turnover rate. Alternative model approaches are currently being analyzed and rely on relative rather than absolute basal area and thus require a truncated Normal distribution. These data show a sigmoidal dominance trend and will thus require use of a nonlinear model. Additional environmental variables will need to be incorporated into this model to better account for variation among transects. In the future, data from four additional sites will be added and model complexity will increase to account not only for variation within and among transects, but also for variation among sites.
References:

JAGS version 3.4.0 (2013). *Just Another Gibbs Samper*. Martyn Plummer.

Tables:

Table 1. Mean process error covariance across all three models. Values did not differ significantly among models, so mean values are presented.

<table>
<thead>
<tr>
<th></th>
<th>Pico</th>
<th>Pipo</th>
<th>Psme</th>
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<tbody>
<tr>
<td>Pico</td>
<td>0.471</td>
<td>-0.138</td>
<td>-0.159</td>
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<tr>
<td>Pipo</td>
<td>-0.138</td>
<td>0.197</td>
<td>-0.001</td>
</tr>
<tr>
<td>Psme</td>
<td>-0.159</td>
<td>-0.001</td>
<td>0.189</td>
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Table 2. Residual term (Gm) values for each model from the predictive loss calculation.

<table>
<thead>
<tr>
<th></th>
<th>Tmax</th>
<th>Tmin</th>
<th>Precip</th>
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<tbody>
<tr>
<td>Gm</td>
<td>16.61175</td>
<td>16.73251</td>
<td>17.46759</td>
</tr>
</tbody>
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Figures:

**Figure 1.** Mean turnover rate by species for each model. Error bars represent 95% CI’s.
Figure 2. Mean climate effect on turnover rate for each model. Error bars represent 95% CI’s.
Figure 3. Observed versus predicted basal area for each model. Solid lines represent a perfect fit (1,1).