Interactive Effects of Environmental Variability and Neighborhood Diversity on Performance of Four Common Deciduous Tree Species in Eastern North America

by

Kirk Acharya

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Faculty advisor(s):
Inés Ibáñez, Professor
Stella Cousins, Research Scientist

Abstract

There is considerable evidence on the benefits of forest diversity for overall stand growth. Diversity has also been shown to buffer forests from climate disturbance. Knowing the species-specific impacts of diversity on tree growth is critical to assess, manage, and potentially design, resilient local forests under global change. We aim to address this knowledge gap using a combination of a dendrochronological study with a predictive modeling framework to understand the effects of forest neighborhood diversity across a gradient of June precipitation. We expected that: 1) under drought conditions increasing levels of diversity would impact species differently depending on their hydraulic strategies and 2) under typical/non-drought water availability, intraspecific interactions would have a more negative effect on growth than interspecific interactions, due to higher competition with resource overlap. We found that species do in fact respond to varying scenarios of diversity differently based on water availability. However, diverse ecosystems were not beneficial to drought tolerant *Quercus* species during high water availability, contrary to our prediction. Neighborhood dynamics are likely influenced by functional traits beyond hydraulic diversity including shade tolerance, water uptake depth, and growth strategy. Our findings indicate a potential trend in which *Quercus* species are released from competition under drought. The future environmental conditions in the region are predicted to have greater variability and clarifying neighborhood interactions helps to understand future trends in forest growth patterns.

Acknowledgements

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INTRODUCTION

There is a mounting body of evidence that biodiversity has a positive effect on forest ecosystem productivity and on other ecosystem services (Morin et al. 2011, Gamfeldt et al. 2013, Forrester 2015). Furthermore, greater species diversity has the potential to mitigate some of the negative impacts associated with climate change in forests (Merlin et al. 2015, Anderegg et al. 2018a, Aussenac et al. 2019, Fichtner et al. 2020). Despite the overall benefits of biodiversity to forest communities, there is considerable variation in the effects of diversity among co-occurring tree species and in the way in which these diversity effects are modulated by environmental conditions (Liang et al. 2007, Haase et al. 2015, Uriarte et al. 2018, Ammer 2019, Bosela et al. 2019, Taylor et al. 2020). Still, knowing the species-specific impacts of diversity on tree growth is critical to assess, manage, and potentially design, resilient local forests under global change (Ibanez et al. 2019). We address this knowledge gap by investigating how the diversity of the forest neighborhood (adjacent individuals) affects the yearly growth of target trees under varying environmental conditions. In our study region, extreme weather events of drought and heavy rainfall are predicted to increase (Hayhoe et al. 2007, Villarini et al. 2011). The study period of 2006 to 2017 experienced ~ 4mm June precipitation between 2011 and 2012 resulting in severe drought indicated by a Palmer Drought Severity Index (PDSI) of -2.46 and higher than average rainfall in 2014 with ~ 15 mm during the month, demonstrating the wide environmental variability predicted to increase (Dai et al. 2004).

In forest ecosystems, biodiversity can benefit tree growth and resilience to environmental variability through both niche complementarity (Hooper et al. 2005, Morin et al. 2011, Forrester 2015, O'Keefe et al. 2019, Searle and Chen 2019) and/or competitive release (Gomez-Aparicio et al. 2011, Clark et al. 2014, Manso et al. 2015, Ford et al. 2017, Oboite and Comeau 2020). These benefits of biodiversity emerge under diverse conditions because there is a decrease in the overlap between conspecific trees in resource acquisition, growth strategies, and life history. When considering performance at the individual level, functional diversity of species can alleviate competition pressure if there are fewer similarly functional species vying for the same resource pools (Manso et al. 2015, Oboite and Comeau 2020). At the community

level, complementarity between species results in higher growth because of a greater efficiency of soil water use and more diversity in shade tolerance and thus canopy architecture (Forrester 2015, O'Keefe et al. 2019). While complementarity between species results in an overall increase in ecosystem productivity due to resource and light use efficiency, it is unclear if all species will have the commensurate increases in growth compared to less diverse stands.

In addition to complementarity, forest stands are shaped by competition (Clark et al. 2011, Clark et al. 2014). Co-occurring tree species compete for light, nutrients, water and space (Gomez-Aparicio et al. 2011); and under global warming competition for water will increase (Fernandez-de-Una et al. 2015). Warming temperatures are not only increasing the demand for water but also increasing loses due to evaporation (McDowell et al. 2008). There has been much attention paid to how tree species diversity might ameliorate the increasing competition for soil water (Anderegg et al. 2018a, Bello et al. 2019, Vanhellemont et al. 2019, Fichtner et al. 2020). Tree species are often classified along a gradient of hydraulic strategies. Anisohydric species, which are typically better adapted to tolerate water stress, keep their stomata open despite drought, in order to maintain positive photosynthetic rates (McDowell et al. 2008). In contrast, isohydric, drought-intolerant species will close their stomata to reduce water loss and maintain less-negative interior water potentials (McDowell et al. 2008). Anisohydric species prioritize carbon assimilation while increasing the risk of xylem embolisms under extreme conditions. Isohydric species minimize the risk of cavitation but increase the risk of carbon starvation due to increased respiration relative to photosynthetic assimilation. This functional trait enables anisohydric species to be more productive during mild droughts, but at the risk of hydraulic failure if drought is extreme, while isohydric species prevent hydraulic failure closing their stomata but with the risk of carbon starvation due to reduced photosynthetic function (Sperry 2003, McDowell et al. 2008, Anderegg et al. 2016, Anderegg et al. 2018b, Choat et al. 2018).

The distinct functional diversity of these two groups led us to predict that productivity of anisohydric tree species will benefit from a diverse neighborhood under drought conditions due to a greater availability of water from the closure of stomata in isohydric neighbors. Conversely, we expect no effect of neighborhood diversity on isohydric species' growth during

drought due to their stomatal closure and subsequent reduction of photosynthetic activity. However, during high water availability, both isohydric and anisohydric species likely benefit from neighborhood diversity when water availability due to complementarity between the diverse water uptake depths, water storage strategy, growth strategy, and

To better understand how forest diversity may differentially affect tree species performance we assess how environmental conditions, i.e., water availability, and biodiversity interact to affect tree growth of tree species on the continuum of more isohydric (Acer) to anisohydric (Quercus) (Matheny et al. 2015, Roman et al. 2015, Mirfenderesgi et al. 2019). Our goal was to quantify the effect of the different neighborhoods surrounding individuals and how these effects might vary depending on water availability. We expected that: 1) under drought conditions increasing levels of diversity would impact species differently depending on their hydraulic strategies, with anisohydric species deriving benefits from diversity under drought conditions, while isohydric species would not benefit from a diversity of neighbors due to their reduced photosynthetic activity. 2) Under typical/non-drought water availability, intraspecific interactions would have a more negative effect on growth than interspecific interactions, due to higher competition with resource overlap. Therefore, both anisohydric and isohydric species would benefit from more functionally diverse neighborhoods. Biodiversity has benefits to community performance, but at the local species level is not entirely clear who benefits most from diversity and how these benefits may change as a function of environmental conditions. Understanding the benefits of biodiversity at the local scale is crucial for improving our predictions of future forest performance and informing effective forest management practices.

METHODS

Study Locations

We conducted this study in two mapped forest stands in southeast Michigan, USA: Stinchfield Woods (42.399 N, -83.925 W) and Radrick Forest (42.289 N, -83.658 W) (Supplementary Material, S1). Both stands are temperate mesic hardwood forests dominated by *Acer* and *Quercus* species. The climate is similar across both sites with growing seasons (June-August) averaging 22.2 °C and 260 mm of precipitation. Mean annual precipitation is

75.84 cm. At each site, we identified all trees within a 100 m^2 plot to species level, measured their diameter at breast height (DBH), and recorded their position on a Cartesian grid (Figure 1., S2). These forests are both mid to late successional secondary growth forests categorized as mixed oak-hickory with a range of microtopography. Stratification of both sites include overstory of *Acer, Quercus, Carya, Prunus, Tilia*, and some *Sassafras*, while the understory consists of largely *Acer* species and *Ostrya virginiana*. There is little shrub layer and a relatively open forest floor or herbaceous layer.

Data Collection

Tree Cores: Field & Processing

Between 2018 and 2019 we identified all *Acer* and *Quercus* individuals larger than 10 cm DBH within the forest stands. We extracted tree cores from these individuals at breast height (1.3 m) using Haglöf 5.15 mm increment borers (Haglöf Inc.; Madison, MS, USA). The north and south side of each tree was cored to the pith, and cores were stored in paper straws until they could be dried. We dried core samples overnight in a 100 °C oven and mounted them afterwards in cradles. Cores were then sanded with progressively finer sandpapers starting at 100 grit and ending at 600 grit for *Quercus* species and 1600 grit for *Acer* species. Broken or incomplete cores were not used for analysis. We digitized the prepared samples using a flatbed scanner at a resolution of 1200 dpi.

Environmental Data

Environmental data for Washtenaw county was obtained from the National Center for Environmental Information (NCEI) Climate at a Glance time series product (https://www.ncdc.noaa.gov/cag/). The datasets include average monthly temperature and total monthly precipitation from 2006-2017.

Analysis

Tree Cores: Measurement & Crossdating

We measured annual ring width (growth) of digitized scans at a precision of 0.001 mm using the Cybis CooRecorder program. We then used Cybis CDendro to crossdate samples and assemble chronologies by site and species, estimating pith using the geometric method if not present on the sample (Duncan 1989). We estimated historical DBH for tree *i* in year *y* using ring width and the diameter of trees in 2017. To measure yearly growth, we calculated Basal Area Increment (BAI) as $BAI_{i,y} = \pi \cdot (\frac{DBH_{i,y}^2}{4} - \frac{DBH_{i,y-1}^2}{4})$ for use in our model.

Data Analysis

We developed a model to explain the impact of species-specific neighborhood effects (NE) and environmental conditions on the growth of individual trees (hereafter 'target trees'). Our timeframe of growth was between 2006 and 2017. This short time period was used to ensure that no major changes in the neighborhood surrounding the target trees had taken place (e.g., a large neighboring canopy tree falling). We first performed exploratory data analysis to assess relationships between growth and environmental variables. April temperature and June precipitation were the variables most strongly correlated with growth and were therefore chosen to be used in model selection. We also included previous year growth to account for lag effects (Ibanez et al. 2018) and DBH to detrend the size-growth relationship (Cook 1990, Bigelow et al. 2020). We assessed several combinations of explanatory variables; below we describe the best model fitting the data (based on deviance information criterion [DIC]; Spiegelhalter et al. 2002) which included site specific random effects and an interaction between June precipitation and NE. For each species independently, we modeled *BAI* for tree *i* in year *y* ($bai_{i,y}$) with a log-normal likelihood:

$$bai_{i,y} \sim Lnormal(R_{i,y}, \sigma^2{}_{i,y})$$

And process model:

$$R_{i,y} = \alpha_{site\,(i)} + NE_i + \beta_1 \cdot JunePrecip_y + \beta_2 \cdot JunePrecip_y \cdot NE_i + \beta_3 \cdot April\,Temp_y + \beta_4 \cdot \log(DBH_i) + \beta_5 \cdot BAI_{i,y-1}$$

Neighborhood effects (*NE*) for tree *i*, NE_i, were estimated for each individual *i* as the sum of the effects of each neighbor *j*, 10 m in any cardinal direction, effects varied for each species of neighbor and as a function of the sizes and distance of the neighbor and target trees:

$NE_i = \sum_{j=1}^{no.neighbors\ i} \lambda_{species\ i,j}(DBH_j/DBH_i)/distance_{i,j}$. Parameter λ represented the effect of species *j* on species *i*. Positive λ values indicated facilitation between species and neutral values indicated complementarity, whereas a negative λ indicated competition. During data exploration we observed that the variance of growth increased with a greater DBH. To account for this, we estimated the variance ($\sigma^2_{i,t}$) as a function of DBH (Lines et al. 2012):

$\sigma^2_{i,t} = a + b \cdot \ln(DBH_{i,t})$

We estimated model parameters within a Bayesian framework from non-informative prior distributions, $\alpha_* \sim Normal(A, \sigma^2_\alpha)$, $1/\sigma^2_\alpha \sim Gamma(0.001, 0.001)$, A,

$\beta_*, \lambda_*, b \sim Normal(0, 10{,}000)$, $a \sim logNormal(1, 0.0001)$.

Simulated neighborhoods

Using parameter estimates from the analysis we created simulated neighborhoods in order to describe the effect of increasing diversity on growth in three scenarios: 1) a neighborhood of species composition representative of our field sites (observed), 2) a simulated higher diversity neighborhood that included an even distribution of the dominant species found across the sites (high diversity), and 3) an scenario without neighbors (no neighbors) (S3). For these diversity scenarios we assumed that target trees had a DBH equal to the respective species' mean DBH in the data (A. rubrum, 19.26 cm; A. saccharum, 25.2 cm; Q. alba, 42.87 cm; Q. velutina, 52.54 cm), while neighbor trees were given the average DBH for the whole data set (13.2 cm). We then used the posterior parameter estimates from the model (mean, variances and covariances) to estimate growth across the gradient of June precipitation experienced at our sites between 2006 and 2017. We used the mean temperature for April (15° C), as exploratory analysis showed that variation in April temperatures did not alter the effects of neighborhoods.

Analyses were performed in OpenBugs version 3.23 (Lunn et al. 2009). We ran three Markov Chain Monte Carlo simulations for 300,000 iterations. Once chains converged, we

estimated the posterior parameter means, standard deviation (SD), and the 95% credible intervals for each variable and simulations values (model code, S4).

RESULTS

Our final analysis included 270 target trees between the two sites. *Acer rubrum* included 78 individuals with an average DBH of 19.3 cm, a minimum of 10.1 cm, and a maximum of 49.4 cm. *Acer saccharum* included 40 individuals with an average DBH of 25.2 cm, a minimum of 12.1 cm, and a maximum of 52.8 cm. *Quercus alba* included 88 individuals with an average DBH of 42.9 cm, a minimum of 19.4 cm, and a maximum of 85.9 cm. Finally, *Quercus velutina* included 64 individuals and an average DBH of 52.5 cm, a minimum of 21.3 cm, and a maximum of 80.3 cm (Figure 1; S2).

Effects of neighbor species identity on growth of target trees

Neighborhood effects varied in sign and magnitude among the target species (Fig. 1; Table 1; see S4 for parameter values). In general, isohydric maple species exhibited negative interactions with their neighbors (i.e., competition), while anisohydric oak species showed none or positive effects of neighbors on growth (i.e., complementarity) (Figure 1). *Acer rubrum* and *A. saccharum* demonstrated significantly positive interactions with *Ostrya virginiana* neighbors, *A. saccharum* growth was negatively affected by *Ulmus americana* neighbors and by congeneric *A. nigrum* neighbors. All neighbor effects were non-significant for *Q. alba* but generally positive. *Q. velutina* growth was positively affected by four neighbor species, while growth was negatively affected by conspecific *Q. velutina* neighbors (Table 1).

Growth effects of temperature and precipitation; interaction with neighborhood effects

Three of the target species showed a significant positive relationship of growth to April temperature and June precipitation (Fig. 2; *A. rubrum, Q. alba,* and *Q. velutina*; *A. rubrum*, *A. saccharum*, and *Q. velutina,* respectively). The interaction between June precipitation and neighborhood effects was negative for all four study species, and significant for *A. saccharum*, *Q. alba* and *Q. velutina* (Fig. 2). This interaction indicates that with increasing precipitation, the negative and positive effects of neighbors would diminish.

Predicted growth in contrasting diversity scenarios

The predictive model framework showed broad similarity among target species' responses to diversity, but individual species had some distinguishing trends (Figure 3). *A. rubrum* showed no response to diversity as the mean growth trends for no neighbors, observed, and high diversity scenarios were all similar across the precipitation gradient. *A. saccharum* exhibited its highest potential growth under the high diversity scenario and its lowest growth in the observed neighborhood scenario (Figure 3b.). *Q. alba* in drought conditions had its highest growth in the high diversity scenario, but with high precipitation the observed neighborhood and no-neighbor scenarios yielded the highest mean annual growth (Figure 3c.). *Q. velutina* mean growth in drought conditions was highest under the observed neighborhood scenario, but growth was similar at high precipitation for all three diversity scenarios (Figure 3d).

DISCUSSION

Several studies have shown that a diversity of functional traits helps to maintain forest performance under drought (Anderegg et al. 2018a, Uriarte et al. 2018, Bello et al. 2019, Fichtner et al. 2020). Still, it is unclear if all species benefit similarly or if the benefits of biodiversity vary among co-occurring species. We used a spatially explicit dendrochronological study and modeling framework to describe the influences of neighborhood diversity on performance of four temperate tree species. We found that the effect of biodiversity on growth varied in magnitude and direction between the study species. We found that while *Acer rubrum* showed little response to neighborhood diversity, *Acer saccharum* benefitted from absence of neighbors and from high neighborhood diversity. *Quercus spp.* benefited from nearby biodiversity only under drought conditions. Land managers looking to enhance growth of these species can focus on promoting beneficial neighborhoods with targeted thinning of species showing negative interactions. Forest or Dynamic Global Vegetation Models (DGVM) can benefit from our results with enhanced clarity of species interactions .

Effects of low precipitation

As we predicted, all species responded positively to more favorable growing conditions, in this case, warmer springs and higher early summer precipitation (Fig. 2). *A. rubrum* is usually considered a very adaptable species, but a recent study corroborated our findings showing that *Acer rubrum* are sensitive to growing season droughts due in part to their hydraulic strategy (Hoffmann et al. 2020). Forest managers should focus less on stand thinning that reduces neighborhood competition to promote growth of *Acer rubrum* and should consider the local edaphic conditions more when planting stands in areas projected to experience increased drought (McCollum and Ibanez, 2020).

Acer saccharum is an important economic and ecological species in temperate forests experiencing decline due to factors including drought (Bal et al. 2015), and our results confirm this vulnerability. Isohydric species like *A. saccharum* rely on stored non-structural carbohydrates to maintain function during drought periods (Kannenberg and Phillips 2020). These stores are built during favorable growing conditions, and as our results show these may be affected by competition jeopardizing the ability of this species to cope with drought (Kunstler et al. 2012).

Effects of diversity in low precipitation years

Temperate forests in the eastern United States are projected to see an increasing frequency of short term droughts with heavier rainfall in between (Hayhoe et al. 2007, Villarini et al. 2013). This increase in weather extremes will test the physiological limits of trees on each side of the hydraulic strategy spectrum and the interactions between these functional types have important implications for performance and future succession. We found partial support for our prediction that under drought conditions increasing levels of diversity would impact species differently depending on their hydraulic strategies. Anisohydric species, i.e., Quercus, benefitted from neighborhood interactions and diversity under drought conditions, while isohydric *Acer rubrum* was not affected by neighborhood interactions and *Acer saccharum* tended to benefit most from neighbors under high precipitation.

Our results imply that forest succession models considering *Acer rubrum* could solely focus on weather and site factors as neighborhood interactions seem to play a lesser role in

determining performance under drought. Bigelow et al. 2020 found that *Acer saccharum* growth was negatively impacted by competition especially under warmer, drier conditions; supporting our conclusion that sugar maples may decline under drought with intraspecific interactions. In addition to hydraulic complementarity, it is possible that *Acer saccharum* performance is benefitting from partitioned canopy structure and shade tolerance between species; a fundamental benefit of forest diversity (Morin et al. 2011). This means that if *Acer saccharum* are cultivated in monoculture, a common practice, the effects of prolonged droughts could be particularly damaging; instead, and to minimize the impact of drought, management of these stands should target higher functional diversity.

Under low precipitation conditions, the high diversity scenario was particularly beneficial for growth of *Quercus alba* but not for *Quercus velutina.* In drought prone areas anisohydric species are likely to benefit from a diversity of hydraulic strategies not only from the complementarity between species, but also the subsequent soil water availability from isohydric species that have reduced photosynthetic activity (Mirfenderesgi et al. 2019, Mrad et al. 2019). Our findings support a body of previous work that has shown diversity as a buffer to drought conditions for specific species (Anderegg et al. 2018a, Bello et al. 2019, Fichtner et al. 2020). We see that anisohydric species benefit from diversity, but also isohydric *Acer saccharums* would benefit from an increase in neighborhood diversity.

Effect of neighborhood diversity during high growing season precipitation

We did not find support for our prediction that all functional types will benefit from diverse neighborhoods under conditions with high water availability. Neither anisohydric nor isohydric tree species benefitted from more functionally diverse neighborhoods under high growing season precipitation (Fig. 4). Isohydric species growth responded similarly to diversity under dry and wet conditions, while anisohydric species experienced either neutral or negative impacts of diversity under high growing season precipitation, potentially due to the contrasting hydraulic strategies and competitive advantage. While droughts are becoming more frequent in temperate forests, they will be punctuated by heavier rainfall events (Hayhoe et al. 2007,

Villarini et al. 2013). These weather extremes will impact growth in tandem with neighborhood interactions.

<u>Contrasting hydraulic traits and community effects</u>

The null effect of diversity on isohydric species may be linked to either a competitive advantage during high soil water availability or a complementarity in water uptake depth when in crowded, diverse neighborhoods. While *Acer* species are less drought tolerant, studies of forest succession in the area have found in mesic conditions isohydric *Acer* species have a competitive advantage over anisohydric *Quercus* species (Kutta and Hubbart 2018, Palus et al. 2018). Along the same isohydric-anisohydric spectrum previous studies have found maple species are able to shift their water uptake between shallow and deeper soil water stores (Brinkmann et al. 2019, O'Keefe et al. 2019, Lanning et al. 2020). Soil water access has important implications under drought, but also may explain buffering of maples from competition or neighborhood interactions during high growing season precipitation, if surrounding species are more acquisitive competitors at shallow soil profiles. For mesic sites, our findings have positive implications for future performance of isohydric species in a wide range of neighborhood diversity and neighborhood density.

Anisohydric oaks in our study responded negatively or neutrally to neighborhood diversity for potentially the same reason that isohydric maples are buffered from biotic interactions under high water availability. Quercus species are prized for their cultural and aesthetic value along with being an important timber product in temperate forests (Hanberry et al. 2012, Knoot et al. 2015, Vander Yacht et al. 2019). Moist, favorable growing conditions have led to a process coined as "mesophication" in many sites (Nowacki and Abrams 2008). This process manifests as the replacement of xeric, shade-intolerant genera, with mesic, shade-tolerant ones (Hanberry et al. 2012, Knoot et al. 2015), and has led to a homogenization of forest species and a reduction in biodiversity that is driven by positive feedback between canopy closure and growth of shade-tolerant genera (Knott et al. 2019). Our findings suggest that effects of environmental conditions are mediated by species hydraulic traits. Understanding neighborhood dynamics in detail will help clarify what is happening to Acer and

Quercus species in mesophy-ing forests (Fichtner et al. 2017, Anderegg et al. 2018a, Fichtner et al. 2020).

Implications of species pairwise interactions

Our study describes the interactions between specific species in our sites, which reveals important information about community dynamics (Table 1; S4). *Quercus* species generally benefitted from heterospecific neighbors while *Acer* species had largely negative interactions with neighbors. The size class of our target species likely contributed to these results beyond drought alone. A. rubrum were consistently in the smallest size classes and surrounded by larger competing neighbors, while Quercus species were generally the largest tree in their neighborhood. These differences in size class likely explains some of our findings considering competition for light as well as belowground resources (D'Amato et al. 2011, 2013). These findings have important implications for the inclusion of NE in modeling of forest succession, but also for management of forest stands to promote growth of desired species. (Ibanez and Rodriguez) showed that specific species combinations should be considered when restoring woody plant communities to enhance growth. *Acer* species are both positively influenced by *Ostrya virginiana* neighbors, which may be a positive feedback when *O. virginiana* creates shade conditions for *Acer* species and rarely grows above the understory (Cox et al. 2016, Goode et al. 2020). The negative effect of *Ulmus americana* on *Acer saccharum* growth could be due to the difference in hydraulic traits, although these are not generally abundant neighbors in our sites (Ellmore and Ewers 1985). When considering biotic interactions removed from climate, *Acer nigrum's* negative effect on A. saccharum growth is likely due to the same shade tolerance and growth strategies vying for similar resources, especially at similar size classes (Woodrum et al. 2003).

Quercus alba in our study had no significant effect of any one neighbor likely due to their placement along the shade tolerance spectrum for oak species (Izbicki et al. 2020). It is possible that under many different conditions neighbors have varying effects on *Quercus alba*, especially when persisting in the understory for prolonged periods. Our findings for *Quercus velutina* with pairwise interactions support our prediction on increased intraspecific

competition (Uriarte et al. 2018). *Quercus velutina* represented the largest size classes in our study and it is possible that whenever they were in close proximity, size was a defining variable for negative interactions (Liang et al. 2007, D'Amato et al. 2011, 2013). The benefit of many different species to *Quercus velutina* is evidence for complementarity between species when considering diversity alone. Our findings present compelling motivation to investigate the pairwise interactions between species in management or silvicultural applications to promote growth of desired species.

Future Studies and Limitations

Our findings address the role of biotic interactions and neighborhood diversity and growth on two genera of importance in the region. While we have evidence for some potential mechanisms, showing a causal relationship is particularly difficult in forest communities with long organismal lifespans and many confounding factors for growth at the site and even microsite level (McCollum & Ibanez 2020). A future study that accounts for growth of all neighbors could show this mechanism, if *Acer* species do in fact ramp down growth during drought conditions and release the *Quercus* individuals in our study. As a general critique of forest community studies, we collected growth and neighborhood data for a relatively short period of time and did not account for mortality over the forests' history. Future studies should aim for long term datasets on growth and mortality to understand forest succession and species interactions. Finally, these results may be interpreted differently if we investigated below ground interactions and differences in microbial communities between the two genera: a worthwhile pursuit for future research.

CONCLUSIONS

Our study has presented evidence that biodiversity and climate interact to influence growth differently at the species level. During drought and high growing season precipitation this relationship between performance and diversity changes with each species. Climate change in the Midwest region is expected to increase drought and storm severity; these changing abiotic conditions along with neighborhood diversity will affect tree growth.

Figure 1. Stem maps of target trees with calculated neighborhood effects. Green signifies positive impacts of neighbors on growth, red negative, and yellow neutral.
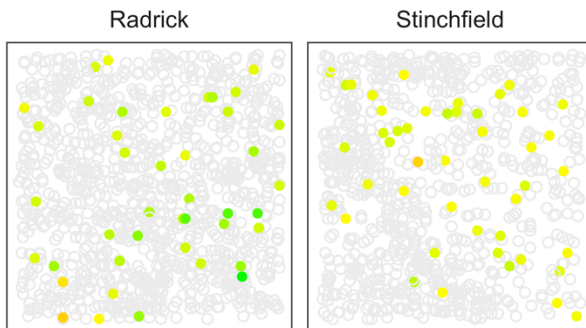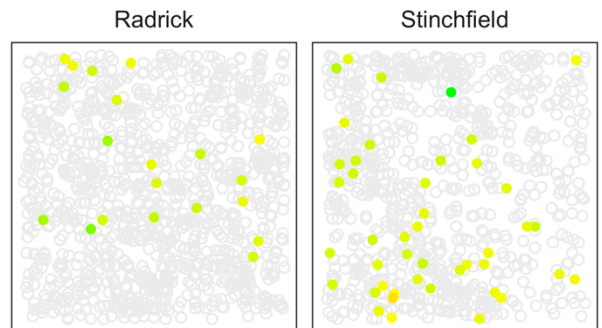
a) *Acer rubrum*
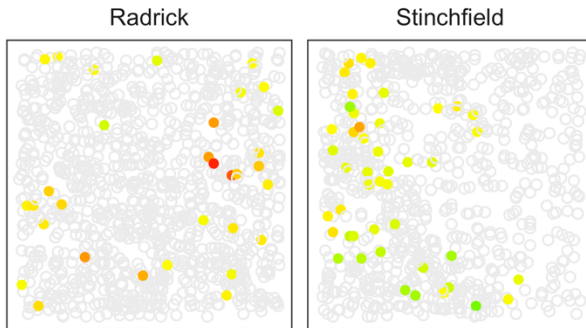
b) *Acer saccharum*
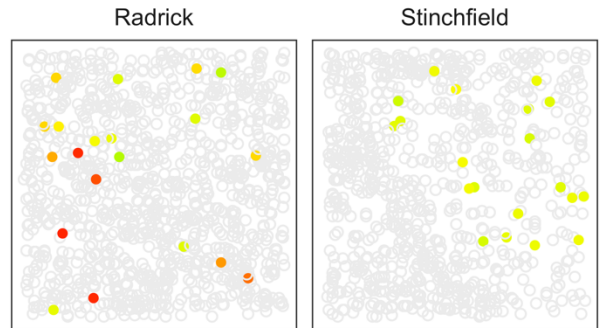
c) *Quercus alba*

d) *Quercus velutina*

Table 1. Neighbor species effects on BAI (parameter λ) for the four target species. Plus, or minus signs indicate direction of effects. Shaded boxes indicate significance (95% CI do not intersect with zero; green positive effect, red negative effect). NA, not applicable if less than 10 neighbors were represented.

Neighbor	n	Target Species			
		A. rubrum	*A. saccharum*	*Q. alba*	*Q. velutina*
A. saccharum	1876	+	+	+	+
A. rubrum	1742	-	-	-	+
O. virginiana	1253	+	+	+	+
A. nigrum	935	-	-	+	+
P. serotina	467	-	+	-	+
Q. alba	345	-	+	+	-
U. americana	321	-	-	+	-
Q. velutina	296	-	+	+	-
P. virginiana	241	-	-	+	-
C. glabra	180	+	+	-	+
F. americana	55	+	NA	+	-
Q. rubra	48	-	+	-	NA
T. americana	45	+	NA	NA	+
S. albidum	29	+	NA	NA	+

Figure 2. Beta parameters by species for April temperature, June precipitation, and the interaction of June precipitation with neighborhood effects. Points above the dotted zero line indicate a positive effect on growth, while points below the dotted line indicate a negative effect on growth. Points and 95% CI that do not intersect with the zero are significant; parameters are standardized about the variable mean.
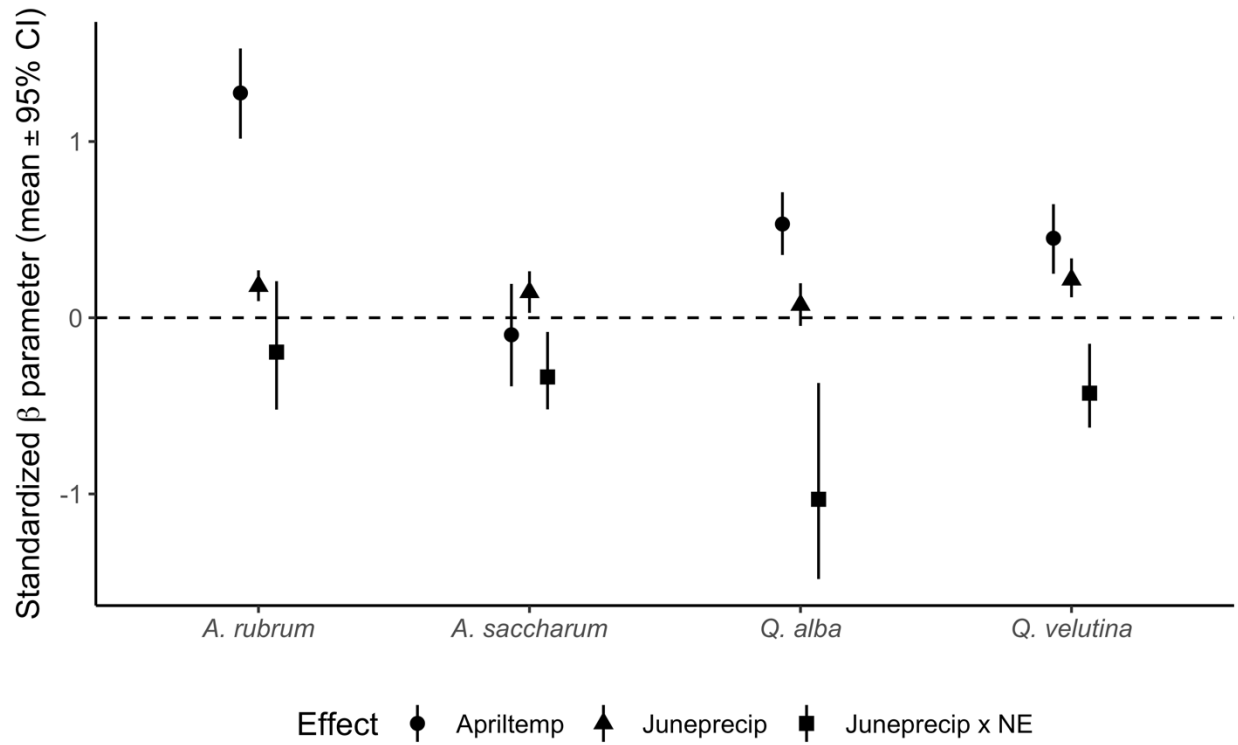
Figure 3. Predictions of growth target species across a June precipitation gradient for the average April temperature observed in the data for each scenario of neighborhood diversity. Lines indicate mean prediction and shaded regions indicate the 95% predicted intervals (PI).
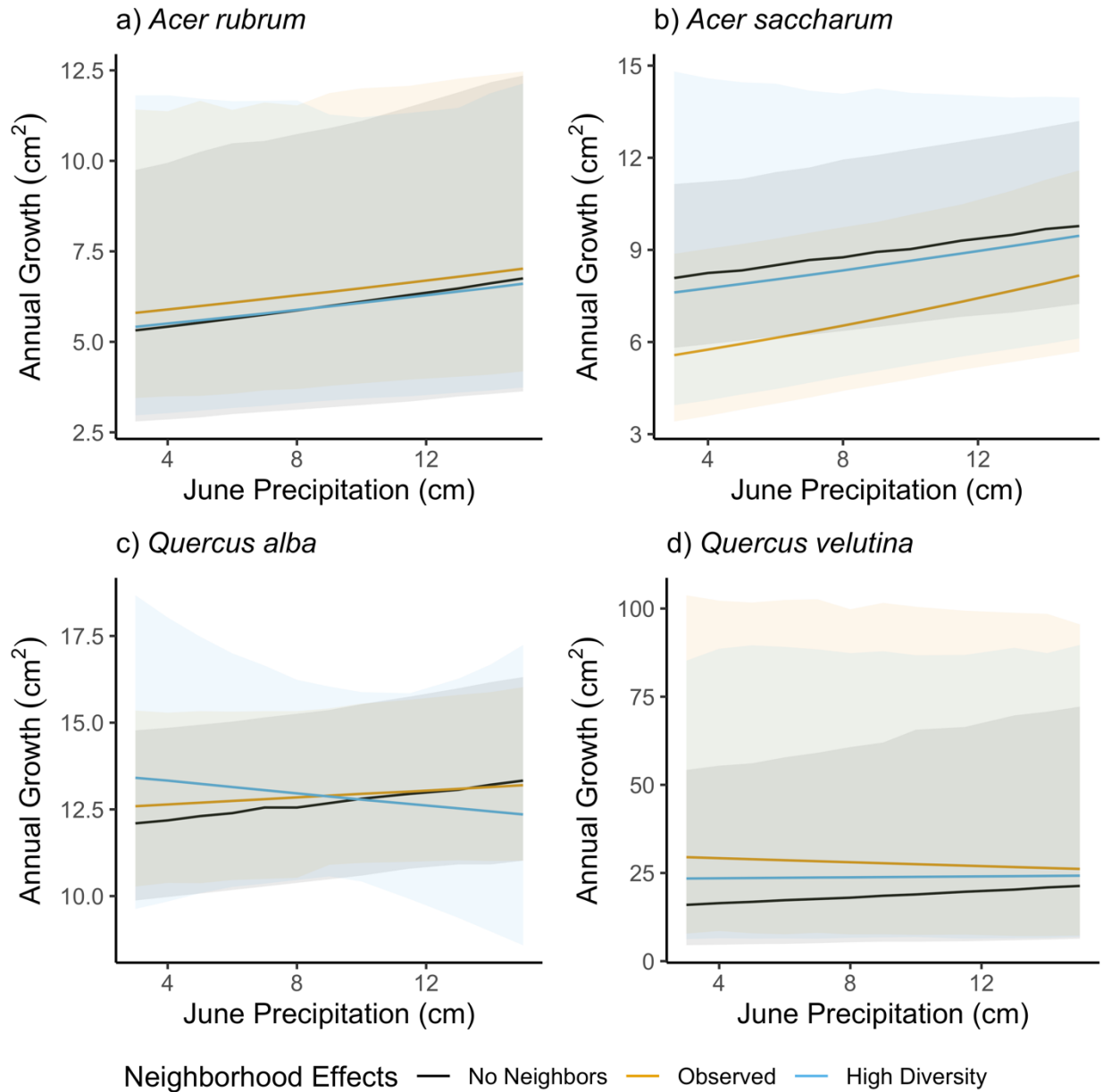
Supplementary Material

S1. Locations of field collection sites within Washtenaw County, Michigan. Included are the forest cover types circa 1800 (Michigan Open Data).
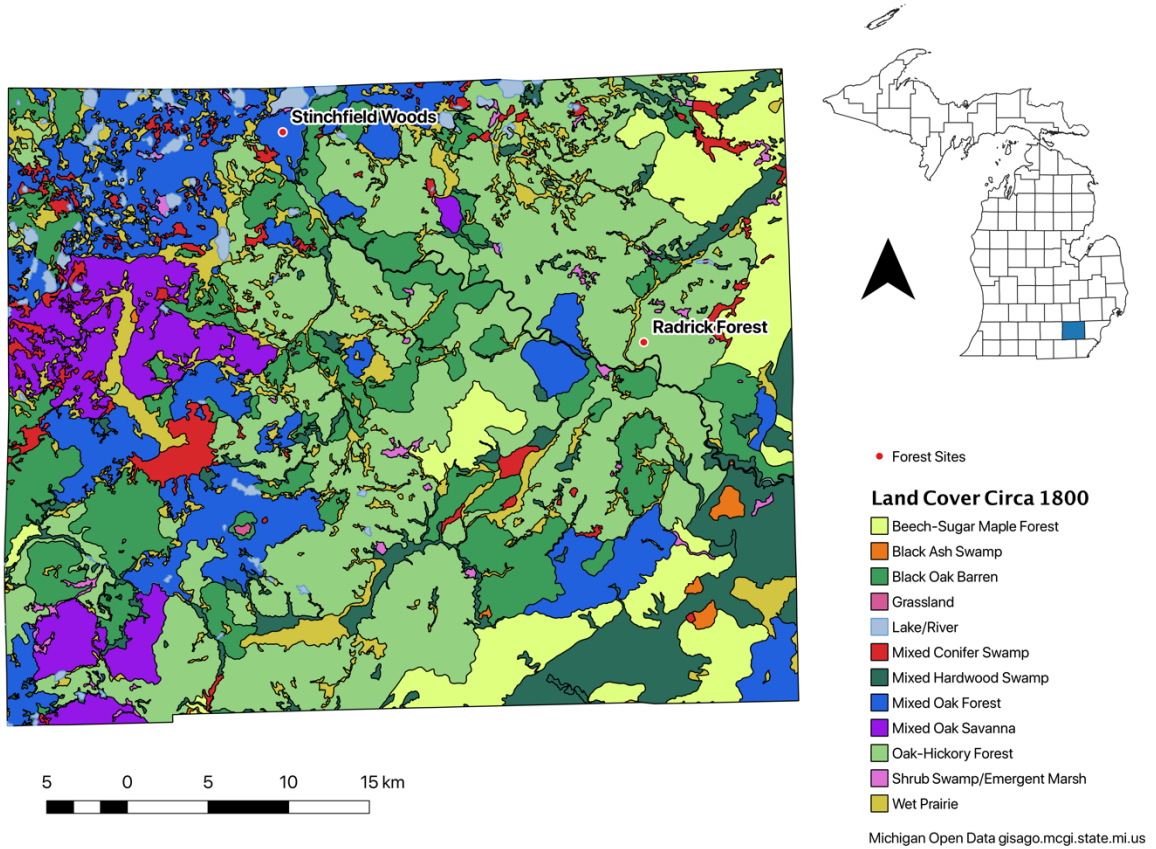
S2. Stem maps of each site with target trees filled in with color, size of point relates tree diameter.
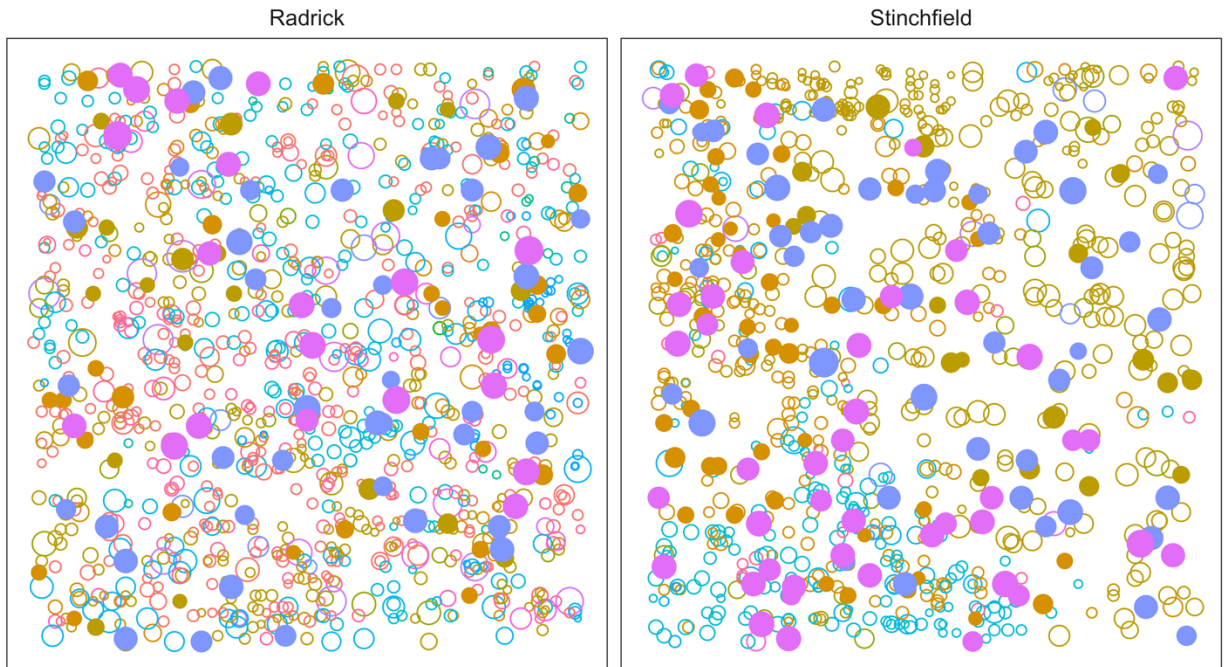
● Acer nigrum	● Carya glabra	● Fraxinus americana	● Prunus virginiana	● Sassafras albidum
● Acer platanoides	● Carya ovata	● Lonicera maackii	● Quercus alba	● Tilia americana
● Acer rubrum	● Cornus florida	● Ostrya virginiana	● Quercus rubra	● Ulmus americana
● Acer saccharum	● Euonymus alatus	● Prunus serotina	● Quercus velutina	

S3. Graphical depiction of neighborhood diversity scenarios used in annual growth simulation across a June precipitation gradient. Size of simulated target tree varied based on average diameter for each species, size of all neighbors was the average diameter of all trees across sites (13.2 cm).
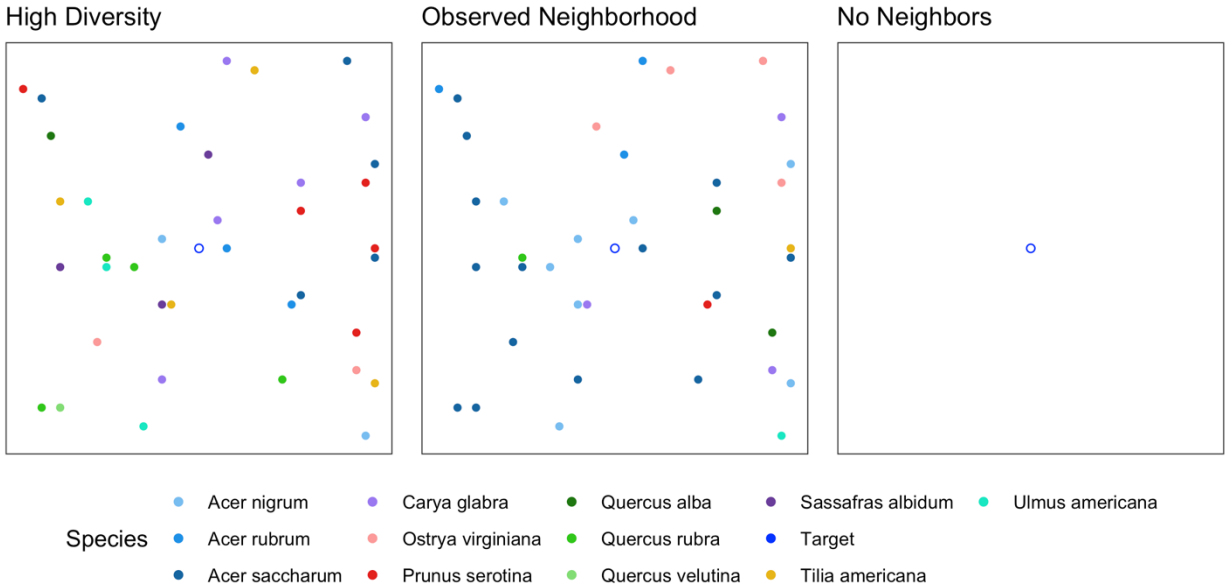
S4. Model Code:

```
model{
for(i in 1:270){                            #Number of individual trees
   for(y in 3:12){                          #Number of years analyzed
      bai[i,y]~dlnorm(R[i,y],tau[i,y]) C(0,) #likelihood
      bai.h[i,y]~dlnorm(R[i,y],tau[i,y]) C(0,) #predictions
R[i,y]<-
AA[sp[i],Site[i]]+NE[i]+beta[sp[i],1]*Juneprecip[y]+beta[sp[i],2]*June
precip[y]*NE[i]+
beta[sp[i],3]*Apriltemp[y]+beta[sp[i],4]*log(dbh[i,y])+beta[sp[i],5]*b
ai[i,y-1]

tau[i,y] <- 1/var[i,y]
var[i,y] <- a[sp[i]]+b[sp[i]]*log(dbh[i,y])  #variance is estimated as
a function of the dbh (tree size)
}}

for(i in 1:270){  #plants analyzed
for(j in 1:NNeigh[i]){  #neighbors
NE0[i,j]<-
(Size[SNN[i]+j]/dbh[i,12])*lambda[sp[i],SpeciesN[SNN[i]+j]]/Dist[SNN[i
]+j]
}
NE[i]<-sum(NE0[i,1:NNeigh[i]])
} #neighbors

for(q in 1:4){  #tag 267 Radrick
for(c in 1:NNeighsim[q]){  #neighbors
#observed
NEsim1[q,c]<-
(Sizesim[SNNsim[q]+c]/dbhp[q])*lambda[spp[q],observed[SNNsim[q]+c]]/Di
stsim[SNNsim[q]+c]
#High Diversity
NEsim2[q,c]<-
(Sizesim[SNNsim[q]+c]/dbhp[q])*lambda[spp[q],highdiv[SNNsim[q]+c]]/Dis
tsim[SNNsim[q]+c]
}}
for(q in 1:4){
NEobs[q]<-sum(NEsim1[q,1:NNeighsim[q]])
NEsim[q]<-sum(NEsim2[q,1:NNeighsim[q]])
} #neighbors predictions

#average NE effect per species
NEp[1]<-(mean(NE[1:46])+mean(NE[157:188]))/2
NEp[2]<-(mean(NE[47:66])+NE[189:208])/2
NEp[3]<-(mean(NE[67:112])+mean(NE[209:250]))/2
NEp[4]<-(mean(NE[113:136])+mean(NE[251:270]))/2
```

```
#priors
for(i in 1:4){
 for(s in 1:2){AA[i,s]~dnorm(A[i],tau1[i])}
for(k in 1:5){beta[i,k]~dnorm(0,0.001)}
a[i]~dlnorm(1,0.01)
b[i]~dnorm(0,0.0001)
for(n in 1:19){lambda[i,n]~dnorm(0,0.1)}
A[i]~dnorm(0, 0.0001)
tau1[i]~dgamma(0.0001, 0.0001)
}

#predictions, growth along a gradient of precipitation and three
neighborhoods

for(y in 1:4){
tp[y]<-1/vp[y]
vp[y]<-a[y]+b[y]*log(dbhp[y])

for(e in 1:12){
```

#NO NEIGHBORS
```
 Bai1[y,e]~dlnorm(Rp2[y,e],tp[y])
     Rp1[y,e]<-
A[y]+beta[y,1]*Junepredi[e]+beta[y,3]*log(dbhp[y])+beta[y,4]*baip[y]+b
eta[y,5]*15
```

#Observed Neighborhood
```
 Bai2[y,e]~dlnorm(Rp8[y,e],tp[y])
     Rp2[y,e]<-
A[y]+beta[y,1]*Junepredi[e]+beta[y,3]*log(dbhp[y])+beta[y,4]*baip[y]+b
eta[y,2]*Junepredi[e]*NEobs[y]+NEobs[y]+beta[y,5]*15
```

#High Diversity
```
 Bai3[y,e]~dlnorm(Rp11[y,e],tp[y])
     Rp3[y,e]<-
A[y]+beta[y,1]*Junepredi[e]+beta[y,3]*log(dbhp[y])+beta[y,4]*baip[y]+b
eta[y,2]*Junepredi[e]*NEsim[y]+NEsim[y]+beta[y,5]*15
}}
}#end model

#inititals

list(
a = c(1,1,1,1), b = c(0,0,0,0),
lambda=structure(.Data=c(0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0), .Dim=c(4,19))  , beta =
structure(.Data = c(0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0),
.Dim = c(4,5)), tau1 = c(1,1,1,1), A = c(0,0,0,0)
)
```

S5. Posterior parameter estimates, mean ± SD and 95% credible intervals (CI)

Parameter	*A. rubrum*	*A. saccharum*	*Q. alba*	*Q. velutina*
AA_1: Site_1	-2.124 ± 0.3521 (-2.873, -1.434)	-0.348 ± 0.3553 (-1.05, 0.3997)	-1.552 ± 0.2785 (-2.147, -1.047)	-2.669 ± 0.5428 (-3.604, -1.647)
AA_2: Site_2	-2.216 ± 0.3683 (-2.988, -1.516)	-0.3571 ± 0.3594 (-1.07, 0.3935)	-1.544 ± 0.2812 (-2.145, -1.039)	-2.859 ± 0.5575 (-3.82, -1.812)
β_1: Effect of June precip. on BAI	0.01977 ± 0.004859 (0.01035, 0.02956)	0.0159 ± 0.00654 (0.003032, 0.02897)	0.008008 ± 0.006798 (-0.005079, 0.02152)	0.02375 ± 0.00619 (0.01277, 0.037)
β_2: Effect of June precip. * NE interaction on BAI	-0.0214 ± 0.02027 (-0.05725, 0.02279)	-0.03689 ± 0.01223 (-0.05704, -0.008833)	-0.1131 ± 0.03177 (-0.1628, -0.04061)	-0.04698 ± 0.01345 (-0.06846, -0.0162)
β_3: Effect of DBH on BAI	0.6712 ± 0.09291 (0.4994, 0.8683)	0.652 ± 0.08225 (0.4773, 0.8122)	0.7719 ± 0.0698 (0.649, 0.9208)	1.125 ± 0.1287 (0.8781, 1.347)
β_4: Effect of prev. growth on BAI	0.06632 ± 0.003582 (0.05916, 0.07329)	0.03651 ± 0.002861 (0.03096, 0.04219)	0.03959 ± 0.002101 (0.03547, 0.04368)	0.02212 ± 0.001251 (0.01973, 0.02462)
B5: Effect of April temp. on BAI	0.08547 ± 0.008628 (0.0681, 0.1024)	-0.006475 ± 0.009801 (-0.02607, 0.01289)	0.03564 ± 0.006217 (0.02386, 0.04773)	0.03023 ± 0.006857 (0.01673, 0.04319)
λ_1: Acer rubrum	-0.01613 ± 0.03929 (-0.09926, 0.05666)	-0.1536 ± 0.1966 (-0.5447, 0.2271)	-0.003387 ± 0.006387 (-0.01601, 0.009537)	0.2097 ± 0.1159 (-0.01806, 0.4397)
λ_2: Acer saccharum	0.1204 ± 0.06478 (-0.000335, 0.2559)	0.07889 ± 0.06389 (-0.04208, 0.2089)	0.000776 ± 0.07989 (-0.124, 0.1812)	0.2624 ± 0.114 (0.04617, 0.4935)
λ_3: Quercus alba	-0.03837 ± 0.03214 (-0.1064, 0.0213)	0.01412 ± 0.03415 (-0.05369, 0.08129)	0.1158 ± 0.1216 (-0.162, 0.3165)	-0.01208 ± 0.1517 (-0.3153, 0.2862)
λ_4: Quercus velutina	-0.01235 ± 0.03138 (-0.0838, 0.04112)	0.00604 ± 0.07312 (-0.1347, 0.1546)	0.05452 ± 0.07914 (-0.09865, 0.2172)	-0.3692 ± 0.1289 (-0.6334, -0.1285)
λ_5: Carya glabra	0.1255 ± 0.09454 (-0.04622, 0.3301)	0.01344 ± 0.05764 (-0.09812, 0.1313)	-0.05416 ± 0.3011 (-0.6688, 0.5272)	0.4815 ± 0.24 (0.013, 0.9625)
λ_6: Ostrya virginiana	0.263 ± 0.07797 (0.1277, 0.4318)	0.7113 ± 0.2095 (0.3137, 1.134)	0.03123 ± 0.2145 (-0.35, 0.4948)	0.1906 ± 0.1461 (-0.09083, 0.485)
λ_7: Prunus serotina	-0.06571 ± 0.04618 (-0.1665, 0.01715)	0.06329 ± 0.07371 (-0.07851, 0.2122)	-0.04957 ± 0.08899 (-0.2325, 0.1226)	0.3721 ± 0.1612 (0.06612, 0.704)
λ_8: Quercus rubra	-0.02928 ± 0.02832 (-0.08706, 0.02552)	0.04175 ± 0.03391 (-0.02336, 0.1108)	-0.01074 ± 0.3401 (-0.6188, 0.7219)	-0.005431 ± 0.364 (-0.7173, 0.723)
λ_9: Ulmus americana	-0.2769 ± 0.2133 (-0.6896, 0.1603)	-0.8968 ± 0.4184 (-1.739, -0.09259)	0.5611 ± 0.4493 (-0.2715, 1.509)	-0.2216 ± 0.6893 (-1.551, 1.18)
λ_{10}: Euonymus alatus	0.02023 ± 0.9008 (-1.81, 1.791)	-0.01797 ± 3.174 (-6.227, 6.211)	0.001118 ± 3.16 (-6.179, 6.227)	1.374 ± 3.128 (-4.731, 7.524)
λ_{11}: Prunus virginiana	-0.4348 ± 0.3448 (-1.123, 0.2478)	-0.5034 ± 1.188 (-2.821, 1.855)	2.014 ± 1.942 (-2.577, 4.965)	-1.967 ± 1.594 (-5.112, 1.171)
λ_{12}: Sassafras albidum	0.02274 ± 0.05868 (-0.09266, 0.1413)	0.2792 ± 0.6388 (-0.9673, 1.553)	-0.1347 ± 0.8965 (-1.419, 1.895)	0.1825 ± 0.5906 (-0.9554, 1.368)
λ_{13}: Acer nigrum	-0.1194 ± 0.1276 (-0.3564, 0.1566)	-0.6084 ± 0.2634 (-1.148, -0.1204)	0.01678 ± 0.02696 (-0.02985, 0.07591)	0.8474 ± 0.2962 (0.2965, 1.455)
λ_{14}: Tilia americana	0.09603 ± 0.5832 (-0.8948, 1.437)	0.479 ± 0.5423 (-0.5633, 1.589)	0.5671 ± 1.222 (-2.155, 2.619)	0.2376 ± 1.074 (-1.786, 2.453)
λ_{15}: Fraxinus americana	0.7249 ± 0.9121 (-0.9387, 2.691)	-1.531 ± 2.874 (-7.145, 4.114)	1.245 ± 2.416 (-3.776, 5.696)	-1.776 ± 3.019 (-7.656, 4.176)
λ_{16}: Acer platanoides	-1.878 ± 1.231 (-4.216, 0.6828)	1.732 ± 3.021 (-4.179, 7.667)	0.01205 ± 3.171 (-6.197, 6.222)	-0.001725 ± 3.164 (-6.181, 6.208)

λ_{17}: Carya ovata	-0.01382 ± 3.142 (-6.178, 6.171)	-0.002713 ± 3.17 (-6.193, 6.206)	0.8634 ± 2.665 (-4.439, 5.994)	0.009499 ± 3.169 (-6.205, 6.212)
λ_{18}: Cornus florida	-0.000319 ± 1.598 (-3.318, 3.01)	-0.006709 ± 3.165 (-6.197, 6.183)	-0.3824 ± 3.167 (-6.525, 5.923)	0.5839 ± 3.113 (-5.539, 6.684)
λ_{19}: Lonicera maackii	1.887 ± 3.13 (-4.254, 8.013)	-0.106 ± 2.867 (-5.701, 5.533)	0.6608 ± 2.489 (-4.229, 5.537)	-0.5884 ± 3.154 (-6.813, 5.598)
a: variance intercept	0.02398 ± 0.04126 (6.78e-08, 0.1476)	0.2472 ± 0.06991 (0.1115, 0.3878)	0.3355 ± 0.07174 (0.1913, 0.4708)	0.4916 ± 0.07761 (0.3414, 0.6468)
b: variance slope	0.0518 ± 0.01449 (0.009376, 0.06478)	-0.03777 ± 0.02139 (-0.07955, 0.004662)	-0.05991 +- 0.0188 (-0.0948, -0.02163)	-0.09933 +- 0.019 (-0.1371, -0.06235)

S6. Model fit for each target species with R^2 values.
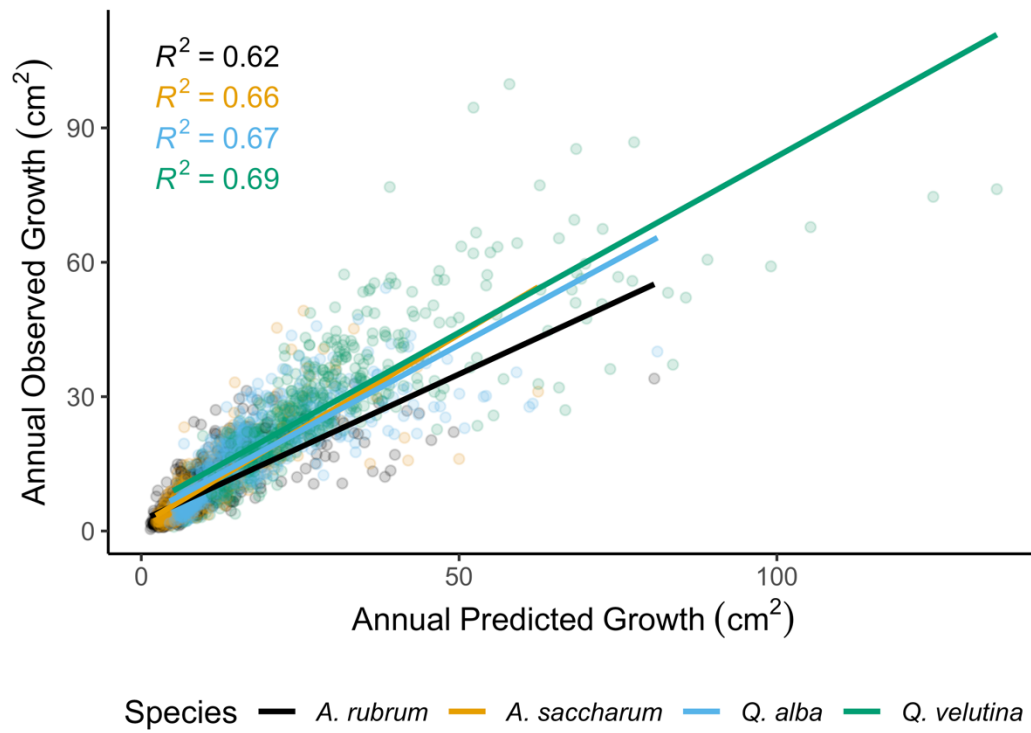
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